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The first part of the report is devoted to a general  
 description of the country, its position, extent,  
 and the nature of the soil. It is a fertile  
 land, and the soil is of a rich and productive  
 nature. The climate is temperate, and the  
 weather is generally mild. The population  
 is increasing, and the country is becoming  
 more and more settled. The principal  
 occupations of the people are agriculture  
 and stock raising. The principal  
 products of the country are wheat, corn,  
 and other grain crops. The principal  
 exports of the country are these crops,  
 and the principal imports are  
 manufactured goods and other articles  
 of foreign origin.



# The Anatomy of *Pentastomum tereticulum* (Baird).

By

**W. Baldwin Spencer, M.A.,**

Professor of Biology in the University of Melbourne.

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With Plates I—IX.

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DURING the summer of 1887-8 the Field Naturalist Club of Victoria arranged for the annual collecting expedition of its members to be made to King Island. The latter lies to the west of Bass Straits, halfway between the mainland of Victoria and Tasmania, and is a wild and, save for two lighthouse keepers, uninhabited island. Whilst collecting we came across very numerous specimens of the copper-head snake (*Hoplocephalus superbus*), and in one of these my attention was drawn by my friend and pupil, Mr. E. Dombain, to the presence of a parasite in the lung, which proved on examination to be a large specimen of some species of *Pentastomum*. Shortly afterwards I killed another snake of the same species, and on cutting the body open found the lung to be crowded with the same parasite. The weather was extremely warm, and, as we were on the tramp, all that could be done was to put the animal into spirits, and trust to finding the parasite again for the purpose of watching it alive. This opportunity has unfortunately not occurred, though since that time I have cut open many "copper-heads" in the hope of finding the *Pentastomum*. Mr. D. McAlpine has been good enough to give me four specimens of the same species of *Pentastomum*, which

he has found in the lungs of a black snake (*Pseudechys porphyriacus*) in Victoria.

On searching through such literature as could be obtained in Victoria I found that Dr. Baird had described a specimen which was obtained in the mouth of a dead copper-head snake in the Zoological Society's Gardens, London, under the name of *Pentastomum teretiusculum*. Though the description is somewhat incomplete, there can be no doubt but that the form with which this paper deals is the one found and first named by Dr. Baird.<sup>1</sup>

Since the time when Leuckart<sup>2</sup> published his classic monograph on the group—now more than thirty years ago—modern methods of investigation have rendered it possible to study more closely the minute anatomy of such an animal as *Pentastomum* (where continuous sections are almost a necessity) than could be done in earlier days, though to those of us who now depend upon such methods the accurate and brilliant results achieved by the older workers are a continual source of admiration.

Despite the recent work of Hoyle,<sup>3</sup> Lohrmann,<sup>4</sup> Stiles,<sup>5</sup> and Macalister,<sup>6</sup> I have thought it worth while to publish the following account of the anatomy of *P. teretiusculum*, which has been made as complete as possible. In doing this I have endeavoured to give (1) descriptions and figures of the external anatomy, (2) schematic representations of the structure,

<sup>1</sup> 'Proc. Zool. Soc.,' London, 1862, p. 114.

<sup>2</sup> 'Bau und Entwicklungsgeschichte der Pentastomen,' Leipzig, 1860.

<sup>3</sup> "On a New Species of *Pentastomum* (*P. protelis*) from the Mesentery of *Proteles cristatus*; with an Account of its Anatomy," 'Trans. Royal Society of Edinburgh,' 1883, with pls. xxvii and xxviii.

<sup>4</sup> "Untersuchungen über den Anat. Bau der Pentastomen," 'Arch. f. Naturgesch.,' 1889. I am unable to refer directly to this work; my knowledge of it is based upon references thereto in Stiles' monograph.

<sup>5</sup> "Bau und Entwicklungsgeschichte von *Pentastomum proboscideum*, Rud., und *Pentastomum subcylindricum*, Dies.," 'Zeit. f. wissen. Zool.,' Band. lii, Part 1, 1891, p. 83, Taf. vii and viii. This paper also contains a full bibliography.

<sup>6</sup> 'Proc. Roy. Irish Acad.,' 2nd series, vol. ii, 1875-7, p. 62: "On Two New Species of *Pentastomum*."



and (3) descriptions and figures of the actual sections and histological preparations, from a study of which the schematic drawings have been deduced.

To students, and those who are engaged in teaching, schematic representations of the most diagrammatic nature are, it appears to me, of great service.

I am much indebted to my friend Mr. W. E. Hoyle for his kindness in sending to me a copy of Leuckart's work, which I was unable to refer to or procure in Australia, and also for his kindness in supervising this paper whilst it was passing through the press.

The structure will be dealt with under the following heads :

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2. External anatomy . . . . .	4	7. Nervous system . . . . .	33
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### 1. Habitat.

The adult form lives in the lungs of the two snakes, *Hoplocephalus superbis* and *Pseudechys porphyriacus*, popularly known respectively as the "copper-head" and the "black" snake. The former is very common in certain parts. In King Island it was not unusual to kill perhaps twelve to twenty in the course of one day's tramp through the scrub. I have myself as yet only found the parasite in the lung of two specimens, and have never seen it save in King Island. On one occasion Mr. McAlpine found it in the lung of a black snake killed not far from Melbourne.

In one copper-head, which to all appearances was perfectly healthy and vigorous, and measured about 4 feet 6 inches in length, there were no fewer than 129 specimens to be counted in the lung and tracheal tube, of which some twenty were males, the rest females, in various stages of growth.

Each parasite lives with the whole of the head buried deeply in the lung wall, and adheres so firmly by means of its hooks

that a considerable pull is necessary to dislodge it. When this is done a definite cavity is left, corresponding in shape and size to the parasite's head. Not one was found loose in the lung, though the fact that Dr. Baird found his specimen in the mouth shows that they must have the power of becoming free and of movement. Like other parasites, this one seems to try to leave the body on the death of the host.

## 2. External Anatomy.

(Figs. 1—5.)

The form of the body is that of an annulated cylinder, bluntly rounded at the anterior and somewhat tapering at the posterior extremity.

It differs slightly in form and much in size in the two sexes, which can readily, as in other *Pentastoma*, be distinguished from each other by the position of the opening of the reproductive organs. During life the whole body is of a bright red colour, as noted by Baird, the colour being undoubtedly due to the blood sucked in from the lung of the host.

(i) The Female.—The specimens vary much in size, some being very small and immature, measuring not more than 12 mm. in length, whilst a large mature specimen will measure 32 mm. in length and 5 mm. in greatest width. Save the anterior end the whole body is annulate, there being from sixty-five to seventy annuli present (sixty-six in the one figured). Occasionally the annuli may be slightly irregular, an incomplete one being wedged in between two perfect ones (fig. 1).

Each annulus consists of an anterior and a posterior portion, and between the two is a slight ridge more or less distinctly marked. This, as will be shown later, can be detected with ease in longitudinal sections. The anterior part corresponds to the annular part, and the posterior to the interannular, as described by Hoyle. With a lens it can easily be seen that the anterior part of each annulus is covered with a number of spots crowded closely together, and showing no arrangement

into definite lines. Such spots are absent on the posterior part of the annulus.

The rounded anterior or head end of the body is not marked by annuli, and its length is about five times the breadth of an annulus.

Mouth.—In the mid-ventral line a little way in front of the first annulus is a distinct papilla, somewhat triangular in shape with the angles rounded off, the whole projecting slightly from the surface. The papilla arises from a depression, and is surrounded by a narrow groove, which is also roughly triangular in general form. The apex of the triangle formed by the groove points forwards: the posterior side is at right angles to the long axis of the body (figs. 2, 5), and forms a slit leading directly into the mouth; in fact, seen from the ventral surface the mouth has simply the appearance of a slight swelling out of the groove. The papilla corresponds to the structure to which Hoyle gave the name of "oral papilla" in *P. protelis*, which Lohrmann also described as the "Mundpapille," but which Stiles in *P. proboscideum* states is to be regarded not as an oral papilla, but as an "Oberlippe." Whilst there is no doubt that it performs the function of an upper lip, it is equally certain that it has the form of a very definite papilla; in fact, "oral papilla" most aptly describes its appearance and structure. In *P. tæniodes* such a structure is apparently absent, the mouth being described by Leuckart as a wide and gaping orifice of oval shape.

Hooks.—On either side of the mouth is placed a pair of hooks. These are prominent structures, with sharp curved protruding points, and bases sunken in special pits on the head surface. The hooks serve for the attachment of the parasite, and each, so far as the external anatomy of the animal is concerned, consists of a strongly curved pointed portion and a broader basal part. The depression in which the latter is placed is bounded by a rounded elevated ridge of the external cuticle; within this, upon the base of the hook, lies a second one, which is prominently marked where it passes across the anterior end of the depression and hook.

**Papillæ.**—These structures, varying somewhat in number and arrangement, appear to be constant features in the anatomy of the Pentastomidæ. Their presence has been described in all forms save *P. protelis*, in which Hoyle was unable to find them, though there can be little doubt that he would have detected them had his material been in a better state of preservation. Even in well-preserved specimens they vary remarkably in distinctness.

The papillæ can be clearly divided into two sets, which may for convenience be described as (*a*) primary and (*b*) secondary.

(*a*) **Primary Papillæ** (figs. 2 and 5).—These comprise only two, and each of these forms a more or less prominent elevation, lying a slight distance anteriorly to the depression which holds one of the hooks placed nearest the mouth—that is, one of the more posterior of the two pairs of hooks. In the retracted state these papillæ are scarcely noticeable, but at other times they project markedly from the surface. Each has, close to its apex, a minute opening, which serves as one of the openings for the duct running forwards from the hook-glands to be afterwards described. Though invisible in surface view, each papilla bears one or more simple sense-organs placed close to the opening of the duct.

These papillæ are the "Tastpapillen" of Leuckart, and were regarded by him as the homologues of antennæ. Lohrmann states that the head-gland (= hook-gland mentioned above) opens upon them; and Stiles, rejecting Leuckart's suggestion of their homology with antennæ, agrees with him in regarding them as sense-papillæ, and says that the head-gland opens to the ventral side of the papillæ. The anatomy of *P. teretiusculum* shows that we are dealing with a form in which we find combined the features described singly by Lohrmann and Stiles. The latter says, "Auf grund meiner Beobachtung betrachte ich diese Papillen gleich Leuckart als Sinnespapillen, finde jedoch keine Veranlassung sie als rudimentäre Antennen anzusehen." As will be shown soon, and as Stiles has already pointed out in the case of *P. proboscideum*, sense-papillæ are present, related in position to the external pair of hooks, as

are the two large ones now described to the internal pair, and these again identical in structure with others having no claim whatever to be regarded as modified appendages. It would appear from the above that very probably this single pair of papillæ, which are directly homologous with the smaller ones, has become specially modified and enlarged in connection with the external opening of the hook-gland, and that, agreeing with Stiles, they are not to be regarded as modified antennæ.

(b) Secondary Papillæ (figs. 2, 3, and 5).—These consist of seven pairs of minute papillæ, which appear under the lens as small white spots on the dorsal surface. They are distributed as follows :

- (1) A pair close to the anterior end of the depression containing the external pair of hooks (figs. 2 and 3).
- (2) A pair placed somewhat posteriorly to the latter (3).
- (3) A pair placed posteriorly to the latter and nearer to the median line (4).

On the lateral surface :

- (4) A pair, one placed to the outer side of each of the external or outer pair of hooks (5).
- (5) A pair, one placed on each side of the body in a line with (4) and the lateral line of the body (6).

On the ventral surface :

- (6) A pair, one placed on each side immediately in front of the first annulus, and corresponding in position to the interval between the two hooks on either side (7).
- (7) A pair, one placed on each side in the first annulus, and corresponding in position to the hook nearest to the mouth (8).

In addition to the above, there can in some specimens be detected what is apparently a line of minute papillæ, of which a pair is present on each segment for perhaps the most anterior eleven. These are placed along what is called the "lateral line," where the body-wall is slightly thinner than elsewhere, and becomes on contraction of the animal thrown

into folds. Similar ones are noted by Stiles as present in *P. proboscideum*; but as in the latter, so in *P. teretiusculum*, they vary considerably, the examination of some specimens leaving no doubt that true papillæ are present, whilst the examination of others will leave equally little doubt that we are dealing simply with structures due to the wrinkling of the cuticle and body-wall. After careful examination I have been unable to detect their presence in sections.

**Reproductive Opening.**—This serves at once to distinguish, apart from the size of the two, the male from the female form. The opening of the vagina is placed on the mid-ventral surface on the eighth annulus from the posterior end (fig. 1), though the modified part around the opening may extend on to the annuli next in front of and behind this one. The opening itself is crescentic in shape, the hinder wall being formed by the anterior part of a low, rounded, and swollen cushion-like structure: the anterior wall is swollen and tumid. The cuticle which lines the opening is thick and yellow coloured.

The anus lies at the very posterior end, between the two lateral halves of the terminal annulus, the cuticle passing in from the exterior.

(ii) **The Male** (figs. 4 and 5).—In this the general form of the body, the hooks, mouth, anus, &c., agree with the description given of the female; the chief differences of importance are (1) the size and (2) the position of the reproductive opening.

The length of a large-sized specimen is about 13 mm.; the greatest width (which occurs just behind the head region) is about 2 mm. Whilst the size of the male is so much less than that of the female, the number of annuli is greater, the average being about eighty-eight, the number varying within one or two of this.

**Reproductive Opening.**—The position of this at once distinguishes the male. It has the form of an oval opening with a raised tumid margin, the whole being placed on the third and fourth annuli in the mid-ventral line, and with the

long axis of the oval at right angles to that of the body. Through the opening can be seen a ridge running across its short axis, and corresponding to the ventral edge of the partition between the two tubes leading down to the atrium genitale; whilst on either side of this ridge, when examined with a lens under strongly focussed light, can be detected a minute rod-like body, which must be the ventral edge of a special chitinous process, which serves, as will be afterwards described, to open up the female aperture prior to the passage of the cirrus itself.

Sensory Papillæ.—The only variation in these, as compared with the female, lies in the presence of an additional pair of secondary papillæ placed just in front of the genital opening, one on each side (fig. 5, 9).

### 3. Structure of the Body-wall.

(Figs. 29, 31, 32, 51.)

Under this head will be dealt with only the cuticle and the cuticle-secreting cells; the muscles of the body-wall will be dealt with under the special head of muscles.

The Cuticle.—The whole external surface of the body is covered with a layer of chitinous material of nearly uniform thickness (average  $\cdot 015$  mm.). This cuticle is continuous with the layer which lines (1) the stomodæum, (2) the proctodæum, (3) the openings of the reproductive organs, (4) the ducts of the excretory glands, and (5) the invaginations containing the hooks. These are described under the sections dealing with the organs with which they are connected.

Stiles has described and figured two distinct layers in the cuticle, a thinner outer and a thicker inner one. In *P. teretiusculum* there can be recognised a very thin external layer, which takes stain more deeply than the main portion, which rarely stains at all. Around each segment runs a pointed ridge dividing the cuticle into a larger anterior and a smaller posterior ring, the latter part of the segment doubtless corresponding to what Hoyle calls the interannulus.

This ridge is formed entirely of the outer layer, and stains deeply. In longitudinal sections it is very clearly marked (figs. 27, 29, *R.*).

The thick inner layer, which, save in the region of the ridge just mentioned, forms almost the entire thickness of the cuticle, shows in sections the presence of great numbers of minute wavy lines, as if it were composed of very thin laminæ—an appearance which may, however, be due to the action of reagents (fig. 51).

All over the head region and in the anterior half of each annulus the cuticle is pierced by numbers of minute pores, which form the stigmata, or the openings of very numerous irregularly arranged glands. Each pore has a circular-raised margin (fig. 31, *st. gl.*).

The Cuticle-secreting Cells (fig. 51, *E.*).—These form a continuous layer immediately beneath the cuticle. Each cell is columnar (the average length is .035 mm.), and each has a somewhat rounded internal end, close to which is placed a distinct nucleus. The cells do not form a columnar epithelium in the ordinary sense of the term, since they are not uniformly closely apposed, but spaces are left between them, through which pass to the cuticle the ends of muscle-fibres and of special strands of connective tissue (*W*). There can be no doubt that their function is that of secreting the cuticle. In addition to this, groups of these cells are specially modified to form the stigmatic glands, the description of which is given under the head of excretory structures.

#### 4. Muscular System.

(Figs. 24, 28—30, 32, 39, 51.)

All authors agree in describing (1) a layer of circularly disposed fibres, (2) a layer of longitudinally disposed fibres, and (3) a layer of obliquely disposed fibres. In addition to these, muscles are developed in connection with the alimentary canal, the reproductive organs, and the hooks, which are somewhat differently developed in different forms.



So far as I have been able to observe, all the muscles of the body are distinctly striated.

**Circularly disposed Fibres (*M. Tr.*).—**These are present all over the body, save in the head region, are placed just within the layer of cuticle-secreting cells, and pass right across the dorsal and ventral surfaces (figs. 12, &c., 29). The layer thins out along two lines which correspond in position to the part of the body-wall which lies midway between the dorsal and ventral insertions of the oblique muscles (figs. 12—23, *L.*). It is this absence of the circular layer of fibres which results in the appearance of a dark line—the lateral line—running along each side of the body. Elsewhere the fibres give the body-wall a dull, whitish, opaque appearance, but here there is little between the cuticle and the body-cavity. The latter being a closed-in and non-illuminated space, and the cuticle through which it is seen fairly transparent, the appearance of a dark line is of necessity produced. The circular layer of fibres is a thin one, and frequently, but not always, only one fibre thick. The fibres are apparently hollow, and are often broken up into fibrils of irregular size, perhaps owing to the action of reagents. Sometimes the fibre appears to be formed of a little group of these fibrils (fig. 51, *M. Tr.*). The layer seems to stop short just beyond the first annulation, as, in longitudinal sections, no circularly disposed fibres are seen in the head region (fig. 24).

**Longitudinally disposed Fibres (*M. Long.*).—**With the exception of the ventral surface of the head, where the hooks arise, these fibres form a layer over the whole surface of the body just within the layer of circularly disposed fibres. In *P. protelis* the two layers are separated by a considerable interval, corresponding in extent to almost the whole thickness of the body-wall, the space being occupied by a large number of cells absent in *P. teretiusculum*. The fibres composing this layer differ from those of the first mentioned, inasmuch as they are not hollow, and show no sign of breaking up, when cut transversely, into groups of fibrils, such as are met with in the circularly disposed fibres (figs. 29, 51,

*M. Long.*). The structure of the muscle fibres is shown in fig. 30. They are seen to have a very characteristic appearance: at regular intervals the customary dark lines pass across the fibre, a light band is present on either side of the dark line, and between two consecutive lines there can be seen, on examination with a high power, what have the appearance of minute rod-like structures lying parallel to each other and to the length of the fibre. Whilst there is no definite sarcolemma present the fibres are bound together by a material, usually of a slightly punctated nature, in which very distinct nuclei are present (*Nu.*). But rarely the outline of cells can be distinguished in this layer, which agrees closely with that described by Leuckart as present in many cases—as, for example, *P. proboscideum*. This layer of muscles is thicker than the circular one, and passes completely round the body, there being no definite arrangement of the fibres into bundles (figs. 12, &c., 24).

*Obliquely disposed Fibres (O. m.)*.—These run obliquely across the body-cavity, their dorsal ends being inserted into the body-wall at a level nearer to the mid-dorsal than to the mid-ventral line, and their ventral ends being inserted on either side of and not far from the mid-ventral line (figs. 12, &c., 28, *O. m.*). They serve roughly to divide the body-cavity into three compartments: (1) a median one stretching from the dorsal to the ventral surface, and containing the alimentary canal, reproductive organs, nervous system, hook-glands, &c.; and (2) two lateral ones, one on either side (*L. S.*). A transverse section of the body thus roughly resembles, in this division of the cœlom into three parts, one through the middle of the segment of such a polychæte worm, for example, as a *Polyophthalmus*, though of course no structures comparable to parapodia are present. The oblique fibres branch and split up into fibrils at either end, and these fibrils pass through between the muscle layers, some apparently passing into the layer of circular fibres, others running through the cuticle (fig. 28).

In young forms especially, a division of these fibres into two groups on each side of the annulus can be clearly seen

(fig. 28). The two groups of fibres, unlike those described in other species, such as *P. tænioides*, do not cross each other, nor do they typically pass from one segment to another. Leuckart<sup>1</sup> has described two bands on each side, one passing downwards and forwards, the other downwards and backwards; whilst Hoyle,<sup>2</sup> in *P. protelis*, finds that only the former of these two groups is present. In *P. teretiusculum* two groups are present, but only in rare instances can any passage of fibres from one segment to another be detected. The fibres pass, in two parallel bundles, in a dorso-ventral direction, and are inserted almost entirely into the wall of the anterior part of the annulus; occasionally an odd fibre, or a terminal branch of one, belonging to the posterior group runs backwards into the very anterior part of the annulus next behind. In the space between the oblique fibres and the body-wall are placed groups of parietal gland-cells (fig. 12, *Pa. gl.*).

Hook-muscles (fig. 39).—There is very considerable difficulty in rightly determining the number and arrangement of these, which accounts for the discrepancies in the various accounts given. The figure drawn represents the results obtained from dissections, and from the examination of some eight series of consecutive sections cut in various directions. Whilst it agrees fairly well with the description given by Stiles,<sup>3</sup> it differs from his in one or two important respects, but to avoid confusion I have as far as possible followed the names given by him.

In connection with the hooks there are four special portions which serve for the attachment of the muscles. These are (1) the upper angle of the base of the hook, (2) the lower angle of the base of the hook, (3) the basal joint, and (4) the special chitinous thickening of the wall in the lower part of the invagination, containing the base of the hook with which it is united (fig. 38, 1—4).

The muscles may be clearly divided into two sets: (1) those

<sup>1</sup> Loc. cit., p. 41, Taf. i, fig. 11.

<sup>2</sup> Loc. cit., p. 172, pl. xxvii, fig. 10.

<sup>3</sup> Loc. cit., p. 143, Taf. viii, figs. 30, 33.

attached to the hook itself; (2) those attached to the basal joint and basal chitinous thickening. In the following description the letters correspond to those used to distinguish the muscles in fig. 39.

(1) Muscles attached to the Hook itself.—These are only two in number.

(a) Extensor of the Hook.—This forms a fan-shaped mass entirely enclosed within the sheath. It arises from the upper and posterior internal surface of this, and its fibres converge as they run forwards, and have a strong tendinous attachment to the upper angle of the hook.

(b) Flexor of the Hook.—This arises from the lower and posterior internal surface of the sheath, and passes forwards as a strong, stout muscle to be attached to the lower angle of the base of the hook. This must correspond to the two muscles described by Stiles as *m. flexor interior et exterior*; but in this form I can only find a single large muscle, which has the same relationship to the lower angle of the hook which the extensor has to the upper angle, except that in the case of the former the attachment to the hook is broad and not tendinous.

(2) Muscles attached to the Basal Joint and Basal Chitinous Thickening.—These are four in number.

(c) Internal and External Protractors.—This, when viewed from above, has a fan shape, and must be equivalent to the *m. protractor externus et internus* of Stiles, and most probably to that described by Macalister<sup>1</sup> as present in *P. imperatoris*, where this author states that “each hook has also a fan-shaped depressor muscle, which is only a specialised part of the longitudinal muscular layer of the body-wall.” The muscle in question is a large one arising from the internal, external, and anterior (with regard to the median line of the body) surfaces of the basal joint of the hook. The fibres spread outwards and slightly downwards to be inserted into the body-wall. The action of this muscle is to pull the whole hook apparatus downwards and outwards, so

<sup>1</sup> Loc. cit., p. 63.

as to cause it to project from the body-wall. In this action it is assisted by the two following muscles.

(*d*) Ventral Protractor.—This is the equivalent of the *m. protractor ventralis* of Stiles, and the *adductor basis unci* of Hoyle. Its fibres are attached to the posterior end of the basal joint, and pass outwards and slightly downwards to be inserted into the body-wall. Its action is to pull the whole apparatus outwards, and to cause the point of the hook to be pulled slightly towards the median line.

(*e*) Dorsal Protractor.—This is the equivalent of the *m. protractor dorsalis* of Stiles, and of the *protractor basis unci* of Hoyle. It is a strongly developed muscle, and arises from the posterior end of the basal joint, nearer to the ventral surface than the last-named muscle. Its fibres run upwards and forwards to be inserted into the dorsal surface of the head, and its action is to pull the hook apparatus slightly outwards, but more still to cause the point of the hook to move towards the ventral surface.

(*f* and *g*) Internal and External Retractors.—These are equivalent to the *mm. retractores externi et interni* of Stiles, and form a series of muscular bands, which arise partly from the ventral posterior end of the basal joint and partly from the basal chitinous thickening. They form strong bands running backwards, the internal ones towards the middle line, the external ones towards the side of the body, to be inserted into the body-wall. Their action is that of retracting the whole apparatus.

(*h*) Ventral Retractor.—This is equivalent to the *m. retractor* or *bursæ ventralis* of Stiles. It arises from the sides of the basal thickening of the hook invagination, and passes outwards to be inserted into the body-wall. It acts as a retractor.

## 5. Alimentary Canal.

(Figs. 27, 32, 50, 59.)

The following five divisions may be distinguished in the alimentary canal:—(1) The mouth with the oral papilla or

upper lip; (2) the pharynx; (3) the œsophagus; (4) the stomach; (5) the rectum. Of these parts the first three are equivalent to the fore-gut, the fourth to the mid-gut, and the fifth to the hind-gut of other Arthropoda.

(1) The Mouth and Oral Papilla or Upper Lip.— This lies in the mid-ventral line (figs. 1, 2, 5), and in both males and females is prominent. The outline of the papilla is triangular, with the angles broadly rounded off and the apex pointing anteriorly. It is sunken in a pit, the sides of which closely embrace it, producing thus the appearance of a groove, which on the posterior side of the papilla is slightly enlarged, indicating the actual mouth opening. A median longitudinal section (fig. 32) shows the relationship well, the groove being cut through anteriorly, and the mouth opening and pharynx posteriorly. The cuticle of the external surface of the body dips down into the groove and covers the surface of the papilla, being especially thick (fig. 32, *Gr.*) when, at the deepest part of the groove, it turns downwards to spread over the papilla. This part serves as an attachment for muscles concerned with the papilla and pharynx.

Hoyle<sup>1</sup> has described two and possibly three sets of muscles in the papilla of *P. protelis*; whilst Stiles<sup>2</sup> and Lohrmann agree in describing, in the forms examined by them, only a single set, viz. those running parallel to the length of the body. In *P. teretiusculum* only the latter are present, and they spread out into a fan-shaped mass, which runs forwards, the fibres converging to be inserted anteriorly into the thickened cuticle at the innermost end of the groove surrounding the papilla (fig. 32, *M 5*). From the bottom of the groove on each side of the papilla anteriorly there is a plate-like projecting of cuticle passing upwards into the body-cavity. To the inner sides of these two plates muscles converge, which run downwards and forwards (fig. 32, *M 6*) from the front and side walls of the pharynx.

From the firm attachment afforded by the thickened cuticle

<sup>1</sup> Loc. cit., p. 175.

<sup>2</sup> Loc. cit., p. 121.

at the anterior end of the groove surrounding the papilla and by the two plates just described, two well-developed muscle-bands pass forwards, one on either side of the median line, to be inserted into the body-wall at the anterior end of the head. The joint action of the three sets of muscles—viz. (1) those of the papilla, (2) those from the pharynx-wall, and (3) those running forwards to the anterior end of the head—necessarily results in a widening of the mouth opening of the pharyngeal tube, whereby a sucking action will be produced and fluid material passed upwards. Not only this, but the surface of the papilla is marked by little rugosities, as is also the cuticle lining the posterior surface of the mouth opening. The fan-shaped mass of muscles within the papilla (fig. 32, *M* 5) is so arranged that, together with the action of the muscles running forwards into the head, the papilla must be rendered capable of at least an up-and-down scraping movement, by which the parasite is probably able to pierce the walls of blood-vessels in the lung of its host.

(2) Pharynx (fig. 32).—This leads directly upwards from the mouth, and after running a short distance turns somewhat abruptly backwards. It may be easily distinguished from the œsophagus, into which it opens.

In *P. proboscideum*,<sup>1</sup> according to Stiles, the cuticle lining the pharynx is thicker and stains more readily than that of the œsophagus. On the anterior wall of *P. tereti-usculum*, as seen in longitudinal section, the cuticle is thin, except immediately opposite to a thick cushion-like pad in the posterior wall to be soon described. On the posterior wall it becomes considerably modified. The layer becomes much thickened in the lower half of the pharynx, and a special portion can be clearly seen as represented in fig. 32. This has the appearance in longitudinal section of a tooth with its pointed end lying close to the mouth. The surface facing into the pharynx bears distinct rugosities, and the upper end appears to have a definite relationship to a curious swollen portion of the wall of the pharynx just where it turns sharply

<sup>1</sup> Loc. cit., p. 123, Taf. viii, fig. 46.

backwards. This tooth-like body (*To.*) is a very distinct structure when the mouth and pharynx are examined by means of sections, or when they are removed from the body and examined whole. In some cases even it separates off from the rest of the cuticle. It is, however, a single median and not a paired structure (unless, which is very improbable, it be formed of two fused lateral halves), and though it certainly suggests the presence of a modified mouth appendage, its very distinctly unpaired nature must, in the absence of any evidence as to its double nature, be taken as negating the idea of its representing such a structure.

At its upper end a curious modification takes place in the wall of the pharynx. The epithelial layer on the inner side, which is elsewhere thin, becomes here much thickened and swollen out (fig. 32, *P. E.*<sup>2</sup>). In addition to this there is present (fig. 32, *P. E.*<sup>1</sup>), just where the pharynx turns backwards, a special layer which lies external to the ordinary epithelial cells and stains deeply. It is apparently cellular in nature, and secretes on its aspect facing into the pharynx a very thin chitinous coat. The outer half of the upper end of the tooth-like structure ends abruptly against this layer, but the inner half of the same structure is continuous with a thin process of chitin which runs up between the external deeply staining layer and the ordinary epithelium. The exact relationship of the parts is shown in the figure, and it would seem as if this special structure were intimately associated with the growth of the tooth-like organ in the hinder wall of the pharynx.

The anterior wall of the latter has, for the most part, only a comparatively thin layer of cuticle, beneath which is the layer of epidermic cells (*E.*) amongst which the muscle-fibres are inserted. The cells are packed somewhat closely together, and appear to lose their distinctly columnar nature. Immediately opposite to the pad-like structure in the posterior wall the cuticle becomes somewhat thickened. On the posterior wall, on the contrary, the cells are very distinctly columnar; in fact, just where the cuticle bends inwards from the external surface at the mouth the cells, which over the body surface are



separated by irregular intervals from each other, increase in length and lie closely side by side. They form a small swelling under the middle part of the tooth-like organ, but at the upper termination of the latter the layer becomes more than one cell deep (.16 mm. in thickness), and, together with the special differentiation above alluded to (fig. 32, *P. E.*<sup>1</sup>), they give rise to a cushion or pad in the posterior wall of the pharynx where the latter turns sharply backwards. It is to this smaller upper part of the pharynx that the most important muscles are attached. From the anterior and side walls arise the bands passing forwards and downwards to the cuticular ingrowths from the side of the papilla; from the posterior wall arise fibres passing downwards and backwards into connection with the longitudinal layer of the body. Another special band from the latter is inserted into the cuticle just at the angle of the mouth (*M.* 7).

There are thus in connection with the mouth and pharynx five main sets of muscles:—(1) Muscles of the papilla. (2) Muscles from the anterior and side walls of the upper part of the pharynx. (3) Muscles forward from the papilla to the head. (4) Muscles from the posterior surface of the upper part of the pharynx. (5) Muscles inserted into the angle of the mouth posteriorly.

The third series assist the first two, and the united action of all five will be, as can be seen on reference to the figure, (1) to distend the cavity of the pharynx; (2) to pull the pharynx downwards; (3) to pull the papilla backwards and slightly upwards; (4) to distend the mouth opening. In this way the pharynx, oral papilla, and tooth-like organ serve as sucking, and the latter two as rasping structures.

(3) *Œsophagus*.—This is some four times as long as the pharynx, from which it runs obliquely backwards and upwards till it reaches the ventral wall of the stomach (figs. 27 and 50). The walls throughout its whole course are formed of a layer of columnar epithelium directly continuous with that of the pharynx, and lined internally by a thin but distinct cuticle. External to the epithelium lies the muscle

layer, which is well developed, and consists for the greater part of fibres running, some obliquely round the œsophagus, others parallel to its length. Just beneath the stomach wall a ring of circularly disposed fibres is present (fig. 50, *M. Æ.*), which acts as a sphincter. The opening into the ventral wall of the stomach is placed some little distance posteriorly to the anterior end of the latter. The œsophageal tube pierces the wall, and the columnar epithelium rises up into a most distinct papilla. On this a funnel-shaped opening is present, leading into the œsophagus, and the epithelium appears as it were to flow over the margins of the funnel, and then to dip down all round under the epithelium of the mid-gut. The papilla is lined all over by a thin layer of cuticle, and just at its base the cavity of the œsophagus always swells out to form a space of the characteristic form shown in fig. 50.

(4) Stomach or Mid-gut.—This forms a straight tube which runs directly from about the level of the mouth to within a short distance of the very posterior end of the body. Its average diameter is .83 mm. The walls internally are thrown into well-marked longitudinal folds, and are lined by a single layer of definite columnar cells (fig. 50, *M. G. E.*). The outlines of these are very distinct, and each contains a spherical nucleus, placed usually nearer to the external than the internal end. The cells rest upon a basement membrane, and external to this lie the muscle layers. The internal one consists of circularly and obliquely disposed fibres, but the more strongly developed is the external one, which consists of longitudinally disposed fibres (*M. Al. Long.*). Leuckart described a longitudinal layer of muscles, but their presence is denied by Stiles,<sup>1</sup> according to whom this layer is merely a connective-tissue coat. In the form now being described I think there is no doubt whatever as to the muscular nature of this layer.

There is present in addition a certain amount of material which may be described as connective tissue, and which is

<sup>1</sup> Loc. cit., p. 124.

composed partly of fibrous material and partly of cells. This connective tissue is continuous with two mesenteries, one on either side, which run off from the alimentary canal to the hook-glands where these are present (fig. 16), and most posteriorly behind the hook-glands pass off to the mid-dorsal line (fig. 21).

In two specimens the cells of the stomach wall differ from those of the others examined, in containing a certain amount of dark brown pigment. This is interesting since Macalister, in *P. imperatoris*, describes the gland-cells as spheroidal, deep brown in colour, and as giving the digestive canal a deep hue rendering it visible through the body-wall.<sup>1</sup>

In his specimens from the lung of *Boa imperator*, Macalister found the alimentary tract empty or nearly so. In *P. teretiusculum* there are almost always present coagulated remains of the blood on which the animal has been feeding.

(5) Rectum or Hind Gut (fig. 59, *H. G.*).—This forms a short straight tube, which runs from the end of the mid-gut to the very posterior extremity of the body. Its walls are relatively thick, and the lumen small. Most internally lies a layer of columnar epithelial cells, with a cuticular lining which is directly continuous at the anus with that on the external surface of the body. The cells dip down (fig. 59) under those of the mid-gut. External to the epithelium is a thick layer of connective tissue and longitudinal muscle-fibres (*M. H. G.*). No trace of circular fibres can be seen.

Embedded in the connective tissue around the part where the hind and mid guts unite together, are a number of cells exactly similar in structure to those which compose the hook, head, and parietal glands. No trace of any duct leading away from them can be detected (*Al. Gl.*).

## 6. Secretory Organs.

(Figs. 6, 7, 29, 32, 51, 52.)

Perhaps the most striking feature in the anatomy of *Pentastomum* is the great development of glandular structures of an

<sup>1</sup> Loc. cit., p. 62.

excretory nature. Though they have been described in various ways and under slightly different names by different workers, there appears to be on the whole a fundamental agreement in the species examined with regard to the distribution and arrangement of the gland masses, though at the same time they are more extensively developed in some than in others.

Leuckart described in *P. tænioides* (1) stigmatic glands and (2) hook-glands. Hoyle, in *P. protelis*, described (1) hook-glands, (2) parietal cells, and (3) stigmatic cells; whilst Stiles, in *P. proboscideum*, has recently described (1) stigmatic glands, (2) parietal glands, (3) head-glands, (4) hook-glands, together with masses of cells round the œsophagus and rectum.

There is a certain amount of confusion in the names, since what Hoyle has described as "hook-glands" in *P. protelis* are the undoubted homologues of the structures to which the same name had been given by Leuckart in *P. proboscideum*, which are present in *Linguatula Diesingii* (van Beneden); whilst to the homologous structures in *P. proboscideum* Stiles gives the name of "head-gland."

In *P. teretiusculum* the arrangement of the gland masses is very similar to that of *P. proboscideum*, and by interchanging the names "head-" and "hook-glands," as used by Stiles, they may be directly compared with those described by Leuckart, Hoyle, and other investigators.

These secretory structures fall into two groups, which are quite distinct in form and function from each other. The one set, comprising the stigmatic glands only, are epiblastic in origin, and simply modifications of the cuticle-forming layer of cells; whilst the others are more deeply lying structures, and derived presumably from mesoblast. The one set is to be regarded as secreting a material useless to the animal, at all events in the adult state; the other as secreting a fluid of considerable importance to the parasite, the nature of which will be suggested later.

The first group comprises only the stigmatic glands. These appear to be present in greater numbers in *P. tereti-*

usculum than in other forms yet described. They correspond in position internally to the stigmata previously mentioned when dealing with the external anatomy. In the head region they form an almost continuous layer beneath the cuticle, longitudinal sections showing them lying closely side by side. On the annuli they are confined to the anterior half of each (fig. 29).

Leuckart<sup>1</sup> described in the young form of *P. tænioides*, in connection with the stigmata, small vesicle-like structures with a definite wall, and containing fluid. In the older forms the vesicle is replaced by a small process formed of a group of cells which hangs down into the cœlom.

Hoyle, in *P. protelis*,<sup>2</sup> has described and figured them as spheroidal in form, with their inner surfaces projecting but little beyond that of the subcuticular epithelium. They take up staining material easily, and each consists of from 6 to 9 cells. The outer aspect is moulded into a kind of short neck which lies within the stigma, and is closed by a fine very darkly stained line.

Stiles<sup>3</sup> describes and figures them in *P. proboscideum* as small groups of clearly marked cells which lie immediately within the stigma, not apparently arranged so as to form a mass of definite shape. They are placed within a depression on the inner side of the cuticle in such a way that their inner ends do not reach to the level of those of the ordinary subcuticular epithelium.

In *P. teretiusculum* the stigmatic glands form a very noticeable feature in all sections of the body-wall, and appear to be more highly developed than in other forms. Each has the definite shape represented in fig. 51, and consists of a cluster of cells enclosed apparently in a common wall of connective tissue. The whole is somewhat flask-shaped, with the neck leading into the stigma (*St. Gl. O.*). The individual cells can in good sections be distinguished, and then, as shown

<sup>1</sup> Loc. cit., p. 33, Taf. i, fig. 7, and Taf. iii, figs. 18—21.

<sup>2</sup> Loc. cit., p. 180, pl. xxvii, figs. 9 and 11.

<sup>3</sup> Loc. cit., p. 119, Taf. viii, fig. 49.

in the figure, each one is seen to be columnar with a somewhat larger club-shaped head, internally containing a distinct round or oval nucleus, whilst the more pointed external end passes to the stigma. The latter has a definite wall, which is doubtless a special modification of the cuticle, but appears distinct from this in section. Just at the mouth of the gland the wall of the stigma is thrown into a slight fold (*R.*), and from this a thin layer appears to pass inwards, which forms the external boundary of the gland. This cannot often be detected as a distinct continuous structure, but traces of it can be seen, and the very definite form of the gland indicates the presence of some such bounding structure.

The stigma is hour-glass shaped, and its external opening projects as a raised lip beyond the surface of the cuticle.

Whilst there can be no doubt that the cells constituting the glands are modified subcuticular cells, it must be noticed that each one is much larger than one of the latter, and that the whole gland projects considerably beyond the level of the inner end of this layer. At times the cells of the glands contain a large amount of protoplasm, at times only a protoplasmic network is present, doubtless owing to the fact that fluid material has been secreted and passed out.

The second group comprises the remaining secretory glands of the animal, all of which are intimately associated with one another. The cells composing them are identical in structure, and are in all probability to be regarded as mesoblastic in origin. Ducts, when such are present, are, on the other hand, lined with a definite cuticle, and to be regarded hence as epiblastic in origin.

For the sake of convenience we may deal with these structures under the following names :

(1) Hook-gland (=hook-gland of Leuckart in *P. proboscideum* and *P. oxycephalum*, hook-gland of Hoyle in *P. protelis*, and head-gland of Stiles in *P. proboscideum*).

Either of the names hook- and head-gland is applicable to this structure, so far as *P. teretiusculum* is concerned, if we simply pay attention to the external opening of the gland ;

but inasmuch as the structure which lies on each side of the body has a definite relationship to the hooks, and, more important still, there is a glandular mass which does lie in the head region, it is advisable to retain the name of hook-gland for the organ now to be described, more especially since in doing this we are retaining the nomenclature of older workers. At the same time it may be pointed out, as will be described soon, that the hook- and head-glands are directly continuous with one another, and the application of two distinct names is merely a matter of convenience.

In *P. teretiusculum* the large secretory gland of the body may be regarded as consisting of an anterior unpaired portion lying in the head region, from which on either side there extends backwards a long branch which lies close beside the alimentary canal, and reaches almost to the posterior end of the body. The unpaired part forms the head-gland, the paired part the hook-glands.

The hook-gland of each side may be described as a long, slightly tapering, finger-like mass of almost the same length as the mid-gut, but not quite reaching either the anterior or posterior extremity of this (figs. 6 and 7). The younger the specimen the more compact is the gland, and in such forms there is often, as described by Hoyle, the appearance of a fine membrane enclosing the mass. In mature specimens such a structure is rarely visible, but on opening the body-cavity the gland on either side may be separated from the other organs as a distinct structure, save at the anterior end. In the mature form, again, they are compressed and pushed out of place by the swollen-out reproductive organs.

In young forms there may be easily recognised a mesentery, which at the anterior end of the gland serves to attach the latter to the dorsal body-wall, another mesentery passing off on the internal side to the wall of the alimentary canal (figs. 20 and 23, *Mes.*<sub>2</sub>). The mesenteries, again, are more difficult to recognise in the adult form, especially in the case of the female.

The gland has a definite relationship in position to certain

portions of the reproductive organs. In the male it lies at the anterior end, completely dorsal to the reproductive organs; but further back, in the region of the testis, it lies below the level of this. The vesiculæ seminales, which arise from the anterior end of the testis, pass through the middle of the gland—a feature which, again, is more noticeable in young forms (figs. 6, 17, 18). In mature forms the vesiculæ are so large in comparison to the glands that the latter appear to be compressed between them and the alimentary canal, and thus the genital ducts have the appearance of passing between the body-wall and the gland, as they are described as doing in the adults of other species (fig. 17). Careful examination, however, reveals the fact that little masses of cells are present, the remnants of the part of the gland lying external to the vesiculæ. Fig. 17, which is a camera drawing representing a transverse section of a young male, will serve to show clearly the relation of the structures at that stage.

In the female (fig. 7) the gland occupies a similar position by the side of the alimentary canal lying beneath the median ovary, though the latter and the glands are both pressed up against the dorsal wall by the swollen and coiled uterus in the adult form. As in the male, so in the female, the ducts leading off from the anterior extremity of the gonad pass on each side right through the centre of the gland (fig. 22, *Od.*).

In *P. proboscideum* Stiles and Lohrmann have described the gland as being composed of two different kinds of cells—a larger and a smaller. Stiles<sup>1</sup> figures the smaller ones as lying close to the duct in the centre, and as being surrounded by a layer of much larger cells.

In the form now being described there is no such distinction into two kinds of cells; some, indeed, are smaller than others, but all, as is not the case in *P. proboscideum*, take stain (borax carmine) in the same way, and there is every gradation in size between the largest and the smallest. They vary in size from .25 mm. to .08 mm., the largest cells being always those found in the parietal glands, though, so far as their

<sup>1</sup> *Loc. cit.*, p. 128, Taf. viii, fig. 47.



structure is concerned, the cells of the head, hook, and parietal glands are not to be distinguished from one another.

The cells have the same fundamental structure as was first described by Leuckart. Each is of large size (fig. 52), and has a distinct nucleus, which sometimes shows a limiting membrane, but often has the appearance of a darkly stained mass of indefinite outline, which almost merges into the surrounding protoplasm. The latter shows a reticulation very similar to that of the cells to be described in connection with the vasa deferentia in the male, and the ducts leading from the receptacula in the female. Very frequently these cells may be arranged in groups of four or more when they are closely apposed. Around a central spot where the cells are all in contact with one another is a light, unstained, somewhat circular area, into which radiate irregular lines of little (when stained with borax carmine) yellowish masses. From the central spot passes off, as figured by Leuckart, a fine thread-like strand, which is in reality, as described by Stiles in *P. proboscideum*, a hollow tube. The latter in some preparations, where the parts of the gland are more or less separated from each other, and the whole is not so compressed as is usually the case, can be clearly seen to run to the main duct. They have all the appearance of being minute tubes continuous with the chitinous lining of the main duct, and doubtless serve to carry to the latter the secretion of these groups of cells. Numbers of the cells forming the gland are apparently independent of each other, though they are all more or less closely packed together. There is nowhere any trace of a definite arrangement of these cells into layers.

The main duct will be dealt with after the description of the head-gland has been given.

(2) Head-gland (= anterior part of hook-gland of Hoyle in *P. protelis*, and hook-gland of Stiles in *P. proboscideum*).—The cells forming the head-gland are directly continuous with those of the hook-gland, and also with the parietal cells, to be afterwards described. In structure the three are identical.

The cells form an irregular mass of no definite shape, which from about the level of the œsophagus (or in the male of the genital opening) passes forwards occupying the spaces intervening between the strongly developed muscles of the head region. The consequence is that there is no body-cavity in the head region, and that the latter is comparatively solid; so that, apart from their excretory function, the cells of the head-gland must be of considerable use in forming a firm support for the body-wall in this region, where are present the most important muscles, the efficient working of which depends upon their having a firm insertion. Stiles and Hoyle describe the continuity of these cells with those of the glands described above as hook-glands, Hoyle giving to them no special name, whilst Stiles restricts to them the name of hook-glands in consequence of their having in *P. proboscideum* a special relationship to ducts opening beside the hooks. This special relationship does not obtain in *P. teretiusculum*, though at the same time they probably pour their secretion partly into the duct opening on the primary papillæ, and partly into those opening by the side of the hooks.

Ducts of the Hook- and Head-glands.—Lohrmann described the ducts of the head-glands as opening on two prominent papillæ on the head. Stiles, in *P. proboscideum*, states that the ducts of the head-gland (= hook-gland as described above) open ventrally to the papillæ, whilst those of the hook-glands (= head-glands as described above) open in relation to the hooks. Leuckart has described the hook-glands (= those described above under the same name) as opening in relation to the hooks, and in the case of *P. oxycephalum* states that the duct passes through the nerve-ring—a relationship which has not, I think, been observed in any other form. In *P. teretiusculum* the ducts are arranged as follows:—In the hook-gland of each side there is for the posterior two thirds of its course a single main duct. Anteriorly this, on each side of the body, breaks up into three branches (figs. 6 and 7, *a, b, c*); of these three one passes to each hook of its own side, and one—the largest—runs on through the head

region to open as described by Lohrmann on the papilla, and not ventrally to this as in *P. proboscideum*, according to Stiles. Of this fact I have satisfied myself after examination of sections of the head of several specimens.

It will be noticed that there is no separate duct for the head- and hook-glands, nor have I been able, after long searching through series of sections cut in various directions, to detect any openings of small ducts from the cells of the head-gland, either into the main duct, which forms a prominent feature as it passes forwards to the papilla of its own side, or into the ducts leading down to the hooks. The latter ducts open, as described by Leuckart, into the invaginations in which the bases of the hooks are placed, and on the ventral side of these (fig. 9, *O. Hk. Gl.*).

In structure each duct consists of a layer of small cubical cells with distinct nuclei (figs. 24, 27, *Hk. Gl. d.*), and is lined internally by a thick chitinous layer, whilst the very fine secondary ducts arise irregularly, are usually very difficult to distinguish, and appear to consist simply of a thin chitinous wall. The main duct runs right on through the posterior part of the gland without dividing, and merely receiving along its course these minute ducts, which pass off, as described above, from small groups of the cells composing the gland.

(3) Parietal Cells (*Pa. gl.*).—These consist of irregularly arranged cells, which in the posterior two thirds of the body are not found in the mid-dorsal or ventral lines, and in mature specimens are nearly entirely confined to the space which lies between the oblique muscles and the body-wall (figs. 12—23, 28). In younger forms and at the very posterior end (fig. 21) they are more largely developed, but are absent in the mid-dorsal and ventral lines. Anteriorly they spread over the whole body-wall internally, and are directly continuous at about the level of the œsophagus with the cells forming the head-gland (fig. 11). As in other forms, there appear to be no special ducts for these cells.

In addition to the above there are present, as mentioned previously, amongst the muscle-fibres and connective tissue

which surround the opening of the mid into the hind gut a few cells evidently similar in structure to the typical gland-cells of the body (fig. 59, *Al. gl.*). They have no ducts. There do not appear to be any special gland-cells connected with the œsophagus such as Stiles describes and figures in *P. proboscideum*, though in this region the parietal, hook-, and head-glands merge into one another, and hence gland-cells lie, but in no regular arrangement, around the œsophagus and pharynx (fig. 32, *Pa. gl.*).

(4) There now remains a special structure, of the nature of which I have not found it possible to speak with certainty. This structure has the form of a somewhat irregularly shaped mass of cells, which lies in the mid-dorsal line immediately above the very anterior end of the mid-gut (figs. 10, 27, *Gl.?*). The cells composing it are small ( $\cdot 025$  mm.), and stand out in striking contrast to the large gland-cells immediately around them. There is apparently no duct connected with them, but they are constantly present, and can be detected in every specimen when sections are cut. They resemble much in appearance the masses of small cells figured by Stiles<sup>1</sup> as surrounding the structures lying within the body-cavity in a young female *P. proboscideum*.

#### Functions of the Gland-Structures.

We have under this head to deal with two sets of structures, which are evidently, as before stated, very distinct from one another, and have different functions to perform. *P. teretiusculum* feeds exclusively upon the blood which it obtains directly from the walls of the lung of the snake in which it lives. This blood it can only obtain by piercing the walls of the delicate blood-vessels and by subsequent suction. To effect these two processes special structures are present. For the piercing of the walls, the oral papilla and tooth-like structure in the posterior wall of the pharynx are amply sufficient, owing to their capability of movement by muscles.

<sup>1</sup> Loc. cit., Taf. viii, fig. 47.

Once the wall of the blood-vessel is pierced and a flow of blood produced, the latter would be drawn up the pharynx and œsophagus by the alternate contraction and expansion of the walls, as described in the section dealing with the alimentary canal. From the œsophagus it would pass into the mid-gut, and its backward flow be hindered both by the sphincter muscle at the base of the papilla, and by the situation of the opening at the apex of a papilla.

Under ordinary circumstances, blood, when withdrawn from the vessels in which it normally flows, rapidly coagulates. Were it to do so after passing into the alimentary canal of the Pentastomum, quite apart from the increased difficulty of digestion after coagulation, a block would be formed and the further passage stopped.

Such an animal, for example, as *Hirudo*, which feeds, as does this *Pentastomum*, exclusively upon blood, is provided with special structures to prevent the coagulation of the blood. It seems, therefore, natural to expect that we should find in *Pentastomum*, as in *Hirudo*, some structure which secretes a fluid having the property of preventing coagulation of the blood. This structure we may, in all probability, recognise in the large head, hook, and parietal glands.

In *Hirudo*, however, there is present a definite series of spaces—blood-vessels or sinuses—which contain fluid into which passes the nutrient material formed in the alimentary canal as result of digestion of the blood sucked in. In *Pentastomum* no such vessels or sinuses are present. The cœlom is extensive, and a long mid-gut is present, lined by hypoblastic cells, though no vessels are present in its walls containing fluid into which can pass the elaborated food material. Instead of this, the blood which the parasite sucks in percolates, in *P. teretiusculum*, at any rate, through the walls of the canal into the cœlom and fills the latter, giving to the whole body a brilliant red colour when alive.<sup>1</sup> Either this is the case,

<sup>1</sup> This red colour is not due simply to the alimentary canal being seen through the skin. In large females, in which the reproductive organs fill up and swell out the body, the whole of the latter is brilliantly red coloured.

or else the body-cavity of the *Pentastomum* contains a blood-red fluid such as is not known in any other Arthropod.

Doubtless, in passing through the canal walls, the blood undergoes some change, but finally it bathes all the organs of the body. The latter must be able, as are the various structures in a Cestode, to obtain from the fluid which permeates them nutritive material, and according to their nature we may suppose that they withdraw certain elements, some of which, according to the nature of the organ, are used to build up new structures, whilst others, useless to the body, are excreted.

The latter function is probably performed by the stigmatic glands, which are widely scattered over the body and open directly to the exterior. Very different in nature from these are, however, the hook- and head-glands, and their function is probably, as above suggested, that of secreting from the blood a fluid material which has the power—just as in the case of the so-called salivary glands of *Hirudo*—of preventing the coagulation of the blood.

Leuckart<sup>1</sup> suggested that the function of these glands was that of producing an irritant material which, when passed out, resulted in the organ in which the *Pentastomum* was parasite, giving out a larger supply of nutrient material. Now in *P. teretiusculum* there is no need, when once the tissues are pierced, of any irritant organ to cause a flow of blood. There is, however, a want of some structure which shall prevent the coagulation of the blood.

Hoyle has suggested that the stigmatic glands may serve to secrete a material which forms the cocoon in the young state. Possibly this may be so, but they are so highly developed in the adult form that they must subserve some special function in the latter, and the only likely one appears to be that of excreting material useless to the animal.

<sup>1</sup> Loc. cit., p. 66.

## 7. Nervous System.

(Figs. 6, 7, 8, 11, 12, 15, 27, 32—36, 53, 60, 61.)

The structure of this agrees in the main with that described by Leuckart in *P. tænioides*, and by Stiles in *P. proboscideum*. There is one large ganglionic mass of a clearly double nature, lying to the posterior side of the œsophagus, about one third of the way down the latter from the point at which it enters the ventral side of the mid-gut. From this central mass a comparatively small commissure (figs. 35, 36, 60, *A.*) passes round the œsophagus, forming a ring in which no trace of ganglionic enlargement or ganglionic cells is to be detected in front of the œsophagus. There is thus nothing comparable to a cerebral ganglion.

From the subœsophageal nerve-mass nine nerves are given off on either side. These are represented somewhat diagrammatically in figs. 35 and 36, which have been drawn after study of dissections, and of very numerous sections cut longitudinally, in both a vertical and horizontal direction, transversely and obliquely.

The following is a list of the branches given off:

(1)<sup>1</sup> Close behind the œsophageal commissure (*A*) arises on each side a nerve which runs forwards and downwards, and joins its fellow on the anterior side of the œsophagus. The single nerve thus formed runs for some distance close to the front wall of the œsophagus, and then sends branches to the oral papilla, and the muscles concerned in moving this, as well as to the strong muscles attached to the anterior wall of the pharyngeal tube.

In *P. protelis*, Hoyle describes the œsophageal commissure as double. This appearance of a double commissure may possibly be due to the union in that form, as in *P. proboscideum* (as described by Stiles) and *P. teretiusculum*, of the two nerves in question.

(2) From the latero-ventral surface on each side a nerve

<sup>1</sup> These numbers correspond to those used in figs. 35 and 36.

arises which runs downwards close to the œsophagus, and supplies the muscles lying just behind the œsophagus, and those which are concerned with the posterior wall of the pharynx.

(3) Above the last and just behind the first mentioned arises a nerve on each side. This runs forwards through the head region, keeping close to the ducts from the hook-glands until it reaches the large sensory papillæ on which open the ducts of the glands (fig. 49). This nerve is a very distinct one, and from it probably, though I have not been able to definitely follow their course, arise branches to the smaller sensory papillæ on the dorsal surface of the head (fig. 34). The sole function of this nerve is that of supplying sense-organs, as, though it runs through the head region where muscles are largely developed, it gives off no branches to these.

The sensory papillæ, and amongst these the "Tastpapillen" of Leuckart, are hence innervated from a post-œsophageal nerve mass.

(4) Just behind the last, and slightly ventral to them, a nerve passes off which runs forward to the level of the œsophagus, and then curves backwards, supplying the muscles at the side of the anterior and middle part of the body.

(5) From about the middle of the length of the nerve mass, and dorsal of the last mentioned, arises on either side a nerve which runs forwards and slightly upwards, and after passing to about the level of the anterior end of the mid-gut divides into two. Each division then passes in amongst the muscles of the head region, and its course becomes very difficult to follow, but after repeated examination of sections cut in various directions, I have been able to trace it into distinct connection with a curious structure which lies in the basal part of each hook. The appearance of this is shown in fig. 33. Between the extensor and retractor muscles of the hook, each of which is attached to the internal surface of the basal joint (*B. Hk.*), runs a fibrous structure which is in direct continuation with the nerve now under consideration. The latter



appears to enter the basal part of the hook, and to swell out, or at least to be in direct connection with a well-marked mass of fibres (figs. 9, 10, 33, *Hk. n.*) with nuclei, which breaks up into strands. The latter pass into connection with the cells forming the layer beneath the cuticle, and at times appear to pass right on to the cuticle itself. This fibrous structure is very evident in all sections of the hooks, though it is difficult to see what its meaning is, while in structure it has a somewhat close resemblance to that of the two nerve-cords which pass along the ventral surface of the body (fig. 61).

(6) This is one of two pairs of small nerves which arise from the dorsal surface of the nerve mass. It runs directly upwards behind the œsophagus to supply the walls of the mid-gut.

(7) This lies close behind the last mentioned, and runs in a similar direction, passing into and supplying the hook-gland by the side of the alimentary canal.

(8) From the ventral surface arises posteriorly on each side a small nerve which runs to the reproductive organs. In the female it runs downwards and backwards, and passes on to the walls of that portion of the organ where the duct from the ovary on each side joins the short tube communicating with the spermatheca, and from which arises the long coiled tube which serves in the young form as a vagina, and in the mature one as a uterus.

In the male a similar nerve runs almost directly downwards, and is distributed to the muscles concerned with the cirrus sacs and the external opening.

(9) The nerve mass is prolonged posteriorly into two large cords which run backwards on the ventral side for nearly the whole length of the body.

In the female they pass between the two oviducts and spermathecae, and then turn downwards and enclose between them the proximal part of the vagina, after which their course lies ventral to the various organs in the body-cavity.

In the male they pass backwards and downwards between the two cirrus sacs, and then run along the body just above

the ventral insertion of the oblique muscles. Certainly in parts, and probably for the whole of their length, they are attached to the oblique muscles by a definite mesentery (fig. 15).

These are by far the largest nerves, and run along the surface in such a way as to suggest at first sight an homology between them and the two halves of the main ventral cord in other Arthropods. There can, however, be little doubt but that they are merely specially backward running nerves, the ventral nerve-chain being concentrated. The two nerves are fibrous in appearance, and contain what are apparently nuclei flattened out and elongated in the direction of the length of the nerve. Externally there is present a covering of connective tissue, which is especially marked in young forms (fig. 61, *Ct.*). As Leuckart first pointed out, the nerve mass is to be regarded as equivalent to a fused series of paired ganglia belonging to a much compressed ventral chain. In its young form it shows clear indications of this in its internal structure, whilst in the adult it is clearly divided into two lateral halves by a slight median ventral and dorsal depression, continuous with broad fissures at the anterior and posterior ends of the nerve mass (fig. 60). Each half of the mass is composed, as stated by Stiles,<sup>1</sup> of an internal mass of fibres surrounded by an external sheath of nerve-cells. The whole is enclosed by a fibrous investment, some of the fibres of which, Stiles says, are of the nature of connective tissue, whilst others are nervous. I have not been able to detect the presence of two such sets of fibres. The layer invests very closely the nerve mass, and is undoubtedly continuous (i) with connective-tissue fibres ramifying within the substance of the cell mass, and (ii) with a coat which surrounds the nerves as they pass off, and which is especially well seen in the case of the long posterior cords when sections of a young specimen are cut (fig. 53). It is of course quite possible that nerve-fibres are present, but the two sets cannot be distinguished in the form now under consideration.

<sup>1</sup> *Loc. cit.*, p. 144.

The nerve-cells are very distinct, and do not form a layer of the same thickness all over. They are more numerous at the bases of the nerves where the latter arise from the ganglia (fig. 60), and are more strongly marked ventrally than dorsally (fig. 53); a double layer of them passes up along the line which corresponds to the internal faces of the two fused ganglia. The cells are, as a general rule, pear-shaped, with a single branch passing off, and a distinct nucleus and often nucleolus. At times two branches may be given off, and more rarely three. Where the nerves arise (fig. 53) can be seen thin and elongate cells pulled out in the direction of the length of the branch, and similar structures (fig. 61) are clearly marked all along the course of the posterior cords, especially in young specimens.

### 8. Sense-Organs.

As described in connection with the account of the external anatomy, there are present in the female eight and in the male nine pairs of papillæ, of which two are much more prominent than the others. These two are the "Tastpapillen" of Leuckart, and on cutting sections are found to contain sense-organs of some nature.

Of the seven pairs of papillæ present in *P. proboscideum*, Stiles states that only two, those placed immediately above the hooks, contain sense-organs, though the others seem to have nerves running to them. Leuckart<sup>1</sup> described at the termination of the special nerve running to the "Tastpapillen" a little swollen mass, containing what he took to be ganglion-cells amongst the nerve-fibres, though he could not with certainty establish the direct connection between the two.

Stiles<sup>2</sup> has described and figured a small oval mass of cells, the outer end of the mass projecting beyond the cuticle, and having a small concavity containing a few small stiff processes. The inner end is connected with a slender nerve.

In *P. teretiusculum* there is no difficulty in detecting

<sup>1</sup> Loc. cit., p. 25, Taf. ii, fig. 1.

<sup>2</sup> Loc. cit., p. 147, Taf. vii, fig. 23.

the sense-organs in connection with the two papillæ close to the hooks, but those of the other papillæ are not so easy to distinguish in sections. I have found them in the female in the papillæ on the ventral surface just in front of the first annulus, and in the male just in front of the genital opening, and probably they are present in all. No trace of them is to be seen along the lateral line previously referred to.

Undoubtedly those on the primary papillæ are the most strongly developed and the easiest to detect. Each has the form of a little mass of modified subcuticular cells (fig. 49). These are elongate, and the outer ones of the group are bent round so as to form a bulb-shaped structure of more or less definite shape. In other cases, as in fig. 34, which represents a sense-organ on the papilla above the anterior hook, the bulb shape is more definite, and there is even present what has the appearance of an external limiting structure which runs across the cells where the nerve enters. Sometimes nuclei can be detected in the cells, but more often they cannot, and the cells are distinguished from those around them by their forming a more darkly stained mass. In one instance I detected more than one little mass on the papilla. The cuticle is continued over the surface of the sense-organ, and there is no trace whatever of any anterior concavity, or of stiff processes such as Stiles describes. On the primary papilla the organ lies close to the opening of the hook-gland; in fact, it may here form an irregularly shaped structure of considerable size. It is supplied by a special nerve which runs along by the side of the duct of the hook-gland through the head region. At the base of the sense-organ it swells out into a mass which contains nuclei, and gives off fibres into the bases of the cells. In all probability branches pass from this nerve to the other papillæ on the dorsal surface of the head, but they are so fine that I have not been able to detect them save just where they enter the base of the sense-organ.

It appears to me impossible to speak with certainty as to the nature of these sense-organs, though their constant presence, and the size of the nerve supplying the one in connection with

the primary papilla, point to their having some important function to perform. It may be noted that they are confined to those parts of the body which come in contact either with (*a*) the host or (*b*), in the case of the male, some other Pentastomum. Those in the head region are so placed that they are in contact with the walls of the pit hollowed out in the lung tissue to contain the head of the parasite. The only other ones are the two placed one on either side of the male genital opening (fig. 5). It is easy to see that in *P. proboscideum*, with their projecting processes, they could act in these positions as organs of touch; but in other forms such processes are wanting, and the cuticle is continuous over the external surface.

Judging by the life led by the parasite, an organ of touch—that is, one enabling it to be conscious of contact with external bodies—would be of importance; whilst it scarcely needs to be provided with more than this, since within the lung it cannot, so to speak, go wrong in piercing the tissues in search of food.

These organs are probably sensitive to such stimuli, for example, as those produced by the flow of blood through vessels close to them, a stoppage in the flow, and hence in the food supply of the parasite, being detected. When this takes place the parasites doubtless relax their hold of the tissues, and wander away in search of parts where the sense-organs are affected in the normal manner by the flow of blood, &c. If the host be dead they may thus naturally wander out from the lung, in the characteristic way in which parasites leave the body of a dead host.

### 9. Reproductive Organs.

(Figs. 6, 7, Sections A—G; figs. 11—26, 37, 40—46, 48, 55—58, 60, 62—68.)

(1) Female.—In the different forms the anatomy of which has as yet been studied the female organs appear to agree

somewhat more closely with one another than do the male. They consist of the following parts:

- a. Ovary.
- b. Oviducts.
- c. Spermathecæ.
- d. Vagina (= uterus of mature form.)

The relations and structure of these have been carefully described by Leuckart; and whilst those in *P. teretiusculum* agree in the main with the description given by him of the organs in *P. tænioides*, there are certain minor differences

(a) Ovary.—In the youngest specimen investigated the ovary has the form of a simple tube, the walls of which are formed of a single row of cubical cells with distinct spherical nuclei, there being no difference in thickness between the dorsal and ventral portions. A mesentery composed of fine muscle- (?) fibres and rounded cells attaches the tube to the mid-dorsal line of the body-wall (fig. 57).

Stiles<sup>1</sup> has figured the ovary of a young form of *P. proboscideum* as having the dorsal wall thicker than the ventral, whilst in the same form no muscle-fibres are present in the mesentery. I am not perfectly sure that such are present in *P. teretiusculum*.

In a somewhat older specimen (fig. 44) the ovary has undergone considerable development. Instead of forming a tube circular in outline it has become somewhat flattened out dorso-ventrally, thus indicating clearly a dorsal and ventral side with lateral portions.

The ventral wall is still, and remains throughout life, only one cell thick; but the individual cells are now columnar, with small distinct nuclei close to their outer extremities. These cells extend up the ventral half of each side. The dorsal portion of the wall has undergone considerable changes; the single layer of cells is no longer visible, but as the result of fission a somewhat irregular mass of minute cells has been formed, or rather the dorsal wall is now composed of a mass in which very numerous small nuclei are present.

<sup>1</sup> Loc. cit., Taf. viii, fig. 47.

From the dorso-lateral parts of the ovary a continuous "crest" of cells has grown out on each side, and into this, at intervals which possibly (but of this I am not quite sure) correspond with the annuli of the body, extend pouch-like diverticula of the central cavity (fig. 44, *L. S. O.*). The section figured passes on one side through one of the latter. In the central cavity is a coagulum, which may perhaps contain spermatozoa, though it is extremely difficult to definitely establish the presence of these.

The cells composing the "crest" on either side are distinct in outline, and each contains a well-marked nucleus. The dorsal mesentery (*Mes.*) is prominent, and composed mainly of rounded cells, and is continuous with a somewhat flattened layer of cells on the dorsal surface of the ovary.

Leuckart described the cells which in *P. tænioides* clearly correspond to those of the "crest" above mentioned as being enclosed in definite follicles. There is no appearance of any such structures in *P. teretiusculum*, either now or at any period, and the crest on each side is formed as a lateral growth from the dorsal wall of the ovarian tube. This dorsal wall may be regarded as a syncytium, the nuclei of which are continually dividing; whilst in the lateral portions the protoplasm becomes aggregated around them to form definite cells, which by constant growth are, as it were, pushed over into the "crest."

There is as yet no trace of any shell round the ova. In the adult form the ovary occupies the same position as in the young one, running immediately above the alimentary canal from the posterior end to a point which lies a little behind the anterior extremity of the mid-gut (fig. 7). It has the same structure along its whole length (fig. 43). The ventral wall is composed of a single layer of columnar cells, in which no nuclei can now be distinguished, and many of which have the appearance of glandular cells which have poured out their contents, the remains of which are most likely represented by small coagulated masses, which lie upon the internal ends of the cells in the lumen of the tube.

The dorsal wall is more definite in shape than in the early stages, being very thick in the central line, and thinning out rapidly towards the sides. It is, as before, formed in reality of a syncytium broken up into irregular masses of protoplasm, each of which contains many small nuclei (*Sy.*).

The lumen is continued laterally into pouch-like diverticula (*L. S. O.*), more prominent and numerous than in the earlier stages; and these are surrounded by a mass composed of protoplasm and nuclei, the outlines of cells being visible in parts.

The upper wall close to the main lumen is distinctly marked, and evidently a continuation of the dorsal wall of the ovary. The nuclei in the mass around the diverticula are of various sizes, and it is evident that in this portion the formation of cells is proceeding.

Compared with the earlier stages (fig. 44) the ovary [has both been compressed dorso-ventrally, and has grown out laterally. The cells forming the original "crest" have become more or less separated from one another, modified as will be described, and spread out over the whole external surface. In the earlier stage the dorsal walls of the diverticula were formed in part by the lateral portions of the syncytial mass which formed the dorsal wall of the ovary. In the fully developed stage it appears as if rapid division of the nuclei takes place in the latter part, which, again, is continuous with an ill-defined mass of protoplasm present on either side, into which project a series of diverticula from the main lumen of the ovary.

The original dorsal wall may thus be regarded as having become divided into two parts:—(1) The central part, containing numberless nuclei, which are here undergoing division; and (2) the lateral portions, into which the nuclei from the former pass, and in which they appear to increase in size, and to be surrounded by protoplasm, with the resultant formation of definite cells.

(b) Oviducts. — These differ only slightly from those described by Leuckart<sup>1</sup> in *P. tænioides*, and more especially

<sup>1</sup> Loc. cit., p. 85, Taf. xi, figs. 17—19.



in *P. subuliferum*, where apparently they are very similar to those examined by Stiles<sup>1</sup> in *P. proboscideum*.

In the young form the two oviducts arise from the anterior end of the ovary, the space in which is directly continuous with that of the oviducts. The walls of the ovarian and oviducal tubes are at first precisely similar in nature, being composed of somewhat cubical cells with distinct spherical nuclei (figs. 57 and 58). In fact, at this stage these parts may be described as having the form of a ring around the alimentary canal, the mid-dorsal portion of which is prolonged backwards. In such forms as the Phalangidæ a ring is present, and the greater part of its walls form ova; whilst in the Pentastomum the formation of ova is confined to the backward growing, median, dorsal portion, whilst the two halves of the ring form oviducts, and unite together to form a common median part ventrally as they do in the Phalangidæ.

As the animal grows, and before eggs pass down, the cells of the oviduct walls become more columnar (fig. 56). External to them is a layer of material of the nature of connective tissue, and not containing muscle-fibres.

In the mature form the two oviducts pass off from the anterior end of the ovary, clusters of ova lying on the upper surface immediately anteriorly to their origin, there being thus no free portion of the ovarian tube in front of the most anterior clusters of ova such as Leuckart describes in *P. tænioides*.

They then pass downwards and forwards, not encircling, but passing right through the middle of the hook-gland on either side (figs. 22 and 24). Having traversed the gland, each one lies to the side of and immediately behind the nerve mass. At this part of their course they run straight downwards, enclosing between them the two large posterior nerves (fig. 60). Turning backwards below the level of the nerve mass, they unite together to form a slightly swollen portion (figs. 40, 41, *Co. Od.* 1), which opens in the median line into a short tube with strongly muscular walls (*Co. Od.* 2), which lies

<sup>1</sup> *Loc. cit.*, p. 138.

immediately above the point of union of (1) the tubes coming from the spermatheca on either side, and (2) the vagina (= uterus of the adult) entering from the ventral surface.

The walls of the oviducts near to the ovary are much more cellular in appearance than lower down. As the duct on each side passes through the hook-gland it is accompanied by a certain number of strongly marked muscle-fibres, which run parallel to its course, but are independent of its walls. The latter are formed of a layer of cells internally, which become somewhat indistinct as the oviduct becomes swollen out with eggs, and external to this a layer of muscle-fibres crossing one another obliquely, and with a general trend in the direction of the length of the oviduct. These fibres lie in an external coat of connective tissue, in which at earlier stages no muscle elements could be determined.

The structure of the walls forming the swollen common portion is the same; whilst immediately in front of this the lumen of the tube narrows, the cells of the internal layer become elongate and thrown into ridges, and, in addition to the fibres mentioned above and internal to them, there is developed a special series of circularly disposed muscle-fibres. The longitudinal fibres are strongly developed, and run backwards in the mid-dorsal and ventral lines, to be continuous with those on the surface of the vagina (= uterus) (figs. 40, 54, *M.* 8).

The portion of the duct provided with this special muscular apparatus is equivalent to that described by Leuckart, which he is without doubt right in regarding as a special structure for the purpose of forcing the ova through from the oviducts into the vagina. The swollen portion with thin walls which lies immediately in front of this, and is directly continuous with the two oviducts, appears not to be represented in his species. In *P. teretiusculum* the oviducts open widely into it, and consequently it is filled with ova. Figs. 40 and 41 represent somewhat diagrammatically the relationship of these parts of the reproductive organs.

(c) Spermathecæ and Spermathecal Ducts.—The

spermathecae are large prominent structures, just as described by Leuckart, Hoyle, &c. They are filled with a dense mass of mature spermatozoa (fig. 22). Their walls are, save where the duct passes out, of uniform thickness, and formed of a very distinct single layer of cylindrical epithelium cells (.1 mm. in length), on the inner surface of which is a fine cuticular layer, whilst their outer ends are embedded in a finely granular material, the whole being covered externally by a layer of muscle-fibres (fig. 55). The function of the latter must be, as stated by Leuckart, that of lessening by their contraction the size of the organ, and of thus driving out some of the contained spermatozoa. The cylindrical epithelial cells are very sharply outlined; their inner ends are granular and packed closely together; their median portions are comparatively free from granules, and each one contains a distinct oval nucleus. Their outer ends are somewhat tapering, spaces being thus left between them, and they are embedded in a granular substance. Leuckart has naturally suggested that they may secrete a material which serves to preserve and nourish the sperm, but in no instance could I detect any trace of the remains of such a material, or any indication of its passage from the cells into the cavity. The presence of the thin cuticular lining, which shows no break or trace of pores, is also against the idea of these cells being secretory in function; though, on the other hand, the peculiar and uniformly granular appearance of their inner ends certainly gives rise to the idea that they are elaborating material of some special nature, probably the chitinous lining.

The ducts of the spermathecae are of a very special and peculiar structure. Each has the form of a short tube running in a curved direction from the spermatheca of its side to the median line, where the two unite together on the ventral side of the common termination of the oviducts. The concavity of the curve faces posteriorly (fig. 41). They are lined internally by a layer of nucleated columnar cells thrown into folds, and very similar to those of the vagina (fig. 54, *Sp. D. E.*) Their internal ends sometimes appear to have a very thin cuticular

lining, though usually this cannot be detected; and in this respect the duct shows a marked difference when contrasted with either the spermathecæ or the fine duct opening into these or the vagina.

External to this layer of cells lies one of muscle-fibres, which are directly continuous with those of the spermathecæ. Where the duct comes in contact with the latter the fibres are especially well developed, and form, as described by Hoyle<sup>1</sup> in *P. protelis*, a strongly muscular papilla projecting into the cavity of the spermatheca, and pierced by a fine tube with a distinct chitinous lining. There is not visible externally a somewhat spherical bulb such as is figured by Leuckart in *P. tænioides* and *subuliferum*,<sup>2</sup> nor is there any swollen part of the duct close to this. External to the muscle layer there lies on the anterior, dorsal, and ventral surfaces, save in the very median line where the two join together beneath the oviduct, a remarkable layer of cells, similar, as pointed out by Leuckart, to those found in a portion of the male ducts. The cells vary in size and are irregularly arranged (fig. 54, *Sp. Gl.*); each contains a large nucleus, which rarely shows a nuclear membrane, and stains deeply with borax carmine. The whole cell is filled by a structure having the appearance of a network, in the meshes of which material of a homogeneous nature is present. Both take stain, the network more deeply. These cells, especially in the nature of their nuclei, resemble somewhat those of the hook-glands, but are precisely similar to certain others which will be described later in connection with the male organs.

Leuckart has described a special network of nerve-fibres in connection with this part, but of these I have been unable to determine the presence in this particular form.

On the dorsal portion of the wall where the two tubes unite in the median line, and immediately above the opening of the vagina and posteriorly to that of the oviduct, there lie two small tubular diverticula, similar in the main to those present in other forms, but apparently smaller than in any yet described.

<sup>1</sup> Loc. cit., p. 187.

<sup>2</sup> Loc. cit., Taf. ii, figs. 17 and 19.

The walls of each consist internally of cells more cubical in form than those of the main ducts, and differing slightly in appearance from these. They have, if any at all, only an extremely thin cuticular layer, and the cavity is elongate from above downwards. They lie embedded in the special muscles which pass backwards from the common portion of the oviduct on to the dorsal wall of the vagina, and are curved in such a manner (fig. 54, *Acc. F.*) that a somewhat oblique section may pass at the same time through the blind end and the lips of the opening into the main tube. Possibly the cells serve to secrete some fluid which is passed into the latter, but, as Leuckart pointed out, their function is uncertain. They are relatively very small in size, and vary in this respect in different forms. They are most conspicuous in *P. subuliferum*, smaller in *P. tænioides*, and smaller still in *P. teretiusculum* (fig. 40, *Acc. F.*). They must be considered as connected with the spermathecal ducts. Possibly they are only active just when spermatozoa are either passing into or out of the spermathecae, for in the specimens examined their contained cavities were quite empty. It is interesting to note that in the younger forms they arise from the spermathecal ducts somewhat farther away from the median line than they do in the adult, thus showing their undoubted origin from these ducts. In this respect the young *P. teretiusculum* resembles the adult *P. tænioides*.

(*d*) Vagina (=Uterus of Adult).—This name may be applied to the tube which leads from the external opening at the posterior end of the body to the junction of the spermathecal ducts and the oviducts. It differs very greatly in length in the young and adult form.

In the young form it has simply the structure of a more or less straight tube, sometimes lying in the mid-ventral line; sometimes, as described by Hoyle<sup>1</sup> in *P. protelis*, pushed up to one side (fig. 23, *U.*). In this stage its walls are composed of an internal layer of columnar cells with a very distinct chitinous lining. External to these lies a layer of connective

<sup>1</sup> *Loc. cit.*, p. 187.

tissue, in which are both obliquely and circularly disposed muscle-fibres. At no stage apparently is there present any mesentery attaching the tube to the body-wall. In the mature form it serves as a uterus, in which the eggs lie enclosed in their shells. The tube undergoes enormous growth, coiling about and occupying the whole body-cavity, in which the hook-glands, alimentary canal, and ovary are pushed up against the dorsal wall. The uterus, as it may now aptly be called, is many times the length of the whole body, though its coils are so intertwined that it is quite impossible to unravel them. For the greater part of its length the walls have become exceedingly thin, the layer of cells on the inner surface being unrecognisable; in fact, the wall has all the appearance of a layer of cuticle internally, with externally a thin sheath of muscle-fibres crossing one another irregularly, and between the two a thin granular layer which is probably to be regarded as the remnant of the cellular layer which is well developed in the younger form.

Just before the genital opening is reached the tube suddenly narrows, and its structure changes completely, in somewhat the same manner as Leuckart has described in the case of *P. tænioides*.<sup>1</sup> The cuticular layer becomes very thick indeed. Transverse sections (fig. 45) show most internally a special thin layer, with projecting portions similar to that of the main portion (*Cu. Vg.*). Between this and the epithelial cell layer lies a special cuticular development (*X.*) showing radial lines, as if each cell had secreted a part longer than itself, all the parts being fused side by side to form a thick layer (.08 mm. in thickness). The cells are columnar and distinct, each with a well-marked nucleus close to its inner end (*Vg. E.*). Externally lies a strong layer of circularly arranged muscle-fibres, and outside these is connective tissue, which encloses a certain number of cells similar in structure to those forming the hook-gland, &c. There are no traces of anything like ducts passing off from these cells (*Gl. Vg.*).

In this portion of the vagina no eggs are seen; the muscles

<sup>1</sup> *Loc. cit.*, p. 87.

of the wall will, by their rhythmic contraction, ensure the passage of the egg to the exterior. Its small calibre, thick cuticular lining, the epithelial and muscular layers, and its straight course distinguish it at once from the coiled thin-walled portion which is crowded with eggs, and serves as a uterus. Possibly it may represent the original vagina of the young form, the uterine portion being an after-growth intercalated between the oviducts and the vagina proper.

(2) Male.—The organs in the male form consist of the following parts, and are more complex than those of the female:

- (a) Testis.
- (b) Vesiculæ seminales.
- (c) Vasa deferentia.
- (d) Ejaculatory duct.
- (e) Cirrus bulb.
- (f) Dilator rod sac.
- (g) Cirrus sac.
- (h) Atrium genitale.

(a) Testis.—This has the form, as in *P. proboscideum*<sup>1</sup> and *P. protelis*,<sup>2</sup> of a single median tube. It lies dorsal to the alimentary canal, and extends for the greater part of the whole length of the body, commencing close to the posterior extremity, and running forwards to a point a little behind the level of the external male opening (fig. 6).

In the young form the tube has a wall composed of a thin membranous layer externally, and internally a thick multicellular layer. In the latter the outlines of the cells cannot be clearly distinguished; possibly it is in reality a syncytium, in which are many small nuclei (fig. 21, *T.*).

In the adult the testis is large, and may occupy up to as much as one half of the space in the body-cavity. The interior is crowded with masses of sperm in all stages of development, and mature sperms are to be met with, attached together in the

<sup>1</sup> Stiles, loc. cit., p. 131, Taf. viii, fig. 48.

<sup>2</sup> Hoyle, loc. cit., p. 182, pl. xxviii, figs. 6—8.

characteristic groups, in all portions. The walls have the same structure in the main as in the young form, but instead of a complete coating of cells (or syncytium) on the internal surface, there are only present irregularly scattered and numerous multinucleate masses, evidently relics of the original continuous layer. These must be continually budding off in other sperm-cells into the cavity (fig. 21, *T*).

The testis thus differs in its structure in important points from the ovary of the adult female, though both agree at an early stage of development in having the form of a single median dorsal tube. In the case of the ovary the cells of the walls give rise dorsally to ova which pass outwards, that is away from the central cavity. In the case of the testis, on the contrary, the cells of the walls give rise over the whole surface to sperm mother-cells, and these pass into the cavity, so that the form of a tube with walls of definite outline is retained in the testis and lost in the ovary.

In the case of the latter, also, at the anterior end its walls and cavity are directly continuous with those of the two oviducts. In the case of the testis the mode of connection with the succeeding portions of the organs—the vesiculæ seminales—is of considerable interest when viewed in the light of the probably originally double nature of the testis. It approximates, moreover, in essential features to that already described by Hoyle in *P. protelis*, and by Stiles in *P. proboscideum*. This relationship is shown diagrammatically in fig. 68, and Sections A—G. At its very anterior end the wall of the testis is continuous with the posterior wall of a chamber formed by the union in the mid-dorsal line of the two tubular vesiculæ seminales. Into this chamber it has a double opening. The anterior wall of the testis is thick and muscular, and ventrally there is placed, at the very front end, in the floor of the cavity, a well-marked double muscular ridge. This is well seen in transverse sections (fig. 18, *V. S. O.*). Each half of the ridge ends in a papilla, on which is a funnel-shaped opening, the broad end leading into the testis cavity, the narrow one into a small canal which leads through the ridge



and testis wall, slanting upwards and forwards as it does so (fig. 68, *G.*). A similar double ridge is attached to the roof of the chamber above mentioned, and this ridge again terminates in two papillæ, each with a funnel-shaped opening—the anterior termination of the tubes leading from the testis cavity (fig. 17, *V. S. O.*). Thus in transverse sections the latter is seen to be continued forwards and above the efferent ducts, whilst that of the common seminal chamber passes backwards and beneath the ducts (fig. 68, *F. G.*). There is around the ducts a strong development of distinctly striated muscles, the ducts themselves having a thick cellular wall.

Along its whole course the testis is attached to the mid-dorsal line of the body-wall by a thin mesentery, and it is interesting to note that just at the very anterior end, where the two tubes above described lead out from the cavity, this mesentery becomes double (fig. 17, *Mes.*). It might have been expected that, as in *P. protelis*, one of these mesenteries would have passed on to each of the vesiculæ, but such is not the case, and the latter have no supporting structures of this nature. The presence of this double communication between the cavities of the testis and vesiculæ, which has now been described in *P. protelis*, *P. proboscideum*, and *P. tereti-usculum*, together with the double nature of the testis for the greater part of its length in *P. tænioides*, indicates that originally the testis in *Pentastomum* was a paired structure, as it is at the present time in certain other Arthropoda, such as the *Aranea*.

(*b*) *Vesiculæ seminales*.—This portion of the reproductive organs is very well developed in *P. tereti-usculum*, and of considerable length (fig. 6). It has the form of a tube bent double upon itself, the upper half running backwards and downwards, the lower half forwards and slightly downwards. It has the same relationship to the hook-gland as the ovary has, and in early stages (fig. 18, *V. S.*), when the tube is a comparatively small one, the upper half is seen to pass downwards right through the middle of the gland. The same feature

has been noted by Hoyle in *P. protelis*, and by Stiles in *P. proboscideum*. In the mature form the portion of the gland between the duct and the body-wall becomes thinned out, and thus, just as in the case of the ovary, but not quite to the same extent, the tubes seem to enclose the alimentary canal and the hook-glands. The two vesiculæ unite at the anterior end of the testis to form the single chamber, into which open the two ducts from the testis which have been already described.

In the mature male the nature of the wall of the vesiculæ, both in the common part and in the two tubes which pass down to the vasa deferentia on either side, is most unmistakable. It consists (fig. 37) of (1) an internal layer of cells, which are most evidently glandular in nature (*V. S. E.*). The outlines are, as a rule, indistinguishable. Internally many of them are swollen out into large globular structures, which have clearly been filled with fluid material to be passed into the lumen of the tube. This fluid will serve for the nourishment of the sperm, with which the vesiculæ are crowded. It may be noted that only ripe spermatozoa are ever found in the vesiculæ. In the inner portion of the layer numerous nuclei are seen, and radial lines indicating doubtless the bases of the cells. Leuckart suggested the glandular nature of these cells in *P. tænioides*; whilst Stiles in *P. proboscideum*, referring to this suggestion of Leuckart's, says, "Ich fand hingegen, dass diese Schicht sich aus ziemlich flachen Zellen zusammensetzt." Hoyle, in *P. protelis*, describes them as columnar. Probably in the majority of forms Leuckart's suggestion will be found to hold good: certainly this is the case in the form under discussion, where their nature is unmistakable. (2) External to these cells lies a thin clear layer, the tunica propria of other authors (*T. P.*). (3) External to this is a strongly developed layer of circularly disposed muscle-fibres (*M. V. S.*). (4) Most externally is a thick sheath of connective tissue (*Ct.*)

(c) *Vas Deferens*.—This is a short tube on each side of the body with very thick walls, which communicates poste-

riorly with the vesicula seminalis, and anteriorly with a short tube called by Stiles the "Cirruszwiebel" (figs. 6 and 8).

Together with the remaining parts of the male organs to be afterwards described, it stands in marked contrast to the testis and vesiculæ in that it possesses a cuticular lining to its duct. It is therefore to be regarded as distinct in origin from these two structures, and as formed from an invagination of epiblast which has united with and opened into the vesiculæ. It is interesting to note in connection with this, that in the specimens of *P. protelis* examined by Hoyle, and which were hence presumably immature, the lumen of the vesicula was not continuous with that of the vas deferens. The two sets of structures are independent in origin, one being formed from mesoblast and the other from an epiblastic invagination, and the union of the spaces contained in the two is apparently in *P. protelis* only established comparatively late in development.

The duct of the vas deferens is formed of a layer of very minute cells with internally a distinct cuticular lining. This duct (fig. 47, *V. D.*) is enclosed in a thick coat of cells precisely similar in structure to those around the duct which in the female organ passes from the union of the oviducts to the spermatheca on either side. Each cell is of fair size (.06 mm.), and contains a darkly staining nucleus, the outline of which is often indistinct, whilst at others a distinct nuclear membrane can be distinguished. The protoplasm is markedly reticulate (in preserved specimens), and the outlines of the cells, which are irregular in shape and vary much in size, are distinct. No muscular elements are distinguishable.

Ventrally to the union of this with the vesicula, it is connected with a tube which may be regarded as a special backward running diverticulum of the vas deferens, and which will now be described.

(*d*) Ejaculatory Duct.—This forms one of the most prominent features in the male organ, and there can be no doubt that its name (Propulsionsschlauch), suggested by Leuckart, is indicative of its function. It arises on each side

of the body, as said, from the vas deferens, ventral to the vesiculæ seminales. The walls of the tube are thick, the cavity relatively small and filled with masses of ripe sperm. The walls consist of an internal layer of columnar cells, the nuclei of which are small and spherical, and lie close to the inner ends of the cells, which have a distinct but very thin chitinous lining, forming, as noted by Stiles, folds and ridges projecting into the cavity (fig. 46). External to these cells lies a clear-looking tunica propria (*M. P.*), and external to this a peculiar and strongly marked layer of muscles running in a longitudinal direction (*M. Ej. D.*). In transverse sections these, as Stiles says, might easily be taken for glandular structures, but longitudinal sections (fig. 26, *Ej. D.*) and whole preparations of the organ leave no doubt whatever as to their muscular nature. Each separate fibre (fig. 46) is very distinct, and has a general longitudinal, and at the same time slightly spiral course. Each one may be described as having a stout ribbon-like form, with one of its narrow edges implanted in the tunica propria. The fibres thus, in transverse section, appear to form a thick layer of slightly curved rod-like structures radiating outwards from the tunica propria, the outer end of each being slightly swollen and granular in nature, the inner end clearer and more sharply defined. When the organ is viewed as a whole the striations on the fibres are very evident, but it is difficult to determine how they occur on the individual fibres.

(e) Cirrus Bulb (= Cirruszwiebel of Leuckart and Stiles). —This is directly continuous with the vas deferens, of which it may be regarded as the terminal part, whilst from its other extremity the cirrus passes outwards. Its walls are thick (fig. 63), and formed of some three layers of cells, which are, however, very indistinctly marked in the adult, though in the young stages, as in *P. proboscideum*, they may be clearly distinguished.

In the immature stages (fig. 63) a transverse section across the cirrus bulb shows externally indications of a cavity (*S.*) bounded by cellular walls which wrap round an internal mass

containing a duct (*S'*). The outer cavity opens into the rod-sac to be described later; the inner duct leads at one end into the vas deferens, and at the other into the cirrus-sac. There are thus three definite layers of cells bounding the two cavities.

The meaning of the outer space is difficult to determine, and in the adult it becomes obliterated, with the result that the central duct remains surrounded by three layers of cells.

The whole structure passes forwards, wedged in between the dilator rod-sac externally and the cirrus-sac internally. The chitin which lines the duct is continued directly into the cirrus of which it forms the internal layer, whilst the outer layer of the latter may probably be regarded as continuous with that lining the external cavity above referred to, though in the young stage, in which this is distinct, there is no trace whatever of a cirrus.

(*f*) Dilator Rod-sac (=Chitinzapfen of Leuckart and Stiles).—This, in important details, agrees more closely with the structure described by Stiles in *P. proboscideum* than with that of other species. It is enclosed in a cavity with strongly muscular walls, which are directly continuous with the tube leading to the common genital opening, and into the inner side of which opens the cirrus-sac (fig. 62, *D. R. S.*).

The sac and its contents form a somewhat complicated structure, and on its inner and dorsal side is fused with the cirrus bulb. The whole consists, in the main, of a muscular mass attached to the outer and posterior walls of the cavity, and on the inner side to the wall of the cirrus bulb. Its free end has a deep concavity, in which lies a tongue-shaped structure (*To.*) which projects slightly beyond the mouth of the former. A hollow space, lined by cuticle, passes inwards from the posterior end of the concavity just external to the tongue, and from its walls the muscles radiate outwards. The inner lining of the concavity is continued downwards into a strong chitinous process flattened out into a somewhat shovel-shaped structure when seen laterally (*D. R.*). This is also continuous with the strong chitinous lining on the inner aspect of the

muscular mass, and as it passes backwards and upwards a groove appears on the surface, the two edges of which rise up so as to leave between them an open canal semicircular in transverse section (figs. 62, 66, *Gr.*) in which opens the cirrus-tube with the cirrus (*C.*), to which reference will be made later.

The relative position of the dilator rod-sac and the opening of the cirrus-sac vary slightly according to the greater or less state of contraction of the latter.

In figs. 62 and 62a an attempt is made to show the structure and relationship of the different parts as gathered from a study of the parts mounted whole, and of longitudinal and transverse sections. At times the dilator rod-sac may be drawn lower down, and its free end cut through without showing, as in figs. 64—66, the opening of the cirrus-sac.

The chitinous covering of the whole mass is directly continuous with that of the cavity in which it lies, though here the chitin is very thin. The walls of the cavity consist of a layer of columnar cells internally, and of a strong development of muscles running obliquely and longitudinally.

From the posterior end of the outer wall of each cavity a strong band of muscle-fibres runs downwards and forwards, to be attached to the ventral wall of the body just in front of the genital opening (figs. 13, 14,  $M_1$ ). The bands run obliquely in such a way that they cross one another just before their attachment, the one arising from the right dilator rod-sac being attached on the left of the median line, and vice versâ.

The name of dilator rod-sac is applied to this part inasmuch as it contains, as described above, a somewhat shovel-shaped chitinous rod which serves as an accessory dilator organ in copulation. The muscles serve on contraction to force the rod downwards and out of the genital opening; whilst the crossing of the muscles serves to cause each rod to press outwards and away from the mid-ventral line.

(*g*) Cirrus-sac.—This lies on either side of the body close to the mid-ventral line, and opens together with the cavity

of the dilator rod-sac into the tube leading to the external opening. Each sac extends backwards to the level of the vas deferens (fig. 8), and has in transverse section a somewhat concentric shape, with a cavity much compressed laterally, owing possibly to the action of reagents (figs. 13—15, *C. S.*). The walls are thick, and composed internally of a layer of very large columnar cells, the internal surfaces of which are lined by a thin cuticle. External to the cells is a strongly developed coat of muscle-fibres which run in a general longitudinal direction (fig. 48).

The cirrus has the form of a long chitinous tube, with walls which are continuous, as before said, with the chitin lining of the cirrus bulb (fig. 67). The cirrus appears to vary in development, though possibly this may be due to the fact that it only reaches its greatest length at a very late period of development. In the specimen, otherwise perfectly mature, of which figs. 64—66 represent sections, it only extended for a very short distance beyond the end of the cirrus tube; whilst in other specimens (figs. 14 and 15, *C.*) it was of great length, and lay coiled up within the sac, as represented by Leuckart and Stiles. In *P. protelis* Hoyle was unable to detect any cirrus, owing doubtless to the immaturity of the forms which he examined. In very young males of *P. teretiusculum* (7 mm. in length) there is no trace of a cirrus. When the latter is fully developed it is of great length, and the terminal part is somewhat larger than the rest, and has the property of absorbing stain. In all mature specimens examined the long chitinous process previously referred to in connection with the dilator rod-sac passes for a considerable distance down towards the genital opening. During copulation these two rod-like processes are probably first of all ejected by means of the strong muscles within the sac and those connected externally with its walls. They open up the vagina, each exerting in consequence of the crossing of the muscles close to their insertion a lateral pressure. The result of the action of these muscles must be (1) that the rod-like process is pressed against the outer wall of the male opening, and (2) that it is similarly

pressed against the outer wall of the female opening. There is thus produced both an internally lying space in the tube on either side in the male down which the cirrus can pass from its sac, and also a median space in the female opening into which the rod-like processes direct the cirri. The projection of the latter is caused by two contrivances; (1) the muscles in the wall of the cirrus-sac, and (2) the sudden ejection of a mass of spermatozoa by the ejaculatory tubes with their remarkably strong muscular walls. The whole arrangement may, in fact, be regarded as consisting of two more or less flexible tubes (the cirri), attached at one end to the wall of a compressible chamber, in which when at rest they lie coiled up with their distal end free. A combined sudden ejection of material through the tubes and compression of the walls of the chamber will inevitably lead to the ejection of the tubes themselves, which then naturally pass along the cavity especially opened for them, and formed by the male genital openings and the vagina of the female.

It is, however, difficult to understand how the cirri when once put out are ever drawn in again. Possibly they never are, but are simply broken off, and then gradually by muscular action of the vagina ejected from the female. This might account for the presence of only an extremely short cirrus in a form such as the one represented in figs. 62 and 66, where the animal was otherwise quite mature.

Copulation in *P. teretiusculum* does not take place till the female is of considerable size, as in form 12 mm. or even more in length there is no trace of spermatozoa anywhere in either the vagina or receptacula. In the snake's lung also each individual has apparently its fixed place, with its head deeply sunken into the tissue of the lung, to which it is attached by its hooks, the deep depression corresponding in configuration with its head end.

On each side the cavities of the dilator rod-sac and the cirrus-sac open into a common tube (fig. 11, *Co.*), the walls of which are formed of (1) an internal layer of cells with a distinct cuticle, (2) a layer of longitudinal muscles-fibres, and



(3) an external layer of strongly developed circularly disposed muscle-fibres (*Mg.*). These two tubes run downwards and forwards, and open into a common atrium genitale (fig. 11, *At. gen.*).

On each side just where the two cavities meet there arises from the dorsal wall a short tube (figs. 11, 12, and 25, *Acc.*), evidently homologous with the accessory gland as described by Hoyle in *P. protelis*. This has the form of a duct running upwards and slightly backwards, and penetrating the substance of the hook-gland in front of the part through which runs the vesicula seminalis, and close to the indefinite point of union of the hook- and head-glands. In this form no connection with the gland or with any special glandular cells can be distinguished.

The duct-walls are composed of columnar nucleated cells, directly continuous with those of the walls of the tube leading down on either side to the atrium genitale. Certainly close to the mouth, and probably along the whole course, the duct has a thin chitinous lining. Each one runs upwards surrounded by the strong muscles (figs. 12 and 25, *M<sub>2</sub>*) which pass from the dorsal surface of this portion of the genital apparatus to be inserted into the dorsal body-wall. What function the structure serves it is impossible to say.

Separating the two tubes leading down into the atrium genitale is a tongue-like structure (fig. 11), the distal end of which has the appearance when the atrium is seen externally of a ridge dividing the latter into two lateral halves (fig. 5). In the upper part of this tongue is placed the nerve-ganglion (fig. 11, *N*).

## EXPLANATION OF PLATES I—IX,

Illustrating Professor Spencer's paper on "The Anatomy of *Pentastomum teretiusculum*."

## PLATE I.

FIG. 1.—Ventral view of a female *Pentastomum teretiusculum*.  $\times 2$ .

FIG. 2.—Ventral view of the anterior end of the body of a female, to show the mouth and the arrangement of the hooks and sensory papillæ. 1. Paired primary papillæ. 2, 6, 7, and 8. Paired secondary papillæ. The division of the annuli into anterior and posterior halves by a distinct ridge is represented.  $\times 12$ .

FIG. 3.—Dorsal view of the anterior end of the body of a female, to show the sensory papillæ. Only the outer pair of hooks are seen. 1. Paired primary papillæ. 2, 3, 4, and 5. Paired secondary papillæ.  $\times 12$ .

FIG. 4.—Ventral view of a male *Pentastomum teretiusculum*.  $\times 4$ .

FIG. 5.—Ventral view of the anterior end of the body of a male, to show the mouth, atrium genitale, arrangement of the hooks and sensory papillæ. 1. Paired primary papillæ. 2, 7, 8, and 9. Paired secondary papillæ.

## PLATE II.

*List of References.*

*A.* Supra-œsophageal commissure. *a.* Duct to primary papilla. *b.* and *c.* Ducts to bases of hooks. *Acc.* Accessory organ, male. *Acc. F.* Accessory organ, female. *At. gen.* Atrium genitale. *C. B.* Cirrus-bulb. *Co.* Tube leading to atrium genitale. *C. S.* Cirrus-sac. *D. R. S.* Dilator rod-sac. *Ej. D.* Ejaculatory organ. *Hd. gl.* Head-gland. *Hk. Gl.* Hook-gland. *L.* Lateral line. *L. S.* Lateral division of body-cavity. *M<sub>2</sub>.* Muscles around male accessory organ. *M. Long.* Longitudinal muscles. *M. Tr.* Circular muscles. *Mes.* Median-dorsal mesentery, supporting testis in male and ovary in female. *Mes<sub>2</sub>.* Lateral mesentery from hook-gland to alimentary canal, and from hook-gland to body-wall. *Mes<sub>3</sub>.* Mesentery to ventral nerves. *N.* Central nerve mass. *O. M.* Oblique muscles. *Od.* Oviduct. *Ov.* Ovary. *Pa. gl.* Parietal gland-cells. *Sp.* Spermatheca. *Sp. D.* Duct of spermatheca. *T.* Testis. *U.* Uterus. *V. D.* Vas deferens. *V. S.* Vesicula seminalis.

FIG. 6.—Diagrammatic representation of the alimentary, secretory, nervous, and reproductive systems of a male *Pentastomum teretiusculum*, seen from the side. For the sake of simplicity the parietal glands have been omitted, and only the portion of the head-gland where it unites with the

hook-gland is shown. The different structures are named. *a.* Duct from hook- and head-glands to primary papillæ. *b* and *c.* Ducts from hook- and head-glands to hooks. 1. Nerve to anterior wall of fore-gut. 2. Nerve to posterior wall of fore-gut. 3. Nerve to sensory papillæ. 4. Nerve to muscles, &c., at side of body. 5. Nerve to hooks. 6. Nerve to mid-gut. 7. Nerve to hook-gland. 9. Ventral nerve. *A.* Œsophageal commissure. The lines indicated by the capital letters A, B, C, D, E, F, G, H, and I indicate the planes of the sections correspondingly lettered.

FIG. 7.—Diagrammatic representation of the alimentary, secretory, nervous, and reproductive systems of a female *Pentastomum teretiusculum*, seen from the side. The alimentary, secretory, and nervous systems as in Fig. 6. The lines indicated by the capital letters K and L indicate the planes of the sections correspondingly lettered.

FIG. 8.—Semi-diagrammatic representation of the reproductive organs of a male *Pentastomum teretiusculum*, seen from the dorsal surface. The lines indicated by the capital letters correspond to those in Fig. 6.

Figs. 6, 7, and 8 are constructed as the result of examination of dissections, and of series of consecutive sections.

Figs. A, B, C, D, E, F, G, H, and I represent diagrammatic transverse sections across the body of a male *Pentastomum teretiusculum*, along the lines indicated by corresponding letters in Figs. 6 and 8. The three muscle layers of the body are represented by thick lines, but in all cases the parietal gland-cells and subcuticular layer are omitted for the sake of clearness.

Figs. K and L represent diagrammatic transverse sections across the body of a female *Pentastomum teretiusculum*, along the lines indicated by corresponding letters in Fig. 7.

### PLATE III.

#### *List of References.*

*a.* Extensor muscle of the hook. *Acc.* Male accessory organ. *At. gen.* Atrium genitale. *b.* Flexor muscle of the hook. *C.* Cirrus. *C. B.* Cirrus bulb. *C. S.* Cirrus-sac. *Co.* Tube leading down on each side to the atrium genitale. *Cu.* External cuticle. *D. R.* Dilator rod. *D. R. S.* Dilator rod-sac. *Gl. ?* Gland of unknown function. *Hd. gl.* Head-gland. *Hk.* Hook. *Hk. d.* Ducts to hooks. *Hk. gl.* Hook-gland. *Hk. gl. d.* Ducts to primary papillæ. *Hk. i.* Invagination in which base of hook lies. *Hk. m.* Hook muscles. *L.* Lateral line. *L. S.* Lateral division of body-cavity. *M<sub>1</sub>.* Muscles connected with dilator rod-sac. *M<sub>2</sub>.* Muscles surrounding male accessory organ. *M<sub>3</sub>.* Circular muscles round tubes leading to atrium genitale. *Mes<sub>3</sub>.* Mesentery to ventral nerves. *M. G.* Mid-gut. *M. Long.* Longitudinal muscles. *M. Tr.* Circular muscles. *N.* Central nerve mass. *O. Hk. Gl.*

Opening of ducts at base of hooks. *O. m.* Oblique muscles. *O. P.* Upper lip. *Pa. gl.* Parietal glands. *Ph.* Pharynx. *V. D.* Vas deferens. 1. Nerve to anterior wall of œsophagus. 9. Ventral nerves.

FIG. 9.—Transverse section across the anterior part of the head of a female. The section shows the ducts of the hook-glands, and the opening of two of these at the bases of the two hooks which lie nearest to the mouth. Zeiss, A, oc. 4.

FIG. 10.—Obliquely transverse section across the anterior end of the body of a female. The bases of the two hooks nearest to the mouth are cut through, and the oral papillæ or upper lip. The very anterior end of the mid-gut is seen, and above this the mass of special gland-cells of unknown function. The cells of the head-gland are sparsely distributed. Zeiss, A, oc. 4.

FIG. 11 (cf. Section A).—Transverse section across the body of a male, just behind the opening of the atrium genitale and almost along the plane A of Fig. 6. The common tube running down from the cirrus-sac and the dilator rod-sac on either side is seen, and lying in this the lower portion of the dilator rod. Between the two tubes lies the hinder part of the nerve mass, and from each one arises the accessory gland. The section is just cut through the part at which the hook- and head-glands pass into one another, and together with the parietal glands form a mass of cells filling up the spaces between the muscles and different organs of the body. Outline drawn with camera, Zeiss, A\*, details with C, oc. 2.

FIG. 12.—Obliquely transverse section across the body of a larger male than that of which a section is represented in Fig. 11. Slightly behind the atrium genitale the oblique muscles commence, and this section is taken in a plane slightly posterior to that of Fig. 11, and just at the very commencement of these muscles. The upper and right-hand parts of the section lie anteriorly to the lower and left, so that the cirrus bulb and dilator rod-sac are seen on the left, and the accessory gland on the right. Ventrally the special muscles concerned with the pulling down of the rod- and cirrus-sacs are cut through, so that this part lies behind the atrium genitale. The very anterior end of the hook-gland is cut through. Outline drawn with camera, Zeiss, A\*, details with C, oc. 2.

FIG. 13 (cf. Section B).—Transverse section across the body of a male through that portion of the reproductive organs where the cirrus bulb, cirrus-sac, and dilator rod-sac are all in contact with one another. The section lies along the plane B. The hook-glands are here distinct from the head-glands. Ventrally the muscles concerned with the pulling downwards of the genital sacs are cut through where they cross one another. Outline drawn with camera, Zeiss, A\*, details with C, oc. 2.

FIG. 14 (cf. Section C).—Transverse section across the body of a male through the plane C. The cirrus bulb on the left side is attached to the upper and inner surface of the rod-sac in which the strong muscular mass

concerned with the rod is cut through. The cirrus-sac on either side is cut through behind its union with the rod-sac, and within it are seen sections of the cirrus. The muscles concerned in pulling downwards the genital sacs are cut through at the base of the rod-sacs. The hook-glands are distinct. Outline drawn with camera, Zeiss, A\*, details, C, oc. 2.

FIG. 15 (cf. Section D).—The transverse section across the body of a male through the plane D. The section is slightly oblique, the right side lying a little behind the left side. On the latter just the very end of the rod-sac is cut through, and the cirrus bulb. On the right side the termination of the vas deferens is cut through, and on each side lies a section through the posterior portion of the cirrus-sac. The two posterior nerves lie on the ventral side, each being supported by a distinct mesentery connected with the oblique muscles. Outline drawn with camera, Zeiss, A\*, details with C, oc. 2.

#### PLATE IV.

##### *List of References.*

*C. S.* Cirrus-sac. *Coag.* Coagulum in body-cavity. *Cu.* External cuticle. *E.* Subcuticular epithelium. *Ej. D.* Ejaculatory organ. *Hk. gl.* Hook-gland. *Hk. gl.<sub>1</sub>*. Portion of hook-gland lying internal to the vas deferens. *Hk. gl.<sub>2</sub>*. Portion of hook-gland lying external to the vas deferens. *L.* Lateral line. *L. S.* Lateral division of body-cavity. *M. Long.* Longitudinal muscles. *M. Tr.* Transverse muscles. *Mes.* Dorsal mesentery supporting the testis in the male, and the ovary in the female. *Mes.<sub>2</sub>*. Mesentery passing from alimentary canal to the hook-gland and from the latter to the body-wall. *Mes.<sub>3</sub>*. Mesentery supporting ventral nerve. *O. M.* Oblique muscles. *Od.* Oviduct. *Ov.* Ovary. *Pa. gl.* Parietal glands. *R. S.* Receptaculum seminis. *T.* Testis. *U.* Uterus. *V. D.* Vas deferens. *V. S.* Vesicula seminalis. *V. S. O.* Opening of *V. S.* into testis. *9.* Ventral nerve.

FIG. 16 (cf. Section E).—Transverse section across the body of a male through the plane E. The very posterior end of the cirrus-sac is cut through on either side, and on the left, which lies slightly in front of the right side, the full width of the vas deferens is cut through. On the right the ejaculatory duct is seen connected with the ventral side of the vas deferens. In the mid-dorsal line the common portion of the two vesiculæ seminales is cut through, though contraction of the walls has obliterated the space. This part is supported by two mesenteries. Each vesicula in reality passes through the hook-gland of its side, though in the adult only remnants of the portion lying to the outer side can be detected (*Hk. gl.<sub>2</sub>*), the inner portion being much reduced in size. Outline drawn with camera, Zeiss, A\*, details with C, oc. 2.

FIG. 17 (cf. Section F).—Transverse section across the body of a male

through the plane F. On the left side, which lies slightly in front of the right, the union of vas deferens and ejaculatory duct is cut through, and on the right the termination of the vesicula seminalis of that side and the proximal end of the ejaculatory duct. Dorsally the vesiculæ seminales are still connected with a common median portion which contains on its roof a ridge pierced by two small tubes leading from the common chamber of the vesiculæ into the testis. The glandular nature of the walls of the vesiculæ is seen. Outline drawn with camera, Zeiss, A\*, details with C, oc. 2.

FIG. 18 (cf. Section F).—Transverse section across the body of a very small young male through the plane F. This section is drawn to show that in the young stages there is no doubt that the vesiculæ pass right through the substance of the hook-gland, though in the adult form the other part becomes so thin by pressure that the tubes appear to encircle the glands. Drawn with the camera, Zeiss, A, oc. 2.

FIG. 19 (cf. Section G).—Transverse section across the body of a male through the plane G. On each side, owing to the bending upon itself of the vesicula seminalis, this is cut in section in two parts. The vesiculæ are full of ripe spermatozoa. Ventrally the two ejaculatory ducts are cut through, and dorsally the median testis, which is somewhat pinched in between the vesiculæ and hook-glands. Outline with camera, Zeiss, A\*, details with C, oc. 2.

FIG. 20 (cf. Section H).—Transverse section across the body of a male through the plane H. This lies behind the region of the vesiculæ, but on the ventral surface the ejaculatory ducts are cut through, and dorsally the testis. The mesenteries passing from the walls of the mid-gut to the hook-glands, and on from these to the body-wall, are distinctly seen. Outline with camera, Zeiss, A\*, details with C, oc. 2.

FIG. 21 (cf. Section I).—Transverse section across the body of a male through the plane I. Of the reproductive organs only the testis is present, and its walls are here made up of a thick layer of protoplasm with nuclei, but with no distinct cell outlines. The section shows that the testis extends beyond the region of the hook-glands, the mesenteries of which serve now simply for the support of the wall of the alimentary canal. Drawn with Zeiss, C, oc. 2.

FIG. 22.—Transverse section across the body of a female which is not fully mature (i. e. the uterus contains no embryos). The section passes through the spermatheca on each side, and beneath these lies the uterus cut in section posteriorly to its union with the oviducts and spermathecal ducts. The two oviducts are cut through as, one on either side, they pass through the middle of the hook-gland. The section lies immediately in front of the anterior extremity of the ovary. Outline drawn with camera, Zeiss, A\*, details with C, oc. 2.

FIG. 23.—Transverse section across the middle of the body of a young

female. The ovary has the normal form, but no shells are yet developed around the eggs. The uterus contains thread-like structures, which may possibly be masses of spermatozoa on their way inwards, but not a trace of any are to be found in the ovarian tube. The body-cavity is largely lined by a cellular material, which also forms the mesenteries. Parietal gland-cells are well developed. Outline drawn with camera, Zeiss, A\*, details with C, oc. 2.

## PLATE V.

*List of References.*

*A.* Supra-oesophageal nerve commissure. *Acc.* Male accessory organ. *Ant.* Anterior half of annulus. *At. gen.* Atrium genitale. *B. Hk.* Basal joint of hook. *Co.* Tube leading to atrium genitale. *Cu.* External cuticle. *D. R.* Dilator rod. *D. R. S.* Dilator rod-sac. *E.* Subcuticular epithelium. *Ej. D.* Ejaculatory organ. *Gl. ?* Gland of unknown function. *Hd. gl.* Head-gland. *Hk.* Hook. *Hk. gl.* Hook-gland. *Hk. gl. d.* Ducts from hook-gland. *Hk. m.* Muscles of hooks. *L. S.* Lateral portion of cœlom. *M<sub>1</sub>.* Muscles from cirrus bulb to body-walls behind male opening. *M<sub>2</sub>.* Muscles around accessory male organ. *M<sub>3</sub>.* Muscle-band from dorsal body-wall to anterior wall of atrium genitale. *M<sub>4</sub>.* Circular muscles around tubes leading to atrium genitale. *M. G.* Mid-gut. *M. Long.* Longitudinal muscles. *M. Tr.* Transverse muscles. *Ng.* Central nerve mass. *Nu.* Nuclei between muscle fibres. *Œs.* Œsophagus. *Od.* Oviduct. *O. M.* Oblique muscles. *Pa. gl.* Parietal glands. *Post.* Posterior half of annulus. *R.* Ridge on annulus. *S. O.* Sense-organ on papilla. *St. gl.* Opening of stigmatic gland. *V. D.* Vas deferens. *V. S.* Vesicula seminalis. 1. Nerve to anterior wall of œsophagus. 3. Nerve to sense-organ.

FIG. 24.—Longitudinal vertical section through the anterior part of the body of a small young female. The section lies to one side of the median line, and passes through the hook-gland, showing the fusion of the hook, head, and parietal glands at the anterior end of the first-named. The longitudinal muscles are seen to run dorsally along the head region, whilst the transverse ones stop short close to where the head unites with the trunk (*x*). The head space is largely occupied with hook muscles. The oviduct runs through the hook-gland, passing as it does so close to the gland-ducts. Zeiss, C, oc. 2.

FIG. 25.—Longitudinal vertical section through the anterior end of the body of a male form. The section is cut to one side of the middle line, and passes through the dilator rod-sac and the accessory gland. The latter runs upwards into the hook-gland, and is surrounded by special muscles which are connected with the strongly developed layer surrounding the sac. Zeiss, C, oc. 2.

FIG. 26.—Longitudinal vertical section through the anterior end of another male form. The section is cut so that the anterior end is nearly median, the posterior more towards the side of the body. By this means the atrium genitale is cut through, together with the side of the dilator rod-sac and the vas deferens. The relationship of the latter to the ejaculatory duct and vesicula seminalis is seen, and also the two arms of the latter.

FIG. 27.—Longitudinal vertical section through the anterior end of the mid-gut of a young female form. Immediately above this lies a special glandular mass of cells, which has apparently no duct of any kind. Posteriorly to the œsophagus lies the large nerve mass, and in front of the œsophagus the nerve commissure is cut through.

FIG. 28.—Longitudinal vertical section through the posterior part of the body of a young female. The section is cut to one side, so as to pass through the length of the oblique muscles, the insertion of which in the body-wall is shown; two bundles of fibres being with rare exceptions confined to the space within each annulus. The parietal gland-cells are seen occupying the lateral compartments of the body. The arrow points to the posterior end.

FIG. 29.—Longitudinal vertical section through the mid-ventral line of the body-wall of an adult female form. The section shows the arrangement of the muscle-layers, a few oblique fibres being cut through. The stigmatic glands are seen to be entirely confined in each annulus to the anterior portion, which is marked off from the posterior portion by the presence most externally of a darkly staining ridge of chitinous material.

FIG. 30.—A small portion of muscle-fibre from the muscle coating of the rod- and cirrus-sacs in the male form. In and amongst the fibres is protoplasmic material, containing nuclei but no distinct cell outlines.

FIG. 31.—Surface view of a small portion of the head highly magnified and seen by reflected light to show the openings of the stigmatic glands, each of which is surrounded by a raised circular rim. The dark spots seen probably correspond to the bases of subcuticular cells.

## PLATE VI.

### *List of References.*

In Figs. 35 and 36 the numbers correspond to those used in the description of the different nerves in the text.

In Figs. 38 and 39 the numbers correspond and indicate the different points of attachment of muscles, and in Fig. 39 the letters correspond to those used in the description of the different hook-muscles in the text.

*B. Hk.* Basal joint of hook. *Cl.* Connective tissue. *Cu.* External cuticle. *E.* Subcuticular epithelium. *f.* Moveable attachment of the hook to the basal joint. *Gr.* Groove around oral papilla. *Hk.* Hook. *Hk. i.* Invagination in



which base of hook lies. *Hk. M.* Hook muscles. *Hk. n.* Hook nerve. *L. M.* Limiting membrane of sense-organ. *M<sub>5</sub>*. Muscles in oral papilla. *M<sub>6</sub>*. Muscles from side of pharynx to ingrowth of cuticle around oral papilla. *M<sub>7</sub>*. Muscle band inserted into posterior angle of mouth. *M. Gl.* Modified stigmatic glands near mouth. *M. long.* Longitudinal muscles. *M. Tr.* Circular muscles. *M. V. S.* Muscles in wall of vesicula seminalis. *O. P.* Upper lip or oral papilla. *Pa. Gl.* Parietal glands. *Pe<sup>1</sup>*. and *Pe<sup>2</sup>*. Modifications of epithelium in posterior wall of pharynx. *S. O.* Sense-organ. *St. Gl.* Stigmatic glands. *To.* Tooth-like structure in posterior wall of pharynx. *T. P.* Membrana propria in wall of vesicula seminalis. *V. S. E.* Glandular epithelium of vesicula seminalis walls.

FIG. 32.—Longitudinal vertical section through the mouth region of a large mature female form. The oral papilla with its special muscles is cut through, and also the muscles (*M<sub>6</sub>*) running forwards from the pharyngeal walls. In the ventral wall of the pharynx is the tooth-like structure (*To.*) which runs upwards, and is connected with a swollen pad composed of an outer and inner layer. Special muscles are connected with the posterior wall of the pharynx, and one band of fibres (*M<sub>7</sub>*) is inserted into the cuticle just at the angle of the mouth. Close to the mouth lies a special group of modified stigmatic cells.

FIG. 33.—Section through the basal part of a hook, and the invagination in which it is placed. Through the centre of the basal part and between the muscles runs a nerve (5) which is continuous with a swollen spindle-shaped mass composed of fibres and nuclei. This breaks up distally, and its fibres are connected with the subcuticular cells in the base of the hook. Zeiss, apo., 4.0 mm., 0.95 apert., oc. 4.

FIG. 34.—Sense-organ on one of the secondary papillæ on the head region. The whole is made of elongate cells in which no nuclei can be seen, and which are directly continuous at their internal ends with a small nerve. A fine limiting membrane appears to invest the organ. Zeiss, apo., 4.0 mm., 0.95 apert., oc. 12.

FIG. 35.—Semi-diagrammatic representation of the nerve-ganglion mass seen from above. The drawing represents the result of examination of dissections, and of continuous series of sections. The different nerves given off are numbered, and their distribution is described in the text under these numbers.

FIG. 36.—Semi-diagrammatic representation of the nerve-ganglion mass seen from the side. Numbers as in Fig. 35.

FIG. 37.—Section across the wall of the common portion of the vesiculæ seminales close to the testis. Externally lies connective tissue and muscle-fibres, and within these lies a layer of columnar cells, the outlines of which cannot be clearly detected. Many of them have their inner ends much swollen out and vacuolate, and contain the coagulated remains of a fluid secretion. Zeiss, apo., 4.0 mm., 0.95 apert., oc. 4.

FIG. 38.—Side view of a hook with its basal joint. The numbers indicate the different parts to which muscles are attached, and the letter *f.* indicates the point on either side which acts as a fulcrum.

FIG. 39.—Diagrammatic representation of a side view of the outer hook of the left side, together with its muscular apparatus. The different muscles are lettered, and they are described under these letters in the text. The numbers correspond to those in Fig. 38. The drawing represents the results of examination of dissections, and of continuous series of sections.

## PLATE VII.

### *List of References.*

*Acc. F.* Accessory gland of female. *C. S. O.* Central cavity of ovary. *C. S. E.* Epithelium of cirrus-sac. *Co. Od<sub>1</sub>*, Swollen portion of united oviducts. *Co. Od<sub>2</sub>*, Thick-walled muscular portion of united oviducts. *Cu.* External cuticle. *Cu. C. S.* Cuticle lining cirrus-sac. *Cu. Vg.* Cuticle lining vagina. *E.* Subcuticular epithelium. *E<sub>1</sub>*, Epithelium around opening of hook-gland on papilla. *Ej. D. E.* Epithelium lining ejaculatory organ of male. *Gl. Vg.* Gland-cells in wall of vagina. *L. S. O.* Lateral pouch of ovary. *M. C. S.* Muscle in wall of cirrus-sac. *M. Ej. D.* Muscle in wall of ejaculatory organ. *M<sub>s</sub>*, Muscle band from upper wall of united portion of oviducts to upper wall of uterus. *Mes.* Mesentery supporting ovary. *M. P.* Membrana propria. *Od.* oviduct. *O. Hk. Gl.* Opening of hook-gland on papilla. *O. V. S.* Opening of vesicula seminalis into vas deferens. *S.* Shell around ovum. *S. O.* Sense-organ. *Sp.* Spermatheca. *Sp. D.* Duct of spermatheca. *Sy.* Masses of protoplasm containing nuclei in dorsal wall of ovarian tube. *U.* Uterus. *V. D.* Vas deferens. *V. S.* Vesicula seminalis. *Vg.* Terminal vagina. *Vg. E.* Epithelium of vagina. *x.* Thick cuticular layer in wall of vagina.

FIG. 40.—Diagrammatic representation of a much enlarged side view of a portion of the reproductive organs of a mature female. The whole of the spermatheca of one side and the upper half of that of the other is cut away. The two oviducts are seen to unite to form a common portion, which is joined ventrally by the uterus, and laterally by the spermathecal ducts. A special muscle band passes over from the common portion of the oviduct to the upper wall of the uterus. A portion of the muscle band is cut away to show the accessory gland.

FIG. 41.—Diagrammatic representation of a horizontal longitudinal section through the portion of the female reproductive organs represented in Fig. 40.

FIG. 42.—Longitudinal section through the junction of the portion of the vagina which serves as a uterus and the terminal vagina to show the sudden thickening which takes place to form the walls of the latter. Zeiss, A, oc. 2.

FIG. 43.—Transverse section across the ovary of a mature female. The

ovary has the form of a tube, the walls of which are flattened from above downwards, and the space is continued into little pouch-like lateral diverticula, through two of which the section passes. The upper wall of the main tube is syncytial in nature; the lower wall is composed of columnar cells. The tube is surrounded by eggs of various sizes, each enclosed in a definite shell. There is no enclosing membrane, and the mesentery arises from the mid-dorsal surface. Zeiss, F, oc. 4.

FIG. 44.—Transverse section across the ovary of an immature female. The upper and lower walls of the tube are distinct as in the mature state, but the lower one is composed of more distinctly nucleate columnar cells. There is no surrounding mass of eggs enclosed in shells, but groups of ova form the walls of the lateral diverticula, only one of which is cut through. The mesentery is cellular in nature. Zeiss, C, oc. 4.

FIG. 45.—Transverse section across the commencement of the vagina. Externally is seen the thick muscular coat, then the layer of columnar epithelium, and internal to this a mass showing radial markings (*x*), and lined internally by a thin cuticular layer thrown into little ridges and points. A few special gland-cells are enclosed in connective tissue externally to the muscles. Zeiss, E, oc. 2.

FIG. 46.—Transverse section across the ejaculatory duct of a mature male form. Externally the layer of very strong muscle slips is cut in section, within this the membrana propria, and within this the layer of columnar epithelium with its chitinous lining, the latter thrown into fine ridges and projecting points. Zeiss, F, oc. 2.

FIG. 47.—Transverse section across the part of the reproductive organs of a mature male where the vesicula seminalis joins the vas deferens. The well-marked layer of glandular cells surrounding the latter is seen, and the duct lined by chitin. The walls of the vesicula have been much distended, and are thin. Zeiss, F, oc. 4.

FIG. 48.—Section across the wall of the cirrus-sac of a mature male. Externally is a strong muscle layer, and within this the deep columnar epithelium with its well-marked cuticular lining. Zeiss, apo., 4.0 mm., 0.95 apert., oc. 8.

FIG. 49.—Section through the primary papilla of a young female to show the relationship of the sense-organ and the opening of the hook-gland. The sense-organ is composed of columnar cells, some of which are nucleated. A large nerve with nuclei amongst the fibres enters the inner side of the organ, which has no definite outline. At its opening the hook-gland is surrounded by a layer, sometimes more than one cell thick, of cubical nucleate cells, and the external chitinous layer is directly continuous with that lining the duct. Zeiss, F, oc. 4.

## PLATE VIII.

*List of References.*

*Acc. F.* Accessory gland of female. *Al. Gl.* Gland-cells in walls where mid- and hind gut unite. *Ct.* Connective tissue. *Cu. Sp.* Cuticle lining spermatheca. *Cu. U.* Cuticle lining uterus. *E.* Subcuticular epithelium. *H. G.* Cavity of hind gut. *M. G.* Mid-gut. *M. G. E.* Epithelium of the hind gut. *M<sub>s</sub>.* Muscle-band from oviduct to uterus walls. *M. H. G.* Muscles in wall of hind gut. *M. Al.* Muscle running forwards from anterior end of mid-gut. *M. Al. Long.* Longitudinal muscles of mid-gut. *M. Al. Tr.* Circular muscles of mid-gut. *M. C.* Sphincter muscle of œsophagus. *M. Tr.* Transverse muscles. *Mes.* Mesentery supporting ovary. *Æs.* œsophagus. *Od.* Oviduct. *Ov.* Ovary. *R'* Ridge in cuticle bounding opening of stigmatic gland. *Sp. E.* Epithelium of spermatheca. *Sp. D.* Duct of spermatheca. *Sp. D. E.* Epithelium of duct of spermatheca. *Sp. Gl.* Gland-cells of wall of duct of spermatheca. *Sp. M.* Muscles of wall of spermatheca. *St. Gl.* Stigmatic gland. *St. Gl. O.* Opening of stigmatic gland. *U.* Uterus. *W.* Special radial strands of connective tissue in the body-wall.

FIG. 50.—Longitudinal vertical section through the opening of the œsophagus into the mid-gut. The œsophagus is lined by columnar cells with a distinct chitinous layer, the cells forming a papilla on the floor of the mid-gut and dipping under the hypoblast-cells, from which they are sharply marked off. The latter are thrown into folds and are columnar in form, with large spherical nuclei. Where the œsophagus enters the floor of the mid-gut the cavity of the former swells out into the definite form represented in the figure, and immediately below this cavity is a band of circularly disposed muscle-fibres.

FIG. 51.—Longitudinal section through the body-wall in the anterior part of an annulus of a mature female. The layers of circularly and longitudinally disposed muscle-fibres are seen, the former consisting of hollow fibres or groups of fibrils. The external cuticle is marked by lines, and immediately within it lies the subcuticular epithelial layer. Masses of these cells are modified to form the stigmatic glands, two of which are cut through. The space immediately within the epithelial layer is occupied by connective tissue, in which nuclei are irregularly scattered.

FIG. 52.—Gland-cells. These are taken from the hook-gland of a mature female, but so far as the structure of the cell itself is concerned those forming the hook, head, and parietal glands are identical. Two small groups of cells are represented, one consisting of two, the other of three cells. The curious clear central space with radiating lines of granules is seen in each, and in the larger one the fine duct which arises from this. Zeiss, apo., 4.0 mm., 0.95 apert., oc. 8.

FIG. 53.—Transverse section across the central nerve mass of a young male. The clear division into two halves is shown, and also the arrangement of the fibres on the inside, and the ganglion-cells on the outside and up the median line.

FIG. 54.—Longitudinal section through a portion of the reproductive organs of a mature female. The section is slightly oblique, so that it passes through the commencement of the uterus and the union with this of one of the spermathecal ducts. It passes also through one of the tubular accessory glands, which curves in such a way that one side of the lips at its opening as well as the gland itself is cut through. The layer of gland-cells around the spermathecal duct is seen, and the muscle-fibres passing forwards from the common part of the oviducts to the dorsal wall of the uterus. The latter is lined by very definite columnar cells, and has internally a chitinous lining thrown into distinct ridges. The chitinous lining becomes very thin in the spermathecal tube. Zeiss, F, oc. 4.

FIG. 55.—Section across the wall of one of the spermathecae in a mature female. Externally lies the layer of muscle-fibres. The epithelial cells are distinct and columnar, with somewhat tapering external ends embedded in a granular material. Internally they have a thin cuticular lining. Zeiss, F, oc. 4.

FIG. 56.—Oblique and transverse sections across the oviduct of a female, the spermathecae of which contain spermatozoa, but in which no shells are formed around the ova. Zeiss, camera, C, oc. 2.

FIG. 57.—Oblique section of a portion of the ovary in a small immature female, in which no spermatozoa are present in the spermatheca or vagina. Both the upper and lower walls have the same structure. Zeiss, F, oc. 4.

FIG. 58.—Transverse section across the oviduct of the same female as that of which the ovary is drawn in Fig. 57.

FIG. 59.—Longitudinal section through the point of union of the mid- and hind gut in a young female. The columnar epithelial cells of the hind gut with their cuticular lining dip underneath the less columnar cells of the mid-gut. Just where the two parts unite a small number of gland-cells are present, embedded in connective tissue external to the muscle layers. Zeiss, F, oc. 4.

## PLATE IX.

### List of References.

*A.* Nerve commissure. *C.* Cirrus. *C. B.* Cirrus bulb. *Co.* Tube leading down to atrium genitale. *C. S.* Cirrus-sac. *Ct.* Connective tissue. *Cu'.* Cuticle covering muscular mass in dilator rod-sac. *Cu. C. B.* Cuticle lining central cavity of cirrus bulb. *D. E.* Epithelium lining dilator rod-sac. *D. R.* Dilator rod. *D. R. S.* Dilator rod-sac. *E<sub>1, 2, 3</sub>.* The three layers forming the walls of the cirrus bulb. *Gr.* Groove on the inner face of the mass in the

dilator rod-sac through which the cirrus passes. *i.* and *o.* Two layers of cirrus. *M. D. R. S.* Muscular mass of dilator rod-sac. *Ng.* Nerve ganglion. *Æs.* Œsophagus. *O. D.* Oviduct. *O. Sp.* Duct of spermatheca. *Sp.* Spermatheca. *S.* Outer cavity of cirrus bulb. *S'.* Central cavity of cirrus bulb. *Tb.* Tongue-like organ in dilator rod-sac. *V. D.* Vas deferens. *I.* Ventral nerve cord.

FIG. 60.—Horizontal longitudinal section through a portion of a mature female ventral to the mid-gut to show the relative positions of the main nerve mass, œsophagus, oviducts, and spermathecae. On one side a small portion of the spermathecal duct is cut through close to its opening into the spermatheca. The double nature of the ganglionic mass is clearly marked, and the absence of any ganglionic swelling in the œsophageal commissure. Zeiss, A, oc. 2.

FIG. 61.—Section along a small portion of one of the large posterior nerves in a young female. Externally is seen a distinct connective-tissue coat, and amongst the nerve-fibres are numerous darkly staining elongate nuclei. Zeiss, F, oc. 4.

FIG. 62.—Diagrammatic representation of the portion of the male reproductive organs where the cirrus bulb, dilator rod-sac, and cirrus-sac are in union with one another. Part of the outer wall of the rod-sac and cirrus-sac and the tube running down from these to the atrium genitale has been cut away so as to show the internal structures. The cirrus bulb fuses with the inner side of the muscular mass in the rod-sac. This muscular mass is covered with a thick chitinous layer, and at its apex and on the outer side (that is left of the drawing) is a depression containing a little tongue-like process (*Tb.*). On the inner (that is right side of the drawing) the chitinous lining is produced downwards into the somewhat flattened dilator rod (*D. R.*), and passing from this towards the cirrus bulb the surface of the muscular mass becomes deeply grooved, and in this groove the cirrus itself (*C.*) passes outwards from the bulb. In the fully developed form the cirrus almost, but not quite, always passes into the cirrus-sac, where it lies coiled up at rest with its free end pointing towards the atrium genitale.

FIG. 62A.—Diagrammatic section through the same parts of the female organs as are represented in solid view in Fig. 62, with the exception that in this drawing the cirrus and cirrus-sac are shown complete. The cuticle is represented by the thick dark line.

FIG. 63.—Transverse section across the cirrus bulb of a not quite mature male. Most internally lies the space continuous backwards with that of the vas deferens, and forwards with that of the cirrus. The chitinous lining is directly continuous with the wall of the latter. The three layers forming the wall of the bulb are indicated by letters *E*<sub>1</sub>, *E*<sub>2</sub>, *E*<sub>3</sub>. Zeiss, apo., 4.0 mm., apert. 0.95, oc. 4.

FIG. 64.—Transverse section across the dilator rod-sac where the cirrus

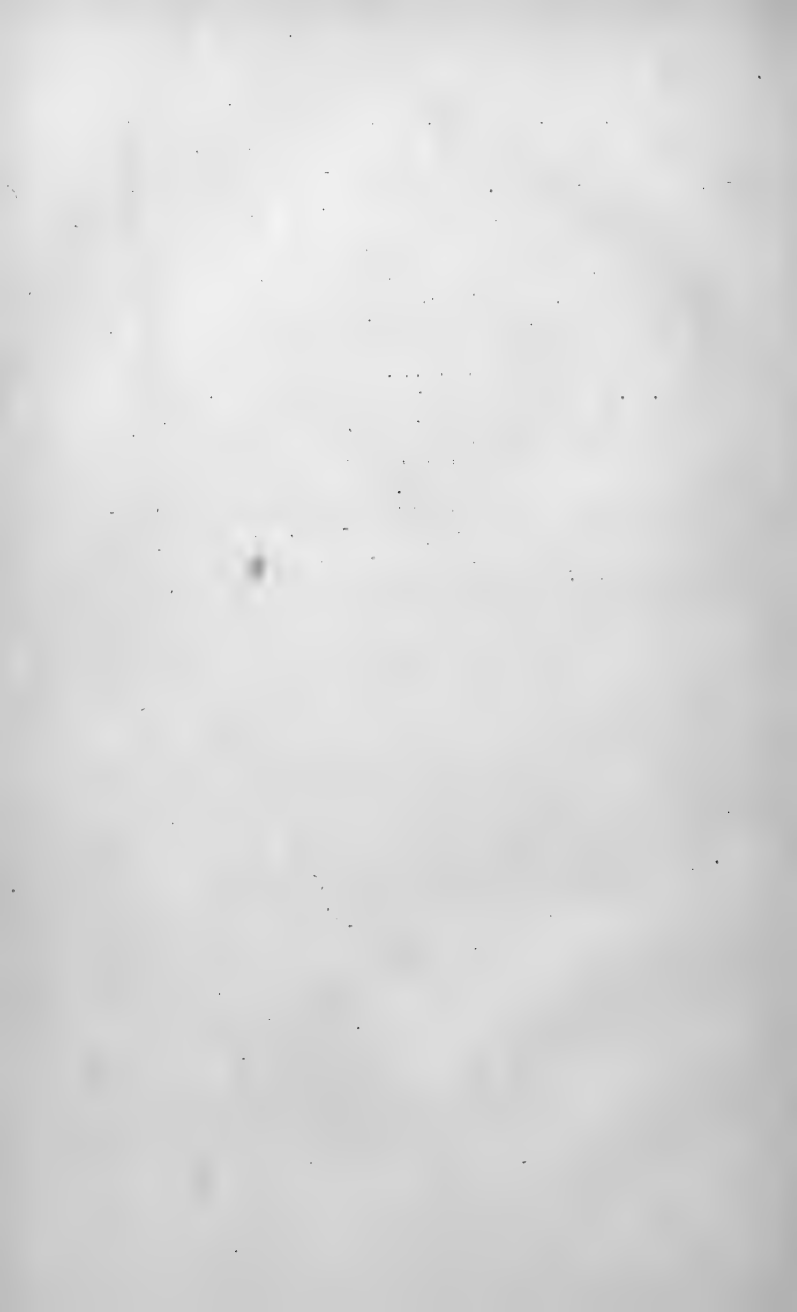
bulb is fused with it. The muscular mass in the rod-sac is attached by one side to the outer wall, whilst the other has a strong chitinous lining. To one side there is seen a trace of the opening into the cirrus-sac, which in this specimen lies somewhat further back than is represented in the diagram in Fig. 62.

FIG. 65.—Transverse section across the dilator rod-sac very slightly in front of the section drawn in Fig. 64. The section passes through the lower part of the muscular mass in the rod-sac where the chitinous layer is thick, and through the root of the tongue-like structure (*To.*), and the cirrus bulb just before the cirrus passes off from this.

FIG. 66.—Transverse section across the dilator rod-sac very slightly in front of the section drawn in Fig. 65. The tongue-like structure (*To.*) is cut through, and the groove formed in the chitinous lining on the inner side, through which the cirrus passes on its way to the cirrus-sac.

FIG. 67.—Transverse section across the cirrus showing the two layers.

FIG. 68.—Diagram to represent the common portion of the vesiculæ seminales and the method of union of this with the testis. A, B, C, D, E, F, G, represent sections along the planes indicated by the lines bearing the same letters in Fig. 68.





On the Minute Structure of the Gills of  
*Palæmonetes varians*.

By

**Edgar J. Allen, B.Sc.,**  
University College, London.

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With Plate X.

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KOWALEVSKY<sup>1</sup> states that when he injected *Palæmon* with a strong solution of litmus, two red stripes appeared on the axis of each gill, the effect being due to the colouring matter having been deposited in two solid strings of cells, which lie on both sides of the axis, near the channels through which the blood flows from the gill lamellæ to the heart (branchio-cardiac canals). Professor Weldon drew my attention to this statement, and suggested that I should endeavour to work out the minute structure of the gills, of which no description, so far as I am aware, at present exists. My observations have been carried on chiefly upon *Palæmonetes varians*, as this form can be more readily obtained alive and kept in confinement in London.

**METHODS.**—The gills of *Palæmonetes* are somewhat difficult to preserve. The use of sublimate and of alcohol failed to give satisfactory results. Specimens preserved in picro-nitric acid, although better, were not good. By using strong Flemming's solution I was, however, finally able to obtain preparations which showed both cell-outlines and protoplasmic structure in an excellent state of preservation. The time

<sup>1</sup> "Ein Beitrag zur Kenntnis der Exkretionsorgane," 'Biol. Centralblatt,' Bd. ix, No. 2, 1889, p. 38.

which the objects must remain in the solution varies from three to twelve or fourteen hours, according to the degree of softness of the chitin. Animals which have recently moulted have their gills well preserved in about three hours. The best average time is from five to six hours. After being hardened in alcohol the objects were stained with Delafield's hæmatoxylin; or they were removed from Flemming's solution to water, and, after a few minutes, transferred to crude pyroligneous acid, where they remained for nearly twenty-four hours. By this process the osmic acid is reduced in the tissue, and no further staining is required (von Mährenthal's method). This latter method is the one which has been chiefly used. After dehydration the objects were sunk in chloroform, and then placed for several hours on the water-bath in a mixture of chloroform and paraffin. They were then embedded in paraffin and cut in the usual way.

ARRANGEMENT OF THE GILLS.—The arrangement of the phyllobranchiate gills of *Palæmon* has been described by Huxley,<sup>1</sup> and P. Mayer<sup>2</sup> has shown that Huxley's description is also true for *Palæmonetes varians*. The second maxillipede bears a podobranchia, the third two arthrobranchiæ, and there is a pleurobranchia above each of the five walking legs.

STRUCTURE OF THE GILLS.—Each gill consists of a vertical axis, bearing on its external surface two rows of lamellæ, each lamella sloping relatively to the axis forwards, upwards, and outwards, making an angle of about thirty degrees with the horizontal. The gills above the thoracic legs taper towards their two ends, the lower ends, however, being less sharply pointed than the upper. The gill above the third walking leg is attached to the body at about the middle point of its axis. Those in front of the third leg are attached slightly above, those behind slightly below the middle points of their axes.

<sup>1</sup> "On the Classification and Distribution of the Crayfishes," 'Proc. Zool. Soc.,' London, 1878.

<sup>2</sup> "Carcinol. Mitt.," 'Mitt. a. d. Zool. Sta. in Neapel,' Bd. ii, 1881.

**THE AXIS.**—A transverse section through the axis of a gill (fig. 1) has a triangular shape, the sections of the lamellæ (*l.*) appearing attached along the two sides of the triangle. The surface of the axis is covered with a layer of chitin (*cht.*), which is thinner than that covering the body of the animal. Beneath the chitin lies the ectoderm (*ect.*), consisting of a layer of cells with large oval nuclei. At the apex of the triangular section the main arterial channel is situated (figs. 1 and 3, *art.*), which runs along the whole length of the axis, and supplies blood to the lamellæ. This artery is lined by a layer of epithelium (*a. ep.*) composed of clear cells with relatively small nuclei. The epithelium, however, only completely surrounds the vessel at irregular intervals (fig. 3, *a. ep.*), it being broken in front, for the most part of its length, to allow the blood to pass into the channels of the lamellæ. The artery then appears to have its outer wall formed by the cells of the ectoderm (fig. 1). At the point of attachment to the body an artery, also lined with epithelium, enters the gill and unites with the main artery of the axis (fig. 4).

In the other two angles of the axis run the main venous channels (figs. 1, 2, and 4, *vn.*), which unite together and enter the body by a common vessel immediately below the artery. Fig. 3 represents a section through this point, which lies a little below that represented in fig. 4.

The venous channels are surrounded by the connective-tissue cells (*con. t.*). The latter are large irregular cells, each containing a small, deeply staining nucleus, an outer layer of protoplasm, and a large, clear vacuole, in which a mass of yellow-coloured concrement is deposited. Around the main venous channels these cells form a more or less continuous layer, which is, however, interrupted at various points. In the other parts of the axis they are arranged somewhat loosely, leaving intercellular spaces, which are in direct communication with the blood-channels, and are filled with blood. Fig. 2, drawn from a section near the end of a gill, in which osmic acid has been reduced by pyroligneous acid, the blood being thereby coloured black, will make this

point clear. It may also be mentioned that blood-corpuscles have been observed not unfrequently in these intercellular spaces. Hence, for the gills at any rate, the statement made by Haeckel<sup>1</sup> and Ray Lankester,<sup>2</sup> that the circulatory system of the Decapods is everywhere closed, does not appear to hold true.

It was in the masses of cells surrounding the venous channels that Kowalevsky found the litmus deposited a few hours after injection, and it seems fairly certain that these cells exercise an excretory function.

That portion of the axis which is not occupied by blood-channels and connective-tissue cells is filled by glandular bodies, which will be treated of in detail when the structure of the lamellæ has been described.

**THE LAMELLE.**—A transverse section through a single lamella is represented in fig. 5. The layer of chitin surrounding it (*cht.*), which is extremely thin, is supported by a number of transverse cells (figs. 5, 6, 7, *tr.*), stretching at intervals across the lamella, and arching over, above and below, until they meet. These cells, which stain deeply, and contain large spherical nuclei, appear to be the formative cells of the chitin. The spaces between them are occupied by large, clear cells (*c. c.*), which, to distinguish them from the transverse ones, may be termed the central cells of the lamella. The protoplasm of these central cells stains much less deeply than that of the transverse cells, but their nuclei are very similar.

Two blood-channels, seen in section in figs. 5, 1, 2, 3, and 4, run along the outer and inner borders of the lamella, that of the inner side (*a. l.*) communicating with the main arterial channel, that of the outer (*v. l.*) with one of the main venous channels of the axis. These channels of the lamella are lined by a thin membrane (*w. a. l.* and *w. v. l.*) on their outer sides, which is probably an epithelium, although the presence of

<sup>1</sup> 'Archiv für Anatomie und Physiologie,' 1857, p. 556. Quoted by Claus, 'Art. Zool. Inst. Wien,' Bd. v, Heft 3, 1884.

<sup>2</sup> 'Quart. Journ. Micr. Sci.,' vol. xxv, p. 518.

nuclei in it has not been made out, owing to the extreme thinness of the layer. That a membrane does actually exist can be seen without doubt, both in transverse and longitudinal sections of the channels.

The blood passing down the inner border finds its way across the lamella through an irregular network of channels, which lie close to the surface on both the upper and under faces of the lamella. These channels are seen in section in figs. 5, 6, and 7, *s. ch.* They are lined on their outer side by the extremely thin arching processes of the transverse cells, on their inner by the central cells of the lamella. Fig. 8, which is drawn from a very oblique section of a lamella, shows this irregular network of channels running across its two surfaces. *a. l.* and *v. l.* are the two channels running along the borders of the lamella, whilst *s. ch.* is the network of surface channels running across.

Owing to the irregularity of arrangement of the transverse cells and of the surface channels, the appearance presented by longitudinal and transverse sections of the central part of the lamella is practically the same (cf. fig. 5 with figs. 6 and 7).

A slight thickening of the lamella occurs along its distal border, and here the surface channels are very much enlarged (fig. 7, *d. b.*). It is probable that all the blood-corpuscles are carried round through these enlarged channels, as the others have never been seen to contain a corpuscle, and appear to be too thin to admit one.

**THE GILL GLANDS.**—In addition to the excretory cells surrounding the venous channels a large number of glandular bodies occur in the axis of the gill. These glands (figs. 1 and 2, *rt. gl.* and *c. gl.*) are spherical in shape, and are composed of large conical cells, each cell having its apex directed towards a common centre. The glands are of two kinds: in the one (figs. 1, 2, &c., *rt. gl.*; figs. 9, 11, and 12) the body of each cell appears as a deeply staining network; in the other (figs. 1, 2, &c., *c. gl.*; fig. 13) it is only faintly stained, and shows a more granular structure in preparations preserved in Flem-

ming's solution. These glands will be distinguished as the reticulate and the clear glands.

The reticulate glands lie, for the most part, just outside the epithelium of the artery of the axis, and are so numerous that two or three of them are found cut across in almost every transverse section throughout the length of the axis. The glands are spherical in shape, a point which can be easily demonstrated by following a series of sections, and which is also proved by the fact that in whatever direction the axis of the gill be cut the section through each gland is circular. The conical cells of which the glands are composed have large, spherical nuclei, which lie near their bases, and a dark spot is seen near the middle of the well-formed network in the protoplasm (fig. 9).

Close to the centre of each gland a spherical nucleus (figs. 9 and 10, *c. n.*) is invariably found, which is easily distinguishable from the nuclei of the cells, both by its position and by the fact that it stains less deeply than the latter. On the opposite side of the centre to this nucleus a duct arises (figs. 9 and 10, *dct.*), which can frequently be followed as far as the edge of the gland, as in fig. 9 (*dct.*), whilst in favorable cases it can be traced into the ectoderm (fig. 11, A, B, C, D, *dct.*), or even to the exterior (fig. 12, B, *dct.*). The most probable explanation of these relations is that the nucleus (*c. n.*) belongs to a central cell which has given rise to the duct of the gland, such modification of a cell into a duct ("drain-pipe cell") being common amongst Crustaceans.<sup>1</sup>

At the centre of each gland a star-shaped figure is always well developed. When viewed under a high power ( $\frac{1}{12}$  oil immersion) this figure (fig. 10) is seen to be formed by the projection of very fine tubes (*tu.*) from the ends of the conical cells into the central cell. The cut ends of the tubes belonging to the cells below can be seen as dark spots in the centre of the star-shaped figure even under the lower power (figs. 9, 11). With the high power these dark spots are seen clearly

<sup>1</sup> Cf. Grobben, "Die Antennendrüse der Crustaceen," 'Arb. a. d. Zool. Inst. Wien,' Bd. iii, 1881.

to represent the cut ends of fine tubes (fig. 10). It is highly probable that in the natural condition all these tubes are in direct communication with the duct.

In preparations which have been treated with pyroligneous acid the protoplasm at the apex of each cell and immediately at the base of the fine tube stains much more deeply than the rest of the cell (fig. 9).

The second form of gland found in the gill (fig. 1, &c., *c. gl.*; fig. 13) differs only slightly from the reticulate form already described. The absence of the well-developed network in the protoplasm is the feature which most distinguishes it from the latter. The clear glands are also slightly smaller than the reticulate, and it will be noticed (fig. 13) that the nuclei are relatively larger, and are situated more nearly at the centres of the cells. The apex of each cell appears less sharply defined, although with a high power it is not difficult to satisfy oneself as to the presence of a fine tube leading from it. The central nucleus and duct can also be made out. The more darkly staining portion of the protoplasm at the apex of each cell, although less marked, extends further back into the body of the cell, and possesses a more definite outline on its outer margin (fig. 13, *d*).

The clear glands are generally (though not invariably, fig. 3, *c. gl.*) situated in the neighbourhood of the venous channels of the axis, whilst, as already stated, the reticulate glands lie for the most part next to the epithelial lining of the artery. These relative positions are so fairly well maintained that it seems impossible to suppose that the two appearances indicate merely different conditions of similar glands performing identical functions.

The presence of glandular bodies in the gill has not, so far as I am aware, been previously observed in any Crustacea. Max Braun<sup>1</sup> has shown that glands of a similar form, which

<sup>1</sup> "Ueber die histolog. Vorgänge b. d. Häutung von *Astacus fluviatilis*," 'Arb. a. d. Zool. Inst. Würzburg,' Bd. ii, 1875. "Zur Kenntniss des Vorkommens der Speichel und Kittdrüsen bei den Decapoden," ditto, Bd. iii, 1876-7.

he regards as salivary glands, occur in the œsophagus, in the labrum, and in the first and second maxillæ of various Decapods, and that the glands situated on the epimera of each segment of the abdomen, which secrete the fluid used to attach the ova to the appendages, have a like structure.

The glands in the labrum and maxillæ of *Palæmonetes* differ but little in appearance from the reticulate glands of the gill. The network in the protoplasm is well developed, but stains less deeply than that in the gill, the nuclei are smaller and lie quite close to the bases of the cells, and the characteristic appearance of the centre of the gland is not quite the same.

Nebeski<sup>1</sup> has described glands found in the legs of certain Amphipoda (*Corophiidæ* and *Orchestia*), and P. Mayer<sup>2</sup> and Claus<sup>3</sup> others found in *Phronimidæ*, which seem to throw light upon the spherical glands of the Decapods. In the *Corophiidæ* and *Orchestia* the glands are described as unicellular, and containing a number of fine chitinous canals, which unite together to form a duct which opens on the exterior. In the *Phronimidæ* each gland consists of either three or five cells. In the case of those with three cells, two of these are large, whilst the third is smaller, and gives rise to the duct which communicates with the exterior. When the gland consists of five cells, four are large, and surround a smaller one, which is the duct cell. All the large cells contain a number of fine chitinous canals, which communicate directly with the duct.

If the network seen in sections of the reticulate glands of the gill of *Palæmonetes* is due to the presence of fine channels which communicate with the duct, the difference between

<sup>1</sup> Nebeski, "Beiträge zur Kenntniss der Amphipoden der Adria," 'Arbeiten a. d. Zool. Inst. Wien,' Bd. iii, 1881.

<sup>2</sup> P. Mayer, "Carcinolog. Mittheilungen," 'Mitth. a. d. Zool. Station in Neapel,' I, i, 1878.

<sup>3</sup> Claus, "Zur Naturgeschichte d. *Phronima sedentaria*," 'Zeitschr. f. w. Zool.,' 1872. "Der Organismus der *Phronimiden*," 'Arb. a. d. Zool. Inst. Wien,' Bd. ii, 1879.



the structure of these glands and of those of the Phronimidæ is very slight. Indeed, the latter may be considered as representing a stage in the development of the former.

Eisig<sup>1</sup> considers that two distinct series of glands occur in Arthropods, the one series being homologous with the crural glands of *Peripatus*, and the parapodial spiral glands of certain Chætopods, and being of ectodermal origin, the other series being the nephridia.

The spherical glands, which are now shown to occur in every segment in Decapods, would seem to belong to the ectodermal series, although the question cannot be finally settled until something is known of their development. One has, however, only to imagine a number of cells, such as the goblet-cells of the leech, gathered into a cluster, one cell taking up the function of a common duct, and such glands as those which have been described in the present paper would be the result.

In conclusion, I should like to express my very best thanks to Professor Weldon for his constant kindness and advice during the progress of this research.

<sup>1</sup> Eisig, "Die Capitelliden des Golfs von Neapel," 'Monographie der Fauna und Flora von Neapel,' Berlin, 1887.

## EXPLANATION OF PLATE X,

Illustrating Mr. Edgar J. Allen's paper "On the Minute Structure of the Gills of *Palæmonetes varians*."

*List of Reference Letters.*

AXIS.—*l.* Lamella. *cht.* Chitin. *ect.* Ectoderm. *art.* Main artery of axis. *a. ep.* Epithelium of artery of axis. *vn.* Main venous channel of axis. *con. t.* Connective-tissue cells. *rt. gl.* Reticulate gland. *c. gl.* Clear gland.

LAMELLA.—*tr.* Transverse cell of lamella. *c. c.* Central cell of lamella. *a. l.* Arterial channel of lamella. *v. l.* Venous channel of lamella. *w. a. l.* Outer wall of arterial channel. *w. v. l.* Outer wall of venous channel. *s. ch.* Surface channels of lamella. *d. b.* Distal border of lamella.

GLANDS.—*duct.* Duct of gland. *c. n.* Central nucleus of gland. *tu.* Tube from end of conical cell. *d.* Deeply staining portion at apex of cell.

All the figures have been drawn with the aid of the camera.

FIG. 1.—Transverse section through the axis of gill of *Palæmonetes varians*.  $\times 240$ .

FIG. 2.—Oblique section through tip of gill. Osmic acid reduced with pyrologneous acid.  $\times 240$ .

FIG. 3.—Transverse section through the point where the venous channel enters the body.  $\times 100$ .

FIG. 4.—Transverse section through the point where artery enters from the body.  $\times 100$ .

FIG. 5.—Transverse section of lamella.  $\times 420$ .

FIG. 6.—Portion of longitudinal section of lamella.  $\times 240$ .

FIG. 7.—Longitudinal section through distal end of lamella.  $\times 240$ .

FIG. 8.—Very oblique section through a lamella.  $\times 240$ .

FIG. 9, A and B.—Two consecutive sections through the centre of a reticulate gland.  $\times 420$ .

FIG. 10.—Central portion of reticulate gland under high power.  $\times 770$ .

FIG. 11, A, B, C, D.—Four consecutive sections through a reticulate gland, showing duct.  $\times 420$ .

FIG. 12, A, B, C.—Three consecutive sections through a reticulate gland, showing duct.  $\times 420$ .

FIG. 13.—Group of three clear glands.  $\times 420$ .

## On the Development of the Optic Nerve of Vertebrates, and the Choroidal Fissure of Embryonic Life.

By

**Richard Assheton, M.A.,**

Demonstrator of Zoology in the Owens College.

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With Plates **XI** and **XII**.

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IN the 'Anatomische Anzeiger' of 28th March, 1891, Froriep described, in a somewhat brief manner, the way in which the fibres of the optic nerve are developed in the embryo of *Torpedo ocellata*. The paper contains twelve outline figures, which satisfactorily indicate that in the case of *Torpedo ocellata* at least certain fibres of the optic nerve arise from nerve-cells or neuroblasts situated in that portion of the optic cup which will form the retina at a later stage of development.

Herr Froriep is, I believe, the first who has published any figures in support of what is not altogether a new idea. In a foot-note to the above-mentioned paper Froriep remarks that Keibel had previously described the centralwards growth of the fibres of the optic nerve from the retina in reptilian embryos.

The original statement of Keibel's was in the form of a communication to a meeting of the Naturwissenschaftlich-medizinischer Verein in Strasburg, and, as I understand from a letter from Herr Keibel himself, there is not a fuller published account than that which appears in the 'Deutsche

medicinische Wochenschrift,' 7th February, 1889, p. 115, which is as follows:—"Ueber die Entwicklung des Sehnerven.—Bei allen Amnioten bilden sich die Nervenfasern in dem unteren, mit der Netzhaut-anlage in Verbindung stehenden Theil des Augenblasenstieles; eine secundäre Lösung der oberen Wand vom Pigment Blatt der Retina und eine Verschmelzung derselben mit der eigentlichen Retina-anlage findet nicht statt. Präparate von Reptilienembryonen (Lac: mural und Tropicidonatrix), welche mit Boraxcarmin gefärbt und mit Picrinsäure nachbehandelt sind, zeigen ferner, dass, bei diesen Thiere wenigstens, die erste Sehnervenfasern von der Peripherie centralwärts wachsen. Es ist demnach höchstens wahrscheinlich, dass sie aus der Retina-anlage hervowachsen, wenn ihr Ursprung dort auch nicht direkt nachgewiesen werden konnte."

The suggestion that the fibres of the optic nerve either develop from cells within the retina and grow towards the brain, or that they develop in the brain, and grow towards the retina, and are not formed by the transformation of the cells of the optic stalk, was first discussed as a matter of theory by His in the year 1868.

His (10) at that time maintained, as he has so ably demonstrated in a more recent work (11), that nerve-fibres are outgrowths from nerve-cells; and holding that there are no nerve-cells along the optic stalk, he suggested that the fibres of the optic nerve must grow from cells probably in the brain along the optic stalk to the retina.

With him in the main agreed W. Müller (20), Mihalkovics, and Kölliker, though they differed as to the direction of the growth of the fibres.

Certain other embryologists, however, were not convinced by what was little more than suggestion; among them was Balfour (1, p. 493), who wrote, "There does not seem to me to be any ground for doubting (as has been done by His and Kölliker) that the fibres of the optic nerve are derived from a differentiation of the epithelial cells of which the nerve is at first formed;" and Balfour's opinion seems to have been held

until the present time by nearly every English writer on the subject.

There are apparently still those who hesitate to accept the more recent views as to the origin of the optic nerve. As examples I will quote passages from the last editions of two widely read educational works, namely, 'A Text-book of Physiology, by Foster, and 'The Frog,' by Marshall.

On p. 1141 of the former work Professor Foster writes: "The cup becomes what we may speak of broadly as the retina, and we may call it the optic or retinal cup; the solid stalk becomes the optic nerve." And again, on p. 1142, "At the time when the epithelial cells of the stalk of the retinal cup are developed into the fibres of the optic nerve these become connected with the elements of the inner or retinal wall of the cup; they pierce the outer wall of pigment epithelium, making no connections with the cells of that outer wall."

On p. 131 of the latter work Professor Marshall writes, "The optic vesicles have already been described as arising at a very early period as lateral outgrowths from the fore-brain; these soon become constricted at their necks, so as to be connected with the brain by narrow stalks, which ultimately become the optic nerves."

In view of this difference of opinion, which still exists concerning the origin of the fibres of the optic nerve, I think an account of a research made some months ago upon this subject in the frog and chick may be of some interest, especially as certain structures connected with the development of the eye and other parts of the nervous system may be more easily understood by appreciation of the fact that the optic nerve and optic stalk are two entirely separate structures.

#### Relation of the Optic Stalk to the Optic Nerve.

The two views held at present are—1. The optic nerve is formed by the differentiation of the cells of the optic stalk into nerve-fibres, which subsequently lose connection with the

inner wall of the optic cup, and, piercing the outer wall, make connection with the outer face thereof.

2. The optic nerve is formed by the growth of nerve-fibres either from the retina (outer wall of the optic cup) or from the brain, along the optic stalk, but outside it and unconnected with it.

The first of these views has been held by Balfour (1), Haddon (8), Foster (6), Marshall (19), &c.; while the second view has been held by His (10, 12), Müller (20), Kölliker (14), Hertwig (9), Orr (21), and more recently supported by Keibel (13), Froriep (7), and Cajal (3).

In the new edition of 'Quain's Anatomy' Professor Schäfer seems to be uncertain which view to take. He writes on p. 79, "The optic nerves take origin as hollow outgrowths of the brain, which afterwards become solid, while nerve-fibres become developed in their walls. Their mode of origin will be further treated of in connection with the development of the eye." On p. 85 Professor Schäfer gives what appears to be an abstract from O. Hertwig's 'Lehrbuch' (9), pp. 402—406, in which Hertwig gives His's more recent opinions on the subject.

His (10) originally considered it probable that the nerve-fibres arose within the brain and travelled towards the retina, but recently (12) has changed his views, and considers it more likely that they arise from neuroblasts within the retina and grow centralwards.

Thus it seems that the tendency of writers of this country is to adhere to the older view in spite of strong evidence in favour of the newer advanced by foreign authors.

Moreover, if we accept the theory that all nerve-fibres are outgrowths from nerve-cells, we have the advantage of knowledge of a peculiarly fascinating nature, and the comprehension of the structure and development of the central nervous system is rendered clearer to both teacher and pupil.

The beautiful works of His, Cajal, and others—but more especially of His—having once taught us what to look for, it is an easy matter with ordinary care in the preparation of

specimens and with thin sections, to find the early commencement of nerve-fibre tracts, arising as they do from definite groups of neuroblasts. I do not doubt that the conclusions of His are correct, namely, that the fibres of the dorsal roots of the spinal nerves and the sensory fibres of the cranial nerves arise as processes from neuroblasts of the spinal ganglia in the one case, of the cranial ganglia in the other case, and grow inwards to the central nervous system.

Similarly also the sensory fibres of the sense-organs may be expected to grow inwards from the sensory epithelium of the sense-organ to the central nervous system.

In no sense-organ can the outgrowths of the fibres to the central nervous system be more easily traced than in the case of the fibres arising in connection with the optic organ; as the distance between the place of origin of the fibres (in the retina) and the final destination of the fibres (the brain) is relatively greater than in such cases as the distance between the olfactory epithelium and brain, or between ganglia of cranial and spinal nerves and the neural tube, in which cases it is exceedingly difficult to trace the centralwards growth of the nerve processes into the brain, though neuroblasts with the nerve processes directed towards the brain may be easily found.

I have paid special attention to the development of the nerve processes in the frog, and so shall describe the development of the optic nerve in that animal at some length.

#### Fate of the Optic Stalk.

I wish first to draw attention to the figs. 1, 2, 3, 8, 9, 10, 11, of Pl. XI, which are camera drawings of sections which seem to me to prove conclusively that the optic nerve is not developed from the optic stalk; that is to say, the nerve-fibres of the optic nerve do not arise by a transformation of the cells of the optic stalk into nerve-fibres.

During the earliest stages of the folding off of the optic vesicles the walls of the stalk are more than one cell thick; but by the time the vesicles are definitely formed, and the

outer wall has apparently begun to be pushed inwards upon the inner wall, the walls of the optic stalk are not more than one cell in thickness, and never become any thicker. The same statement may be made about the inner wall of the cup itself. From the time that the optic vesicles first form—that is, during the folding up of the neural plate—till after the fibres of the optic nerve have appeared, the optic stalk is hollow from end to end. With the folding off of the optic vesicles the optic stalk diminishes in diameter, and consequently the lumen also diminishes.

When the fibres first appear (in tadpoles of  $6\frac{1}{2}$ — $7\frac{1}{2}$  mm. in length) along the outer and ventral border of that part of the stalk nearest the optic cup, the lumen is still continuous throughout (figs. 6 and 7), but the greater part of the cavity between the outer and inner walls of the optic cup has become obliterated by the approximation of those two walls (fig. 12). The lumen of the optic stalk is first obliterated in tadpoles of about 10—11 mm. at the point at which the optic stalk and nerve pierce the dense tissue now forming at the side of the brain. At this point the optic stalk becomes squeezed, the lumen obliterated. Close to the brain the lumen persists for a long time, and is not entirely obliterated until the tadpole has attained a length of about 40 mm.

Fig. 1 is a horizontal section of the eye of a tadpole 10 mm. long, in which the fibres of the optic nerve can be seen along the whole length of the optic stalk, and for a short distance into the brain. It is, however, not possible to trace them at this stage across to the opposite side of the brain. There is as yet no chiasma. The two indentations (*CH.*, *CH.*) are caused by the choroidal fissure.

From the end of the cleft nearest the brain the fibres of the optic nerve are seen issuing (*OP. N.*), and alongside the nerve, but quite separate from it, is the optic stalk (*OP. S.*), the lumen of which is continuous with the cavity of the primary optic vesicle at *C. OP. V.* In the next few sections fibres of the optic nerve can be traced into connection with those arising from cells within the retina, such as are seen at *N. F.*



Fig. 2 is a camera drawing of the optic stalk and nerve of the same tadpole, but of the left instead of the right side. In this figure the optic nerve and stalk, cut across at right angles to their longitudinal axes, are seen lying between the band of dense tissue (*TR. CR.*) and the brain (*BR.*).

The evidence here, again, is to prove the optic nerve to be entirely independent of the optic stalk, except that the two structures lie closely apposed to one another.

A section transverse to the longitudinal axis of the nerve-stalk, taken at any point between the eye and brain at this stage, would give a similar figure.

The cells of the wall of the stalk on the side on which the nerve lies are as large and in every way similar to those on the opposite side, whence it is impossible to maintain that the nerve-fibres are developed by the differentiation of the cells of the stalk in situ into nerve-fibres.

Fig. 3 shows the connection of the optic nerve and stalk with the brain.

On reaching the brain the stalk and nerve separate, the cavity of the optic stalk becoming continuous with the optic recess in the floor of the third ventricle, while the fibres of the optic nerve can be traced as far as the middle line across the great ventral commissure (*M. COM.*), but at this stage can be traced no further. In later stages (20 mm.) the fibres may be easily traced to the opposite side of the brain, and later (30—40 mm.) up into the optic lobe of the opposite side.

At the stage I have been describing the optic chiasma cannot be said to exist; or if some of the fibres have indeed crossed, they form such small bundles that they cannot be recognised.

Figs. 5, 6, 7 represent much earlier stages (tadpole, 7 mm.), by which time the nerve-fibres have just made their appearance, and figs. 8, 9, 10, 11 represent considerably older stages (tadpole, 23 mm.).

Figs. 5, 6, 7 are placed with their dorsal surfaces towards the top of the page, and are figures of sections taken close to the eye.

Figs. 1, 2, 3 are placed with their anterior surfaces towards

the top of the page, and are figures of sections taken close to the eye, midway between the eye and brain, and close to the brain, respectively.

Figs. 8, 9 are placed with their dorsal surfaces towards the top of the page, and are figures of sections taken close to the brain.

From a study of these figures it will be seen that the optic nerve lies at its retinal end ventral to the stalk; but as it nears its cerebral end it lies along the posterior border of the stalk, and even in later stages (fig. 8) lies almost dorsal to the stalk.

The history of the relation of the stalk to the nerve in later stages is as follows:—In tadpoles of 11—12 mm. the trabecula cranii cartilage growing up under the optic stalk and nerve causes the lumen of the stalk to become obliterated at that point, from which point the obliteration of the whole lumen gradually proceeds. The last part to remain open is the part nearest to the brain, which in tadpoles of 23 mm. is still open (fig. 8).

As the nerve-fibres increase in number they seem to tend to grow in between the cells of the walls of the stalk (fig. 9), and eventually (fig. 10) the walls of the stalk become completely broken up, and the cells remain separated from one another, and lie among the fibres of the optic nerve as in fig. 10. Fig. 11 is a longitudinal vertical section of the optic nerve of a 23 mm. tadpole. Very possibly this breaking of the optic stalk is caused not so much, if at all, by the nerve-fibres growing in amongst the cells, but primarily, by reason of increase in distance between the eye and brain, the stalk becomes stretched and broken up.

It might be argued that the nerve-fibres grow out of processes from the cells of the stalk, but of this there is no trace at any time. The cells of the stalk never show any processes, such as are easily and distinctly seen in the neuroblasts of the rest of the nervous system, and excepting a considerable diminution in size (which is common to almost all cells of all parts of the animal), the cells of the optic stalk of a 40 mm.

tadpole do not materially differ in shape or character from those of the tadpoles in which nerve-fibres have not yet appeared.

I cannot see that there can be the slightest doubt that the nerve-fibres of the optic nerve are developed from some part other than the optic stalk. Hence we are bound, I think, to conclude that the fibres must be outgrowths from cells in either the brain or in the retina.

### Origin of the Fibres of the Optic Nerve.

I believe that with the exception of Froriep's (7) researches mentioned at the beginning of this paper, and Keibel's (13) short statement, and of His's (12) expressions of opinion, there is no actual evidence published of the growth of the fibres along the optic stalk, either towards the brain or towards the eye.

His's (12) evidence, though perhaps not complete, is very strong, for he finds in human embryos of five weeks (13 mm.) the first trace of nerve-fibres in the retina as follows :

“Ich selber finde die ersten Nervenfasern der Retina bei menschlichen Embryonen von etwa 5 Wochen (13 mm.). Zu der Zeit zeigt die Retina an ihrer Innerseite ein von den Müllerschen Fasern durchzogenes weites Raumsystem. Die Fasern bilden eine erst dünne, scharf auslaufende Schicht, und sie treten unter spitzen Winkeln aus der austossenden Zellenlage hervor. Hier liegen kleine retortförmig gestaltete Neuroblasten, die mit ihren umgebogenen Spitzen in die Fasern sich fortsetzen. Die zuerst gebildeten Opticus fasern entstammen somit den Zellen der Retina und wachsen centralwärts. In die inneren Körnschicht dagegen finden sich zahlreiche Neuroblasten welche ihre Spitzen nach auswärts behren.”

All three authors, however, agree that the growth of the nerve-fibres is from the eye to the brain.

In support of their views I may add the result of my own observations on the frog.

Before explaining my figures on this point I must mention the beautiful work of Cajal (3).

The author, who made use of the Golgi and Weigert-Pal method, describes the result of his observations on the optic lobes of adult birds and of advanced embryos, amongst which were chicks of the tenth day of incubation and upwards.

Cajal finds that the great majority of the fibres of the optic nerve end in the optic lobes, in many fine-branched twig-like endings, but in no case do these endings anastomose or become directly connected with nerve-cells.

In an earlier paper (4) he described the termination of the nerve-fibres in the retina as of two kinds. I quote from the first-named paper (3), in which he on p. 338 gives a short account of his previous work :

“ Dans cette membrane les fibres du nerf optique se terminent de deux façons ; par les cellules, c'est à dire, se continuant avec les cylindres-axes des éléments de la couche ganglionnaire, et par des ramilles variqueuses et indépendentes situées à la rencontre des couches réticulaire interne et des grains internes. De ces deux espèces de terminaisons, seules les dernières peuvent ainsi se qualifier, car les premières ne sont point de véritables terminaisons, mais plutôt des origines de fibres dont la fin arborisée doit se trouver dans le lobe optique. Si la doctrine de l'indépendance des éléments nerveux est certaine, le lobe optique devra nous montrer, de même que la rétine, des cellules d'origine, et des arborisations terminales.”

Cajal (3), in what he calls the tenth layer (couche 10, equivalent to the ninth granular layer of Stieda [24] and fifth zone or zone fusiform cells of Bellonci [2]), finds cells of an ovoid or spherical shape with a protoplasmic expansion running inwards and outwards. The inward or inferior one seems to end quickly, while the outer or superior runs outwards as far as the layer of fibres of the optic nerve. From the latter process arises an axis-cylinder which enters the layer of optic nerve-fibres—couche 1 of Cajal. With reference to these cells, and fibres arising from them, Cajal says on p. 248,—

“Comme nous venons de le voir ici déjà nous rencontrons les origines cellulaires de quelques fibres optiques lesquelles, d’après nos recherches sur le rétine des oiseaux pourraient bien être celles qui finissent dans la couche des grains internes par des arborisations libres, courtes et fortement variqueuses. Nous ignorons si, parmi les fibres du nerf optique, il en existent d’autres d’origine centrale.”

Hence it seems almost certain from the study of the adult condition, at any rate in birds, that the optic nerve is composed of two kinds: (1) those which have arisen from cells in the retina and have grown centralwards; (2) those which have arisen in the brain and grown outwards.

From a study of the development of the eye and optic nerve of *Rana temporaria*, I am convinced that at any rate a very large proportion of the nerve-fibres of the optic nerve arise as outgrowths of cells in that portion of the optic cup from which the retina will be formed, which processes grow centralwards at first along the ventral, then along the posterior border of the optic stalk, and entering the brain immediately posterior to the optic recess cross along the ventral surface of the middle commissure to the opposite side, where they turn dorsalwards and slightly backwards to the roof of the mid-brain.

In tadpoles of about 7 mm. in length, or a little earlier, the first trace of the optic nerve may be seen.

Many of the cells of the retinal portion of the optic cup may be seen to be pear-shaped, with their end drawn out into processes which are directed towards the centre of the optic cup.

It is not possible to follow the individual fibres, but all are directed towards the ventral rim of the optic cup, over which, at any rate, a large number pass and run along the ventral border of the optic stalk, some for a greater, others for a lesser distance.

Fig. 4 is from a sagittal section of a tadpole (of  $7\frac{1}{2}$  mm. in length), and therefore a section transverse to the longi-

tudinal axis of the optic stalk, taken at the point where the fibres are crossing the ventral lip of the optic cup.

It will be seen that the fibres pass through a cleft, or rather, I should say, the walls of the optic cup have grown up round the bundle of nerve-fibres since they passed over the rim, for there is no such apparent cleft before the fibres are developed. Fig. 5 is a section of the optic stalk from the same series as fig. 4, but taken between the eye and brain, close to the former. Here on the ventral border is seen the bundle of fibres, and the wall of the optic stalk is slightly bulged in along the line of the fibres. The bundle here is rather smaller than in fig. 5.

In fig. 6, which is also from the same series of sections, but taken nearer the brain, the bulging in of the optic stalk is not so marked, and the bundle of fibres considerably diminished in size. Between this section and the brain the fibres become less and less distinct, and in sections of the optic stalk close to the brain no trace of nerve-fibres can be seen (fig. 7). Such is the case in tadpoles of 7—8 mm. in length. In tadpoles of 8—9 mm. the nerve-fibres can be seen along the whole of the stalk.

In later stages fibres may be traced to the upper regions of the mid-brain, though of the actual terminations I have nothing to say. Possibly the appearance of concentric bands of white matter of a molecular appearance in the roof of the optic lobes is concomitant with the branching of the terminations of the fibres that have reached that part of the brain; but, as far as my own researches go, that is merely conjecture. These molecular layers are first visible in tadpoles of 17—20 mm. in length. I consider, however, that the fibres have reached the upper part of the optic lobes in younger tadpoles—those of 12—15 mm.

The optic fibres begin to grow as soon as those from any other part of the nervous system, and grow very rapidly. As the eye itself increases in size the bundle of fibres lying along the optic stalk increases also.

The fibres whose addition causes the increase in size of the

bundle arise as outgrowths from neuroblasts (fig. 13, *N.*, Plate XII) near the rim of the optic cup, for along this rim a constant proliferation of cells takes place as long as the eye increases in size.

Fig. 13 shows the main features in the structure of the retina of a tadpole of 13 mm., and is as far as possible a camera drawing.

Towards the centre of the cup the development of the retina is furthest advanced.

The two walls of the optic vesicle are closely approximated, and the originally inner wall is reduced to a single layer of pigmented cells (*P.*).

These pigmented cells are directly continuous with the walls of the optic stalk, and thereby with the epithelial lining of the neural tube. These cells represent the epidermic layer of the epiblast, so that from this part of the optic cup it will be seen that the nervous layer is entirely absent.

In the originally outer wall of the optic vesicle there are many cells derived from the nervous layer, and the epidermic cells are greatly elongated and to a certain extent branched, and form the supporting elements only of the retina.

The relation of these two parts is shown diagrammatically in fig. 12, which represents a rather earlier stage (tadpole, 9 mm.).

The further discussion as to the fate of the nervous and epidermic layers of epiblast I defer to a paper on the development of the central nervous system of the frog, on which I am at present engaged.

I think, however, that there is no doubt that the spongioblastic elements are all derived from the epidermic layer, and the neuroblastic from the nervous layer of the primitive epiblast.

To return to the section. Next to the pigment layer are seen the developing rods and cones. The former are more developed than the latter, and already their processes, which project into the cavity of the optic vesicle, show the division into inner and outer limbs.

Connected with the outer molecular layer are certain neuroblasts of the inner nuclear layer (*X*).

Among the cells of the outer nuclear layer are some with long, broad prolongations (*FR.*), the radial or Müllerian fibres of the adult.

These fibres are not easily traced to the "outer limiting membrane" in the centre of cup, but may be more easily seen towards the rims, where the rods and cones are not so crowded (*FR'*). Compare these with the cells marked *SP* in fig. 12.

Certain neuroblasts (*NI.*) of the inner nuclear layer seem to send processes into the inner molecular layer, but my observations do not enable me to say whether they break up into fibrils, or whether they pass through and on to the brain.

Within the inner molecular layer comes a double row of cells, the ganglionic layer. In many cases these cells are produced into short deeply staining processes towards the inner molecular layer, and break up at once into fine fibrils (*G.*).

The growth of these processes seems to be the prime cause of the appearance of the inner molecular layer.

These processes just described appear to be a later development than the process from the opposite pole, which forms a fibre of the optic nerve.

These are seen at *N*, near the rim of the cup, as thick black prolongations, while the other pole is still round, and shows as yet no signs of the processes described above, which form, at any rate in part, the inner molecular layer.

So also, if the other elements of the eye be traced through the section, it can be noticed that as they near the rim they are less and less differentiated, until they all merge into a mass of rapidly dividing cells, each one very like to his neighbour.

### The Choroidal Fissure.

At one point of the rim, however, there is no proliferation of cells, and therefore at this point the wall of the optic cup does not grow. This point is that over which the fibres from



the retinal neuroblasts pass on their way towards the brain (fig. 12, *CH*).

It is quite inaccurate to talk of the fibres of the optic nerve becoming connected with the elements of the inner or retinal wall of the cup after piercing the outer wall of pigment epithelium (Foster, 6), as the development shows that the fibres never really pierce either wall, but, from the moment of their first formation, they are on the outside of both. It is only by the subsequent growth of the rim of the optic cup that the bundle of nerve-fibres becomes surrounded by the walls of the cup, and so apparently pierces it. It does in reality pass over the edge of the cup, just as much as do the fibres in such an eye as that of *Pecten*.

It has been usual to regard the choroidal fissure as essentially an embryonic feature, present chiefly for the purpose of admitting mesoblastic tissues into the optic cup for the formation of and nourishment of the vitreous body, and to be due to the manner of invagination of the optic vesicle.

Some authors have recognised a further meaning in that the optic nerve is thereby brought into connection with the retina (v. Hertwig, 9, p. 404).

I have never, however, seen it suggested that the choroidal fissure represents a stage in the evolution of the eye, as seems to me more than probable, and that it was due entirely to the eye having a deep-seated cerebral origin, and having only subsequently grown towards the surface.

Whatever may have been the first origin of the eyes of Vertebrates, whether they arose, as has been suggested by Balfour (1), as patches of the epidermis sensitive to light, before the sinking down and folding up of the central nervous system, or whether, as Lankester (15, 16) suggested, they are derived from such an eye as that found within the cerebral vesicles of certain Ascidians, it is clear that they were of myelonic origin, and much more deeply placed than at present in adult Vertebrates.

In either case the light must have fallen directly upon the sensitive cell; that is to say, the light reached the eye from

the opposite direction to what it does in Vertebrate eyes of the present day.

That is to say, the light-perceiving portion of the sensory cell would be directed towards the cavity of the brain, and the transmitting portion or nerve-fibre towards the exterior, as indeed is the case in the larval Ascidian eye.

When we realise that the nerve-fibres of the present Vertebrate eye really pass over the edge of the cup, and do not—morphologically speaking—pierce it, we are able to imagine the probable steps in the evolution of the eye far more easily than otherwise.

It can hardly be supposed that such eyes perceived any image; it was merely a case of distinguishing light from dark. On the closure of the neural tube in the one case, or on the commencement of opacity in the other, and more light therefore reaching the light-sensitive cells from the opposite direction to that heretofore, any variation (1) which brought the sensory patch nearer the skin (origin of optic vesicle), (2) which brought the skin nearer the sensory patch, i. e. depression in the skin (origin of lens), would tend to be preserved.

As yet the eye would not be a cup, it would only become so in connection with the formation of the lens.

Round the depression in the skin the light-sensitive area might expand, and by the growth of its edges round the depression in the skin would form a cup.

While these changes were in progress the nerve-fibres having now to pass over one part of the edge of the area to reach their cerebral destination, would prevent the growth of the edge at that point, and consequently a gap would be left.

As soon as a lens was formed and an image thrown upon the retina, a gap would be disadvantageous to the perception of the image as well as to the retention of the vitreous body, which no doubt existed as early as the lens; but until such a time I do not see why a choroid fissure should not be a permanent feature; and indeed it seems to me that a consideration of the manner in which the Vertebrate eye was evolved almost necessitates the occurrence of a gap at a certain stage.

### Development of Optic Nerve in Chick.

I have followed also the development of the optic nerve in the chick, and find that the mode of development is essentially similar to that described above for the frog, *Rana temporaria*.

In chicks of four days thick nerve-fibres may be found in the retina, radiating towards and into the just beginning choroidal fissure, but can be traced no further. In five-day chicks the fibres are thinner, and can be easily traced into the choroidal fissure, but along the optic stalk near to the brain there is no trace of nerve-fibres.

In six days fibres can be traced all the way to the brain.

#### SUMMARY.

1. The optic stalk takes no part in the formation of the nervous parts of the organ of sight.

2. The optic stalk becomes broken down and the cells composing it separated from one another, partly by the mechanical stretching due to the growth of the optic nerve, partly by the growth in between the several cells of the nerve-fibres.

3. The optic nerve is developed independently of the optic stalk, the nerve-fibres lying along the posterior border of the stalk, and at first entirely outside it; but on the breaking down of the stalk some of the nerve-fibres grow in between the cells.

4. The great majority of fibres forming the optic nerve arise as outgrowths from nerve-cells in the retina, and grow towards and into the brain.

5. According to Cajal's researches certain fibres also exist which would seem to grow from the central nervous system to the retina, but these I have not been able to find.

6. The nerve-fibres pass over the ventral edge of the optic cup, and thereby cause the formation of the choroidal fissure.

7. The choroidal fissure of the embryo represents a condition in the evolution of the eye which was persistent in the adult prior to the formation of a lens.

It has only secondarily been made use of as a means of ingress for the mesoblastic tissues.

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## EXPLANATION OF PLATES XI & XII,

Illustrating Mr. Richard Assheton’s paper “On the Development of the Optic Nerve of Vertebrates and the Choroidal Fissure of Embryonic Life.”

### *Alphabetical List of Reference Letters for all the Figures.*

*BR.* Brain. *B. V.* Blood-vessel. *C.* Cone. *C. OP. V.* Cavity of the optic vesicle. *CH.* Choroid fissure. *CH’.* Choroid fissure, outer end. *D.* Growing rim of optic cup. *FR.* Radial fibres. *G.* Cells of the ganglionic layer of the retina. *L.* Lens. *L. C.* Cavity of lens. *M. COM.* Middle commissure. *MES.* Mesoblastic sheath round optic nerve and stalk. *MO.* Outer molecular layer. *N.* Neuroblast. *NI.* Inner nuclear layer. *OP. N.* Optic nerve. *OP. RC.* Optic recess. *OP. S.* Optic stalk. *OP. S’.* Cells of optic stalk separated. *P.* Pigment layer of retina, i. e. posterior wall of optic vesicle. *R.* Rods. *R. CH.* Edge of choroid fissure. *RS.* Rim of optic cup. *TR. CR.* Trabecula cranii. *X.* Neuroblast of inner nuclear layer.

FIG. 1.—Horizontal section of the right eye of a 10 mm. tadpole.

FIG. 2.—From a horizontal section of a 10 mm. tadpole. In this the optic stalk, *OP. S.*, and optic nerve, *OP. N.*, are cut across transversely to their length.

FIG. 3.—From a horizontal section of a 10 mm. tadpole. The optic nerve and optic stalk are seen separating at their junction with the brain.

FIG. 4.—From a sagittal section of a 7 mm. tadpole. The figure shows

the ventral edge of the posterior part of the eyeball; the optic nerve is seen passing through the choroidal fissure.

FIG. 5.—From the same series as Fig. 4, taken nearer to the brain. 7 mm. tadpole.

FIG. 6.—From the same series as Figs. 4 and 5, taken about midway between eye and brain, nearer to brain than Fig. 5. 7 mm. tadpole.

FIG. 7.—From the same series as Figs. 4, 5, and 6, taken still nearer to the brain.

FIG. 8.—From a sagittal section of a 23 mm. tadpole, taken near to the brain. Optic nerve and optic stalk cut transversely.

FIG. 9.—From a sagittal section of a 23 mm. tadpole, as Fig. 8.

FIG. 10.—Same as Figs. 8 and 9, but taken nearer to the eye.

FIG. 11.—From a transverse section of a 23 mm. tadpole. The optic nerve is cut "sagittally;" the cells of the broken-up optic stalk are seen scattered over it.

FIG. 12.—Semi-diagrammatic figure of a solid section of an eye of an 8 mm. tadpole. The optic nerve-fibres are seen on the cut surface to be processes of neuroblasts (blue). They pass over the ventral edge of the optic cup (the choroidal fissure). The edge of the choroidal fissure is seen at *R. CH*, the mosaic-like pattern being the pigment-cells of the hinder wall of the optic vesicle. The optic stalk is seen to be hollow, and quite separate from the optic nerve. The cells of the walls of the optic stalk pass into the pigmented cells of the outer wall, and the spongioblasts of the inner wall of the optic cup, *SP*. The blood-vessel which enters the optic cup is seen cut off at *B. V*.

FIG. 13.—A section of the retina of a 13 mm. tadpole. A description of this figure is given in the text. Prep. Perenyi's fluid; aniline blue-black.

## The Larva of *Asterias vulgaris*.

By

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With Plates XIII, XIV, and XV.

THIS work was undertaken at the suggestion of Professor W. K. Brooks for the purpose of getting, if possible, some further hint upon the significance of the larval form in Echinoderm phylogeny. It was carried on from October, 1889, to April, 1891; from June to October, 1890, at the Laboratory of the United States Fish Commission at Wood's Hall, Massachusetts, where the living animals were studied, and for the remainder of the time in the Biological Laboratory of the Johns Hopkins University, where the work was upon the preserved material. My heartiest acknowledgments are due to Professor Marshall McDonald, U.S. Fish Commissioner, for the advantages furnished at the Government Laboratory; and to Professor Brooks, of this university, who has so kindly placed at my service the preserved material, the preparations, and drawings, which formed the basis of his recent paper before the National Academy (4).

The material was obtained by means of the surface net, and was supplemented by that obtained by artificial fertilisation. The larvæ reared by the latter process were kept in glass beakers containing fronds of *Ulvaceæ*, which served both for aëration and by the liberation of zoospores furnished to some extent food for the developing larvæ. The larvæ were daily transferred with a pipette to beakers of fresh sea water. The

time most favorable for finding an abundance of sexually ripe starfish at Wood's Hall is the month of June and in early July. The larvæ are to be found in considerable numbers at the surface during June, July, and August. Those thus obtained were immediately examined, figured as live objects, and then killed separately and hardened for sectioning. All the stages of larval development have been studied (1) in the living condition; (2) as total preparations; (3) the results confirmed by sectioning. For killing I found that Kleinenberg's picric salt gave the most satisfactory results, particularly in the younger stages. Flemming's, followed by Merkel's fluid, gave excellent results, as did also Perenyi's fluid. Oil of cedar or of origanum proved most satisfactory for clearing.

OOGENESIS.—The ovary is a very large compound racemose gland, with a great number of spherical alveoli. When sexually mature it completely fills up the cavity of the arm. Its colour at this time is a delicate tint of salmon. In a cross-section of an alveolus is shown an external covering, the peritoneal membrane, consisting of a single layer of cubical cells (fig. 1, *p. e.*). Next, internal to this, is a muscular layer of considerable thickness (*m.*). This is made up of fibres running in every direction; the outer and inner parts, however, are made up chiefly of fibres running nearly at right angles to each other. Within this muscular layer, and lining the lumen of the alveolus, is the germinal epithelium (*g. e.*), showing cells in various stages antecedent to their separation to form ova. In the earlier stages the size of the nucleus is large in proportion to the cytoplasm, but later the cytoplasm increases very rapidly. In fig. 1 the lumen is completely filled with mature eggs, which have assumed various shapes from mutual pressure. The spaces between the ova are filled by branching cells and fibres of connective tissue. Each egg has a thin gelatinous external membrane, which upon contact with the water swells by imbibition to a considerable thickness.

The condition of the ovary a few weeks after the discharge of the eggs is shown in fig. 2. The lumen is seen to be traversed by the radiating branched cells, while the germinal



epithelium is very much thicker, and crowded with nuclei of various sizes, which will form the next crop of eggs.

SPERMATOGENESIS.—The testis (fig. 3) differs histologically from the ovary only in a less development of the muscular layer (*m.*) of its wall, and in the smaller size of the cells of the germinal epithelium (*g. e.*). These cells separate from the epithelium, and by the increase in size and final separation of the germinal epithelium-cells behind them are pushed towards the centre of the lumen. These separated cells are the sperm mother-cells of the spermatozoa (fig. 3, *s. m. c.*). Their diameter is many times less than that of the ova at a corresponding stage. Each sperm mother-cell, in its progress towards the centre of the lumen, divides into two smaller cells. In the further progress towards the centre of the lumen each of these smaller cells divides again into two. Thus from the sperm mother-cells are formed four very small cells (fig. 3, *sp.*), each of which, without further division, is directly changed into the form characteristic of the spermatozoon. Each sperm mother-cell gives rise to four spermatozoa, and not to a large or indefinite number. The entire sperm mother-cell apparently passes into the four spermatozoa, with no traces of the "residual corpuscles" supposed to be the homologues of the polar bodies. This fact is of interest when compared with Hertwig's recent results upon *Ascaris* (15).

CLEAVAGE.—The facts of the process of maturation, fertilisation, and cleavage have been carefully studied by others. Sufficient here to add that, as in many other groups, the four cells arising by the first two divisions become pressed together, so that two have their apices directed towards the centre, truncated, so to speak, while the other two have sharp points; and the arrangement is such that the two opposite cells are alike, while the two adjacent cells are unlike.

The plane of bilateral symmetry is plainly indicated in the 8-cell stage (fig. 4). In the 16-cell stage the difference in size between the cells of the ectodermal and entodermal area is conspicuous (fig. 5). Throughout the process of cleavage I watched carefully for some particular cell to which the origin

of the mesenchyme could be referred, but with negative results.

**MESENCHYME FORMATION.**—About twelve hours after fertilisation cleavage is completed, and results in a ciliated cœloblastula, which spins around within the egg membrane; soon by the rupture of the egg membrane the blastula becomes free-swimming, and immediately seeks the surface of the water. Then appear the first traces of mesenchyme formation. In the region of the more columnar cells, the future entoderm, one and then more cells push out into the segmentation cavity, and become amœboid mesenchyme-cells. Usually the entire cell pushes out from the entoderm, but frequently there is a transverse division, and only the inner half becomes amœboid (fig. 6). Somewhat later this portion of the sphere becomes flattened (fig. 7) and is gradually invaginated. During the progress of the invagination amœboid mesenchyme-cells in great numbers wander into the segmentation cavity from the walls of the invaginated portion (fig. 8); some of these amœboid cells are formed by division of the entoderm-cells as above described, while the majority are in no way distinguishable from the cells which remain as the permanent entoderm. The stage where only one, two, or three mesenchyme-cells are present is quickly followed by the appearance of others which arise from any part whatever of the entodermal area (figs. 6, 7, and 8), and I am led to believe that the condition in *Asterias vulgaris* is the same as that found by Metschnikoff, and by Korschelt (21) in other Echinoderms, i. e. the absence of two bilaterally symmetrical "Urmesenchymezellen"—a view in opposition to that of Hatschek, Selenka, and Fleischmann.

My observations on *Asterias vulgaris* in regard to the time of the beginning of mesenchyme formation relatively to the process of gastrulation differ from those of Metschnikoff in *Astropecten*, inasmuch as I find that the mesenchyme formation precedes and continues throughout the progress of the invagination. No traces were found of the bilaterally symmetrical rows of cells comparable to the mesoblastic

bands of Annelids, as described in other Echinoderms by Hatschek, Selenka, and Fleischmann. As the invagination progresses the spherical form of the larva changes to ovoid, the long axis corresponding with the antero-posterior axis of the future Bipinnaria. The gastrula travels through the water with two motions, one of translation in the line of the long axis of the body, the blastopore directed forwards; the other of rotation around this axis. At the completion of invagination the gastrula is much elongated (fig. 9). The archenteron, extending backwards about two thirds of the length of the embryo, is somewhat tubular in form; its blind end is bent towards that side which later proves to be the dorsal surface of the Bipinnaria. At this blind end is a considerable enlargement, where the cells by becoming flattened and losing their cilia acquire a character different from the columnar ciliated cells of the rest of the archenteron.

In section the ectoderm-cells are seen to be flatter and smaller than those of the entoderm, but the one grades insensibly into the other (fig. 9). At the pole opposite the blastopore is a point where the cells are distinctly more columnar than in any other part of the ectoderm. This point is found to become the apical pole of the Bipinnaria (fig. 9, *a. p.*).

FORMATION OF THE ENTEROCÆLS.—The mesoderm in *Asterias* as in most other Echinoderms has a twofold origin, though morphologically a sharp distinction between them in this case is not to be made: (1) mesenchyme formation; (2) enterocœl formation. The enterocœls arise as two bilaterally symmetrical diverticula of the blind end of the archenteron (fig. 10, *et.*). In position they are lateral and slightly dorsal. The time of complete separation shows much individual variation, in some cases being complete before, in others just after the formation of the larval œsophagus. A. Agassiz (2), working upon *Asterias vulgaris*, found that the stomodæal invagination united with the archenteron before the enterocœls separated from the latter. Metschnikoff (26) agrees with this, as does also Götte (10) for *Asterias glacialis*. Ludwig (25) says, "In most Echinoderms the separation of

the enterocœls occurs before the formation of the larval mouth. Asterids form an exception. Still this condition occurs in some Asterids, e. g. *Asterina*." It would seem as if too much importance has hitherto been attached to this point, since it is subject to so much individual variation.

After separation from the archenteron the enterocœls increase slightly in size and move nearer to the dorsal wall of the larva, now appearing as ovoid vesicles with walls formed of flattened mesenchyme-like cells, which send out branching processes; these processes uniting with the branches of the mesenchyme-cells, which form an anastomosing network within the segmentation cavity, serve as supports for the enterocœls.

FORMATION OF THE WATER-PORES AND PORE CANALS.—Soon after the completion of the larval digestive tract by the fusion of the stomodæal ingrowth with the evaginated portion of the archenteron (fig. 11) begins the formation of the water-pores and the pore canal. On the dorsal wall of the enterocœl a diverticulum is formed. The cells of this diverticulum take on a cubical form; the cells of the rest of the enterocœl wall retain the flattened branching appearance characteristic of mesenchyme (fig. 16). Above this upward projection of the enterocœl wall there appears a proliferation of the dorsal ectoderm. This as a solid plug extends downwards, meets, and fuses with the upward projection of the enterocœl; a cavity becomes formed in this ectodermal portion, and through it the cavity of the enterocœl is put in communication with the exterior. In this manner a right and a left water-pore and pore canal are formed. The walls of the pore canal are formed of columnar cells, which become ciliated. The pore canal is thus found to be made up of mesodermal and ectodermal elements. These observations are very unlike those described by Bury in his account of the mode of formation of the pore canal and water-pore in another Echinoderm. He says, "Examination of the living animal under a very high power shows that this pore is formed by a single elongated cell, perforated throughout its length and lined with cilia" (5,

p. 411). The condition above described, having two bilaterally symmetrical water-pores, is found in larvæ three and a half to four and a half days old (Pl. XIV, figs. 14 and 23). In a short time (eight to twelve hours after formation of the pores) the ectoderm pushes together, closing the external opening of the right water-tube; but the rest of the tube persists for some time, retaining its characteristic appearance. Fig. 19 is one of a series of sections of the larva at the stage after the closure of the right water-pore, but with the pore canal still present. In the sections succeeding the one here figured the water-tube of the right side (*w. t.*) was seen to end blindly. These observations were all made upon the living larvæ and confirmed by sections.

The presence of a right and a left water-pore has been noticed by several Continental investigators, but has been by them set aside as pathological. There is reason to believe, however, that this is a true ontogenetic character, and of very considerable phylogenetic significance. In figs. 21 and 22 I have drawn two sections of a series made by Professor Brooks, showing the bilaterally symmetrical water-pores and pore canals found by him in several larvæ of the same stage as that figured in side view in fig. 14, and in dorsal view in fig. 23. The specimens shown in section (figs. 21 and 22) were taken in the surface collections at Wood's Hall. The sections are cut in a plane nearly parallel with the dorsal surface of the larva. In fig. 22 the section is seen to pass through the postoral and the preoral regions. In the postoral part are seen the two water-tubes cut transversely (*w. t.*). In fig. 21 only the postoral part is figured. The section passes through the water-pores (*w. p.*). Figs. 14 and 23 are drawn from living specimens obtained by artificial fertilisation. Specimens with two water-pores can be found in considerable numbers among larvæ three and a half to four and a half days old; but normally two water-pores are not present in larvæ after that age. In examining a number of larvæ of that age we could not expect to find a very large percentage with two water-pores, firstly on account of the individual variation in rate of

development, and secondly on account of the briefness of the time in which both pores are functional. However, a number having two water-pores were isolated, and upon subsequent examination of these the right pore was found to have closed, while in two instances the process was observed.

But these facts, taken with the finding in the surface collections of several undoubtedly normal individuals of a similar age with two bilaterally symmetrical water-pores and water-tubes (in one specimen the water-pore on the right side was found to be obliterated, though the pore canal still persisted), and the exceeding rarity of older larvæ with two water-pores, lead to the belief that this stage is a definite one in the ontogeny, and not a pathological condition, as has hitherto been assumed by the Continental students.

#### FORMATION OF THE CILIATED BANDS.

Circumoral Band.—From the time of the completion of the segmentation until the formation of the larval digestive tract, all the cells of the surface, of the œsophagus, and intestine are ciliated. These cilia serve for locomotion, and for propelling water through the digestive tract. But very early this condition of general ciliation gives way to the restriction of the cilia to definite band-like areas. Often even before the completion of the œsophagus the ectodermal cells of the ventral surface become flattened, and lose their cilia. There are left, however, two narrow transversely extending ciliated areas projecting slightly above the surface, one upon the bulging portion of the body anterior to the mouth, the other posterior, between the mouth and anus (see fig. 13, *c. o. b.*). As the area where the cilia have disappeared extends dorsally these two bands lengthen, the postoral one being of greater length. The original body cilia disappear last at the apex of the preoral lobe. Fig. 11, Pl. XIII, shows a stage where the end of the two parts of the ciliated bands pass into this remnant of the original general ciliation. Later, by the further disappearance of the original cilia the two ends of the preoral portion unite with the corresponding ends of the postoral


portion, thus forming a single continuous bilaterally symmetrical ciliated band, by Semon named the circumoral band. The course of this band is shown in figs. 12 and 14, *c. o. b.* Whether the two legs of the band touch, fuse, or remain separated at the apex of the preoral lobe is somewhat difficult to determine. Semon in *Asterias rubens* finds that they touch; in *Asterias vulgaris* I am inclined to believe that they are separated (see figs. 23 and 25).

At the apex of the preoral lobe (fig. 15) the ectoderm-cells are elongated over a small area. The outer part of the cell is clearer with fine granules, while at the base of the cells are what appear to be the cut ends of fibres, suggesting nerve-fibres. This may possibly be regarded as a very simple apical plate. It is the same as that referred to above in case of the gastrula (fig. 9). The direction of locomotion has become reversed. At first the blastopore was directed forwards; now the blastopore has become the larval anus, and is near the posterior end. The reversal of direction in locomotion takes place at the time of the formation of the mouth.

**Adoral Band.**—At first the entire surface of the larval œsophagus is ciliated. The first trace of that ciliated band immediately surrounding the mouth and sending a loop into the œsophagus, called by Semon the adoral band, is a thickened circular ring of ectoderm closely surrounding the mouth opening (fig. 12, *a. o. b.*). Later, with the formation of the depression of the body-wall around the mouth the circumference of this ring increases, and is seen to surround the rim of this oral depression (fig. 17, *a. o. b.*). It is to be noticed that up to this time there is no connection whatever between the circumoral and this adoral ciliated band. But later the transverse preoral portion of the circumoral band becomes pushed towards the hinder end of the larva, and finally vaults over the oral depression, and almost covers the mouth (figs. 24 and 30, *c. o. b.*). In this way the anterior part of the adoral band comes to touch and fuse with the posterior transverse preoral portion of the circumoral band. Thus the connection between these two bands is secondary, and not primary as was

at first supposed by Semon in his earlier work (36), but corrected in his recent paper (38).

The cilia of the œsophagus are found to disappear except over a certain area, forming a loop-shaped ciliated band extending posteriorly and ventrally into the œsophagus, with its anterior end in connection with the above-described ciliated band bounding the rim of the oral depression, and with this circular band constituting the adoral ciliated band.

Now to return to a further consideration of the circumoral band. How does this band, at first single and continuous (fig. 14), reach the condition shown in figs. 24, 30, and 29, the condition characteristic of the Bipinnaria? The change occurs in the six days old larva. The original single bilaterally symmetrical circumoral ciliated band (fig. 14, *c. o. b.*) by a transverse division at the apex of the preoral lobe of the ) (shaped portion, and by fusion of the divided ends takes a  form; so that a plane passing between the links of the band, after the division and subsequent fusion of the broken ends, lies at right angles to its first position. At first perpendicular to the dorsal and ventral surfaces of the larva, it is after the division parallel with them (figs. 25 and 26). There are thus formed from this single band two complete bands: the upper (see fig. 26) bounds the dorsal and postoral area; while the lower (*p. v. a.*) comes to lie entirely upon the ventral surface, bounding the preoral ventral area (fig. 30, *p. v. a.*). The whole history of the ciliated bands can be followed in figs. 13, 11, 12, 14, 23, 25 and 26, 24, 30, and 29.

By this division of the original single circumoral band into the two ciliated bands characteristic of the Bipinnaria ontogenetic proof is given, as pointed out by Semon (38), of the correctness of Gegenbaur's hypothesis that the two ciliated bands of the Bipinnaria are equivalent to the single band of the Auricularia (see Balfour's 'Embryology,' vol. i, pp. 554 and 557). Semon calls the stage with the single bilaterally symmetrical ciliated band the Auricularia stage of the Bipinnaria.

The ciliated bands in cross-section (fig. 34, *c.o.b.*) show a



distinctly marked difference from the rest of the ectoderm. In the young larva all the ectodermal cells are cubical and ciliated; with the loss of the general ciliation the ectodermal cells become flattened and more irregular in outline, except in the region where the cilia persist as the ciliated bands. Here a great change has taken place. The cells become very much crowded together. The nuclei appear to be restricted to the deeper part, while the external part is formed of granular or finely fibrillated substance. The external surface is thickly ciliated, with many cilia on the free surface of each cell.

FURTHER HISTORY OF THE ENTEROCÆLS.—The appearance of a larva six days old, seen from the dorsal side, is shown in fig. 20. The anus no longer has a terminal position (fig. 11), but by the bending of the intestine it has come to lie some distance forwards upon the ventral surface. The œsophagus, formed by the union of an entodermal evagination of the archenteron with the stomodæal ingrowth of the ectoderm (fig. 11), has elongated somewhat. The oral depression has become more pronounced, and the circumoral ciliated band has become divided at the apical pole, in the manner described above, into the two bands which characterise the Bipinnaria. Before this time the enterocœls have elongated somewhat. The right water-pore has disappeared, and only the left enterocœl has an opening to the exterior. At a considerably later stage (fig. 30) the enterocœls have extended anteriorly as two cylindrical tubes, nearly parallel and slightly dorsal to the œsophagus. The anterior end of the tube is solid, and its tip is formed of branching mesenchyme-like cells. Posterior to this the walls are thin, and formed of flattened cells and mesenchymatous muscle-fibres (fig. 32). In a stage a little older than fig. 30 (fig. 28) these two cylindrical tubes have extended further forwards and into the preoral lobe. The right and left enterocœls have united just in front and dorsal to the mouth. At the point of union the tubes are still solid (fig. 33). At a little later stage the cavities have united, and the two enterocœls stand in open communication with each other by their union in the preoral lobe. They later grow

forwards and increase in size until they almost completely fill the cavity of the preoral lobe (figs. 24 and 29, *el.*). The appearance of the enterocœls in cross-section is shown in fig. 34, *el.*

Meantime the posterior ends of these cylindrical tubes have extended backwards and also dorsally and ventrally, so that they come to overlies the stomach and intestine. Ventrally and posteriorly the right and left enterocœls fuse together. On the left side, just posterior to the pore canal, there early appears a constriction (fig. 18, *x*) which finally narrows and separates the left enterocœl into two parts; the anterior, opening to the exterior at its posterior end by the pore canal and water-pore, extends forwards into the preoral lobe, where its cavity communicates with the right enterocœl, and the posterior part, the left posterior enterocœl, whose cavity is ventrally in connection with the posterior part of the right enterocœl. In the case of the right enterocœl I have often noticed a constriction, but have never found it divided into an anterior and a posterior portion as is the left enterocœl. In studying the living animal it should be noticed that the walls of the enterocœl are contractile, and that a temporary constriction may occur at almost any point. Fig. 18 is a diagram made from a reconstruction of a series of transverse sections of a larva. The outline of the left enterocœl (*el.*), previous to its division into the anterior and posterior enterocœls, is marked by the dotted line. It does not show the posterior ventral fusion between the right and left enterocœls. The hydrocœl has not yet formed.

#### FURTHER HISTORY OF THE MESENCHYME.

The amœboid cells arising from the entodermic area press into the segmentation cavity. This cavity is filled with a transparent, jelly-like substance, and in this the mesenchyme-cells, by their long, delicate, anastomosing processes, form a network which serves for supporting the archenteron and the enterocœls. Mesenchyme-cells apply themselves to the walls of the body, of the digestive tract, and of the enterocœls, and

there flatten and form a discontinuous covering for these organs. These mesenchyme-cells, in the later history of the larva, become differentiated into small fibres, which function as muscle-fibres. This differentiation takes place very early upon the walls of the entodermic portion of the œsophagus, where they form a circular and a longitudinal layer. The gulping movements brought about through the agency of these œsophageal muscles are very violent, and take place at intervals of fifteen to twenty seconds. A contraction starting behind the mouth travels towards the stomach, accompanied by a simultaneous longitudinal contraction of the œsophagus. As the final act the end of the œsophagus at its union with the stomach is violently pushed into the latter, and the contents of the œsophagus, driven down in front of the circular constriction, are suddenly belched into the stomach.

Differentiation of the mesenchyme-cells into muscle-fibres also takes place in the walls of the enterocœls, but no very definite layers were made out.

On the inner surface of the dorsal wall of the young Bipinnaria mesenchymatous muscle-cells and fibres are seen extending from the dorso-lateral portion above the stomach forwards along the median line (figs. 14 and 23, *m. m.*). These fibres have probably to do with the very considerable motion of which the preoral lobe is capable; the motion is in a dorso-ventral direction, and is accompanied by the formation of two or more wrinkles of the dorsal surface at the narrow part of the body of the larva. These fibres I judge to be the same as those described by Semon (38) as bilaterally arranged masses connected by a single commissure, and which he seems a little inclined to consider as a part or the whole of the larval nervous system, though he speaks of the possibility of their being muscular in function. However, the fact that they arise from mesenchyme-cells makes for the view that they are muscular tissue.

In the older larva (fig. 24) there is a small aggregation of mesenchyme-cells, in the main posterior to and just to the right of the pore canal. Its position is shown in fig. 18 (*s. v.*).

At the earliest stage in which I have yet found this it is close to the mesenchymatous lining of the body-wall; whether it arises from the lining of the wall or not I cannot yet positively say. Later a lumen is formed in the midst, and by the increase of the lumen the cells of the wall become flattened. The earliest stage which I have yet seen is shown in fig. 34, *s. v.* Successive stages in the growth are shown in figs. 27 and 31. In a Bipinnaria like fig. 29 the schizocœl vesicle, figured in fig. 31, measured .04 mm. in its antero-posterior diameter. Of the ultimate fate of this schizocœl, or of its identification with the schizocœls hitherto described, I am not certain.

#### GENERAL CONSIDERATIONS.

Morphological opinions upon the significance of the larval form of the Echinoderms fall into two diametrically opposite classes: (1) that the larval form has been cœnogenetically acquired, or (2) that it is ancestral in character.

The arguments which make for the former are chiefly based upon the necessity for better means of distribution, and in the free-swimming larval form is found a means secondarily acquired for the purpose of effecting this distribution. This view necessarily presupposes that the ancestor of the Echinoderms was sedentary; but this fundamental supposition does not seem to be well grounded. Even though the ancestors of the Crinoids appearing in the Cambrian seem geologically to be oldest, it by no means follows that we find in palæontology a correct phylogenetic record. From the nature of the case, too, we could gain from palæontology little knowledge of the phylogenetic stages previous to the time when the hard calcareous skeletal parts appeared, and these skeletal parts are seen to be structures which have undergone exceedingly great cœnogenetic modifications. Palæontology, therefore, far from giving us a record of the phylogenetic series of ancestral forms, furnishes little more than a history of the skeletal parts of some of the later descendants. No transitional adult forms uniting the Echinoderms with the other animal groups are known; as a group they stand widely iso-

lated. Even the numerous attempts to unite them with the other classes through the agency of larval forms have been more or less unsatisfactory.

We are asked to believe that in the life-history a form has been secondarily interpolated for the purpose of securing a wider distribution through a prolongation of the free-swimming condition. There is no doubt but that many characters of the larva are cœnogenetic modifications, but these are of little importance when compared with those which appear to be ancestral. (1) The cleavage, total and very nearly equal, and the ciliated cœloblastula, offer simple ancestral conditions, and furnish means at the same time for wide distribution. (2) The mode of mesenchyme formation found in the Echinoderms is probably more primitive than the formation of the third germinal layer in the form of mesoblastic bands; and the derivation of this middle layer from any part whatever of the entoderm is antecedent to that condition where it is restricted to two special cells, the mesoblasts. The nature of the mesenchyme, too, filling up the cleavage cavity with its network of branching cells, is evidence of its primitive character. (3) The formation of enterocœls by archenteric diverticula is characteristic of ancestral forms. And in this larva we find this simplest condition of complete separation of enterocœls and archenteron, passing directly into corresponding parts of the adult. (4) The enterocœls open to the exterior very early by definite pores. The presence of two bilaterally symmetrical water-pores at a certain stage in the ontogeny, and the subsequent disappearance of the right pore, seems to point distinctly to the ancestral significance of the larval form; for we are not justified in supposing that such a character is newly acquired, but that it is ancestral, as Professor Brooks has pointed out (4). It can only be in course of elimination from the ontogeny. The cause of this disappearance of the right pore may be traced to the subsequent connection between the two enterocœls by fusion in the preoral lobe. (5) The formation of the pore canals from ectodermal and mesodermal elements is similar to the condition

described for the nephridia of certain worms, e. g. by Bergh for *Criodrilus*. From the simple conditions in the formation of the mesodermal elements above described is justified the belief that the condition here found is phylogenetically antecedent to that of the Annelids.

The function of the water-pore is difficult to determine. That its function in the adult as the stone canal is excretory is claimed by Hartog (19), but opposed by Cuénot and H. Ludwig. Bury saw exhalent currents but never inhalent, though, as he says, this does not prove that there are not inhalent currents. He found that the movements of the cilia are in such a direction as to cause an exhalent current. From Bury's observations, and by elimination, one is almost forced to ascribe to it, at least in the larva, the excretory function, though in the adult this may be obscured by other functions; and the pore canal and water-pore of the Echinoderm larva seem in many ways to be comparable to the nephridia of Annelids, and to be ancestral in character.

The Echinoderm larva is a form which has developed along the phylogenetic line, and is in many ways differentiated and capable of free existence—an animal with a well-differentiated digestive tract, and having locomotor apparatus, enterocoels, excretory system, and well provided for respiration; to these have been cœnogenetically added transparency as a protective adaptation, and the formation of long arms for protection, but primarily as a means of increased locomotor powers. The great length of the arms has probably been acquired since the time when the metamorphosis began to be accelerated by its earlier beginning; i. e. originally metamorphosis did not begin until after the larva had become fixed to some support, but secondarily the beginning has been pushed forward, so that it now occurs long before fixation. The long arm-like projections of the larva are to be explained through the necessity for increased powers of locomotion on account of the weight of the adult starfish developing in the hinder end of the larva. But the greatest of the cœnogenetic modifications is that whereby the typical larva acquires the dif-

ferent forms characteristic of the various groups—the larval form distinguished as *Auricularia*, *Bipinnaria*, and *Pluteus*. The fact that all these forms are modifications of a single typical form was long ago pointed out by Johannes Müller. The recent work by Semon (38) has completed the confirmation.

It seems pretty certain that the radial symmetry of the Echinoderms has been derived from bilateral symmetry through the influence of a sedentary mode of life. May we not be justified in supposing that such an animal as the typical Echinoderm larva above described may upon becoming sedentary have been modified in adaptation to its mode of life, even so much as now appears between such a larva and an adult Echinoderm, and that the process of change as now shown in the metamorphosis is in its general character an expression of the course of phylogeny, but subjected to exceedingly great distortion by the constant tendency towards abbreviation, by the dropping out of details from the ontogeny, and by greater or less shifting of the relative times of formation of the various organs, particularly in the time of appearance of radial symmetry, which has been constantly carried forward to earlier appearance in the ontogeny. After assuming the sedentary condition there came in as further adaptive modifications changes in the function of organs. The greatest of these changes concerns the enterocœls; to their earlier function, probably excretory, has been secondarily added that of locomotion, of relation (feelers, tentacles), and also to some extent of respiration.

It seems more probable that the ancestral Echinoderm arose by the adaptive modification of a more primitive free-swimming form than that a larval form has been acquired for the purpose of distribution. The Echinoderm ancestor was probably a free-swimming animal, in general characters not far removed from the ancestors of the Turbellarians; a creature with a well-differentiated digestive tract, ciliary locomotor apparatus, excretory system, respiratory surface not localised; cœnogenetically modified by the acquirement of transparency,

long arms, and particularly by modification of the external form by changes in the direction of the ciliated bands, as pointed out by Johannes Müller, into the forms characteristic for the various Echinoderm groups. In their ontogeny the Auricularia and the Bipinnaria have travelled together for some distance, as shown by the fact lately pointed out by Semon (38) that the Bipinnaria passes through an Auricularia stage. We may suppose that the bilateral form after a period of free-swimming life became sedentary, and after this the bilateral symmetry became more or less disguised by a radial symmetry. From this sedentary form, the Pentactea of Semon, the ancestors of the present Echinoderm groups have been derived. The earliest arising were the Synaptidæ through some archaic form; next came off the ancestors of the Holothurians, and later the ancestors of the Crinoids, and latest the ancestor of the Echinids, Ophiurids, and Asterids. We are certainly justified in applying to the tentative theory of Echinoderm phylogeny the principles which are accepted in attempts to trace the phylogeny of other classes, namely, that it is not to be expected that many of the ancestral forms connecting the groups are to-day accessible for study, either alive or as fossils; and in view of the failure of the numerous and carefully formulated theories of Echinoderm descent it seems necessary to believe that the various groups were derived from one another only through intermediate forms between each group, which forms, however, probably persisted but a comparatively short time, and palæontological evidence of them is very scanty, or in the vast majority of cases entirely wanting. The corresponding stages, too, have been for the most part eliminated from the ontogeny.

The groups of the Echinids, Ophiurids, and Asterids, and a part of the Holothurids have been cœnogenetically modified for a creeping life, the original excretory system assuming the locomotor in addition to the earlier acquired sensory and respiratory functions. The early appearance of radial symmetry in the free-swimming larva shown in the radial out-pushings of the hydrocœl wall at that stage of the ontogeny



generally spoken of as the beginning of metamorphosis may be regarded as cœnogenetic precocious formation for the purpose of shortening the metamorphosis. Examples of further abbreviation of the metamorphosis are found in the case of the so-called viviparous Echinoderms, where it is carried to an extreme degree.

JOHNS HOPKINS UNIVERSITY;  
May 1, 1891.

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## EXPLANATION OF PLATES XIII, XIV, & XV,

Illustrating Mr. George W. Field's paper on “The Larva of *Asterias vulgaris*.”

### *List of Reference Letters.*

*a.* Anterior. *an.* Anus. *ap.* Apical plate. *ar.* Archenteron. *a. o. b.* Adoral ciliated band. *b. c.* Branched cells. *bl.* Blastopore. *c. t.* Connective tissue. *c. o. b.* Circumoral ciliated band. *d.* Dorsal. *E<sup>1</sup>.* Median anal-paired arm. *E<sup>2</sup>.* Dorsal anal-paired arm. *E<sup>3</sup>.* Ventral anal-paired arm. *E<sup>4</sup>.* Dorsal oral-paired arm. *E<sup>5</sup>.* Ventral oral-paired arm. *E<sup>6</sup>.* Unpaired anterior arm. *Ec.* Ectoderm. *El.* Enterocœl. *ge.* Germinal epithelium. *int.* Intestine. *m.* Muscle. *mes.* Mesenchyme. *m. m.* Mesenchymatous muscle-fibres. *mo.* Mouth. *n.* Nucleus. *O.* Ovum. *o. d.* Oral depression. *æ.* Œsophagus. *p.* Posterior. *p. b.* Polar bodies. *p. c.* Pore canal. *pe.* Peritoneum. *p. l.* Preoral lobe. *p. v. a.* Preoral ventral area. *sh.* Stomach.

*s. m. c.* Sperm mother-cell. *sp.* Spermatozoa. *st.* Stomodæum. *s. v.* Schizocœl vesicle. *v.* Ventral. *v. d. a.* Ventro-dorsal area. *w. p.* Water-pore. *w. t.* Water-tube.

All the figures are camera drawings except Fig. 18, which is a diagram of a reconstruction from serial transverse sections; and Figs. 25 and 26, which are not drawn to scale.

### PLATE XIII.

FIG. 1.—Cross-section of an alveolus of the ovary; the eggs are nearly ready to be discharged. Only one half of the section is figured. Perenyi; Mayer's cochineal preparation.  $\times 145$ .

FIG. 2.—Cross-section of an alveolus of the ovary after discharge of the eggs. Perenyi; alcoholic borax-carmine preparation.  $\times 145$ .

FIG. 3.—Cross-section of an alveolus of the testis. Only a small segment is drawn. The oval cells near the centre (*sp.*), directly without farther division, become changed into the shape characteristic of the spermatozoa. Perenyi; Kleinenberg's hæmatoxylin preparation.  $\times 1000$ .

FIG. 4.—Egg in eight-celled stage, showing the bilaterally symmetrical division into a right and a left half.  $\times 400$ .

FIG. 5.—An egg in sixteen-celled stage, showing the relative size of ectoderm and entoderm cells at this time. Perenyi; Kleinenberg's hæmatoxylin preparation.  $\times 400$ .

FIG. 6.—Optical section of living blastula soon after its escape from the egg-membrane, showing first appearance of mesenchyme-cells.  $\times 240$ .

FIG. 7.—Same at beginning of invagination.

FIG. 8.—Mesenchyme formation during the progressing invagination. Optical section of living animal.  $\times 240$ .

FIG. 9.—Longitudinal section of completed gastrula. Perenyi; Kleinenberg's hæmatoxylin preparation.  $\times 240$ .

FIG. 10.—Optical section of the living gastrula, looking down somewhat obliquely upon the blind end of the archenteron, to show the formation and relation of the enterocœls.  $\times 400$ .

FIG. 11.—Living specimen, seen from the right side; to show the mode of formation of digestive tract and of the circumoral ciliated band.  $\times 70$ .

FIG. 12.—Young larva, seen in ventral view, showing the original relation of the adoral (*a. o. b.*) and the circumoral (*c. o. b.*) ciliated bands. Picric salt; Delafeld's hæmatoxylin preparation.  $\times 110$ .

## PLATE XIV.

FIG. 13.—Showing manner of formation of the ciliated band by the disappearance of the general ciliation. The dotted portions represent the ciliated areas. Living specimen.  $\times 240$ .

FIG. 14.—Larva four days old, seen from the right side, showing the right water-tube and pore. Kleinenberg's picric salt; Delafeld's hæmatoxylin preparation.  $\times 145$ .

FIG. 15.—Longitudinal section through the apex of the preoral lobe, to show the ectodermal thickening, *ap*. From a specimen of about the same age as Fig. 11. Perenyi; Kleinenberg's hæmatoxylin preparation.  $\times 600$ .

FIG. 16.—Section showing mode of formation of the water-pore and pore canal. Similar conditions were observed in the living specimens. Perenyi; Kleinenberg's hæmatoxylin preparation.  $\times 600$ .

FIG. 17.—Larva of five days, seen in ventral view to further show the history of the relation of the adoral band to the preoral portion of the circum-oral band, and the formation of the oral depression. Kleinenberg's picric salt; Delafeld's hæmatoxylin preparation.  $\times 70$ .

FIG. 18.—Diagram of a reconstruction from serial transverse sections, to show the form and position of the left enterocœl soon after its union in the preoral lobe with the right enterocœl. As seen from the left side. *x*. The point where the constriction will appear which divides the left enterocœl into an anterior and a posterior.

FIG. 19.—Longitudinal section, parallel with the dorsal and ventral surfaces, of a larva in same stage as Fig. 14, but just after the closure of the right water-pore. The pore canal persists, but in the sections following the one here figured it is found to end blindly. Perenyi; Kleinenberg's hæmatoxylin preparation.  $\times 240$ .

FIG. 20.—Larva of six days, at the stage when the division of the circum-oral band takes place (see Figs. 25 and 26), showing the dorsal surface. Only the left water-pore is now present. Kleinenberg's picric salt; Delafeld's hæmatoxylin preparation.  $\times 70$ .

FIG. 21.—A longitudinal section, parallel with the dorsal surface, through the two water-pores. The part of the section through the preoral lobe is not here figured, though it is in Fig. 22.  $\times 350$ .

FIG. 22.—The second section, ventralwards from that shown in Fig. 21. It shows the bilaterally symmetrical water-tubes, which in Fig. 21 are seen to open on the dorsal surface.  $\times 350$ .

FIG. 23.—From the living animal, four days old, showing the dorsal mesenchymatous muscle-fibres which move the preoral lobe. It also shows the bilaterally symmetrical water-pores.  $\times 145$ .

## PLATE XV.

FIG. 24.—A *Bipinnaria*, a little older than Fig. 28, seen from the right side. Kleinenberg's picro-sulphuric cedar; oil preparation.  $\times 70$ .

FIG. 25.—Surface view of the tip of the preoral lobe of a four days old larva, before the division of the circumoral ciliated band into the two bands characteristic of the *Bipinnaria*.

FIG. 26.—The same view of a larva six days old, after the division of the circumoral band.

FIG. 27.—Part of a transverse section of a *Bipinnaria*, a little older than that shown in Fig. 24, showing a later stage of the schizocœl (*s. v.*) and its relative position. Perenyi; Delafeld's hæmatoxylin preparation.  $\times 600$ .

FIG. 28.—A stage a little older than Fig. 30. The characteristic arms have begun to form. The enterocœls have united in the preoral lobes, but the cavities have not yet become continuous. From the living specimen, viewed from the dorsal surface.  $\times 70$ .

FIG. 29.—A *Bipinnaria* about five weeks old, seen from the ventral surface. Kleinenberg's picro-sulphuric; alcoholic borax-carmin preparation.  $\times 70$ .

FIG. 30.—*Bipinnaria* about eighteen days old, seen in ventral view. Shows the formation of the preoral ventral area (*p. v. a.*), and the position and form of the enterocœls. From the living specimen.  $\times 70$ .

FIG. 31.—Portion of a longitudinal section parallel to the dorsal surface, from a *Bipinnaria* of about the same stage as Fig. 29, to show a later stage of the schizocœl. Kleinenberg's picro-sulphuric, Delafeld's hæmatoxylin preparation.  $\times 600$ .

FIG. 32.—The growing anterior tips of the enterocœls, drawn from the living specimen. Same stage as Fig. 30.  $\times 240$ .

FIG. 33.—The union of the enterocœls in the preoral lobe. Same stage as Fig. 28. From the living specimen.  $\times 240$ .

FIG. 34.—A transverse section of a *Bipinnaria* at about the same stage as Fig. 24, at a point just anterior to the water-pore (a tangential piece is cut from the pore canal, *w. l.*), to show the origin of the schizocœl, *s. v.* Kleinenberg's picro-sulphuric, Kleinenberg's hæmatoxylin preparation.  $\times 240$ .

The Development of the Genital Organs, Ovoid Gland, Axial and Aboral Sinuses in *Amphiura squamata*; together with some Remarks on Ludwig's Hæmal System in this Ophiurid.

By

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With Plates XVI, XVII, and XVIII.

THE work which forms the subject of the present memoir was carried on at the Zoological Station at Naples during the six months from October, 1891, till April, 1892.

My original intention was to study the development of the genital organs in an Echinoderm, following a suggestion of Mr. Sedgwick. On my arrival at Naples I found that *Amphiura squamata* was the only form available for my purpose, since this viviparous Ophiurid is the only Echinoderm which breeds in late autumn (as, indeed, it does at every other season of the year as well).

In tracing the origin of the primitive germinal cells I was led, as the sequel will show, to examine the development of the ovoid gland, the "Centralgeflecht des Blutsystems" of Ludwig, together with the sinuses in connection with it; and, as far as I can make out, a systematic account of the history of these problematical organs is presented in this paper for the first time.

Before proceeding to describe the methods employed, I shall say a word or two as to the suitability of *Amphiura squa-*

mata as an object for this study. It has both advantages and disadvantages. The former are (1) that it breeds the whole year round; (2) that it retains the young in its genital bursa till a very late stage of development; and (3) that the adult is of such a small size as to render it a very favorable object for microscopic study. Hence it will be understood that one can always obtain an unbroken series of stages; and those phases frequently occur which in other Echinoderms are most difficult to obtain, viz. those immediately following on the close of the larval period. On the other hand, the great disadvantages are (1) that the Ophiurids are probably the most modified group of the Echinoderms; (2) that the development of *Amphiura squamata*, being more or less direct, is likely to be somewhat altered; (3) that the embryos are excessively small, my earliest post-larval stages having a diameter of only about  $\cdot 2$  mm., whilst the unsegmented eggs of *Antedon rosacea* have a diameter of  $\cdot 3$  mm.

With regard to the second disadvantage mentioned above, one must remember that a larval form can be recognised though much simplified in comparison with the ordinary Ophiurid Pluteus; and that the organs treated in this paper are less likely to be modified in their development, since they are all post-larval. The small size of the embryos forced me to give up the attempt to investigate the origin of some of the sinuses, such as the "radial perihæmal" and the "perihæmal ring sinus." So also I can make no statements with certainty as to the origin of the subneural sinus; except this, that Cuénot (6) is most certainly wrong when he asserts that it is formed by an involution of the ventral ectoderm of the arm. As a matter of fact, the nerve-cord has attained its deep position from the time of the very first appearance of the arms, and the figure which Cuénot gives has no counterpart in nature. All the sinuses mentioned are at first exceedingly narrow slits, considerably less in diameter than the nuclei of the surrounding tissue; and as the cell plasma of Echinoderm mesoderm is difficult to stain, one can realise how easy it is to be mistaken about the extent and communications of such



cavities. Added to all this, the cœlom in *Amphiura squamata* is represented at first by a mass of mesenchyme; and as this condition of things is certainly not primitive, I do not think that even if reliable results as to the development of cavities originating before the cœlom clears were attainable, they would be of much phylogenetic importance. I hope to be able to find something more instructive when I study their history in a larger and more typical form.

#### Methods.

I. Fixing.—The following is a list of the preserving fluids employed. Corrosive sublimate in distilled water; corrosive sublimate in sea water; corrosive sublimate three parts, glacial acetic one part; chromic acid; picric acid; Flemming's fluid; glacial acetic; alcohol of 30 per cent.; hot alcohol of 70 per cent. with a few drops of corrosive sublimate; osmic acid from about  $\frac{1}{8}$  to 1 per cent.; osmic acid followed by Müller's fluid for eighteen to twenty hours.

The result of my experiments is this:—The only liquid which gives reliable results is osmic acid, though its use is attended by disadvantages. It renders the animals very brittle, and has little penetrating power. When used in too strong solution, or for too long a time, it is followed by considerable shrinkage. I have found, however, that when it was followed by Müller's fluid this shrinkage was entirely prevented, and the brittleness, though still considerable, was very much less. Alcohol I rejected on account of the imperfect preservation it gave. Corrosive sublimate would give very fair results if it were possible to render its solution quite neutral, but this is very difficult. In no case, however, could one obtain the beautiful differentiation of tissues as to their staining properties which is yielded by osmic acid.

All liquids which decalcified as well as fixed were of no use, on account of the cavities which the evolution of gas produced in the still soft tissues. The method I finally adopted was as follows:—The animals were killed in a solution of osmic acid of about  $\frac{1}{2}$  per cent. allowed to act for ten minutes or more, of

1 per cent. acting for five minutes only; they were then rinsed with water and transferred to Müller's fluid for eighteen to twenty hours, then put at once into alcohol of 30 per cent., and brought slowly up into alcohol of 90 per cent. In the latter they were hardened for a night; then two or three drops of nitric acid were added to some fresh alcohol of 90 per cent., so as to give roughly a solution of from  $\frac{1}{2}$  to 1 per cent. of acid, and the animals were immersed in this till decalcification was complete, a process which occupied not more than twenty hours.

I found that Müller's fluid itself has a slow decalcifying action, and in some cases the acid alcohol was unnecessary. For this reason, were I doing the work again, I should prefer to stop the action of the osmic acid with ammonium picro-carminate instead of Müller's fluid, so as to avoid even the slight and easily recognisable "artefacts" produced by the latter. Glacial acetic acid gave fair results, and I used it to confirm results obtained by osmic acid. Strange to say, it has little or no decalcifying effect, and the suddenness of its action and its penetrating power are unsurpassed. But it is apt to cause swelling of the tissues, and of course on transferring the animals to alcohol one gets a solution of acetic acid, which then decalcifies before the tissues are hardened.

II. Stains.—Double staining was used in order to be certain about the boundaries of sinuses, since the ordinary plasma of Echinoderms stains with great difficulty.

As a nuclear stain I used Dr. Mayer's paracarmine. The great advantages about this are that it acts rapidly, and that all superfluous stain can be extracted by 70 per cent. of alcohol, which can be allowed to act for an indefinite time. I allowed my earlier stages about twenty minutes in the stain, adults and later stages an hour or two. An hour or two suffices to remove all surplus stain, provided the alcohol be changed several times. The plasma stain was applied on the slide. I used two, both of which gave good results, viz. solution of picric acid in turpentine and Dr. Mayer's oxidised hæmatoxylin or "hæmatëin." The advantage of the former is that it can

be used with the shellac method of mounting, and the danger of staining the mounting agent, as in the case of glycerine and albumen, is avoided. On the other hand, hæmatëin gives more differentiation. For embryos preserved in glacial acetic acid I used Dr. Mayer's hæmalaun, which gives a blue nuclear stain, and at the same time colours much of the plasma a faint yellow.

III. Cutting and Mounting.—Embryos fixed and stained according to my standard method were embedded in paraffin, and cut into series of sections in a plane parallel to the line joining the madreporite with the mouth, and at the same perpendicular to the plane of the disc.

A word or two on their orientation may not be out of place here. The young were in all cases extracted from the mother, and the madreporite found by examination with the dissecting microscope. Then, if the arms were long, all were broken off except that which was opposite to the madreporite; but if they were short and comparatively stiff only this arm was broken off. In the case of my earliest stages, where the arms were undeveloped, it was necessary to break off one point of a pentagon, and often it occurred that the animal (if only about .22 mm. in diameter) was destroyed or the breakage went obliquely, so as to mislead one afterwards. In general, out of three series of sections of this stage only one was satisfactorily orientated. This orientation had in all cases (except in the latest stages) to be performed on the living animal. When the animals had been embedded the paraffin was cut away, so as almost to lay them bare on one side, and the position of the madreporite was thus recognised, and the orientation of the block effected. Fresh paraffin was then melted on to the exposed place.

I must here raise an emphatic protest against the method employed by Cuénot (6), who professes to give an account of the origin of the ovoid gland and its surrounding sinus in *Amphiura squamata*, and is naturally quite wrong. He cuts a number of adults containing embryos, and then finds conclusions on casual sections of the contained young. The preserving fluid in this case penetrates neither rapidly nor

effectively, there is no control over the orientation, and it is impossible to get thin enough sections. I found it necessary to use for my youngest and most important stages sections  $3\frac{1}{4} \mu$  thick (five teeth of the rocking microtome). Above a diameter of  $\cdot 3$  mm. my sections were  $4\frac{1}{2} \mu$  thick (seven teeth), and only for adults and the oldest stages did I use sections  $7 \mu$  thick (ten teeth).

Sections perpendicular to the disc, but transverse to the axis of the stone canal, and horizontal sections were also used, but proved to be not nearly so instructive as those orientated as described above; they were useful, however, in determining some minor points.

My results are founded on perfect series of sections with finely differentiated stain and clear, sharp outlines. The sections themselves are clearer and more diagrammatic than the figures I have been able to make of them. In fact, I obtained preparations which for distinctness of outline and diagrammatic alternation of colour could hardly, I think, be surpassed by the use of osmic acid, Müller's fluid, paracarmine, and hæmatin.

It will be most convenient to first of all detail my results, and then to examine and discuss the literature; and as the ovoid gland precedes in development the genital organs, it will be well to commence with it.

#### Ovoid Gland.

I. Structure.—This has been described by Cuénot (4), Hamann (7), Apostolides (1), Ludwig (11), and Köhler (9). They agree in describing a pyriform mass enclosed in a space limited by a strong membrane, and almost filling it. Most agree in finding a supporting network of fibres with meshes partly occupied by cells, partly forming lacunæ. This mass sends out a prolongation, gradually becoming like ordinary connective tissue, towards the nerve-ring. On the dorsal surface of the latter it enters into connection with a structure called the hæmal ring. At its lower end the gland is prolonged into a curious string of tissue enclosed in a prolongation of the sinus which surrounds the gland. This string (the

genital rachis) is ventral in the interradii, but at the sides of the radii it mounts to the dorsal surface, thus passing over the genital bursæ, which are involutions of the integument close to each side of the arm. On the interradiial side of these bursæ the rachis bears the ovary; on the radial side it gives off a branch terminating in the testis, which runs into the short extension of the body-cavity into the arm, called by Russo (11) the testicular chamber.

Fig. 2 *a* is a longitudinal section of the disc passing through the ovoid gland of an adult. Fig. 2 *b* is another section from the same series, and fig. 2 *c* is a horizontal section of the gland of another individual.

In the centre of the organ one sees the stone canal (*st. c.*) with its characteristic columnar epithelium, which dorsally passes into the flattened epithelium of the water-vascular ring (*w. v. r.*). A section of the pore canal (*p. c.*), leading to the madreporic pore, is seen in the body-wall. I find three spaces in connection with the ovoid gland, and, as they have all been confused together under the name of axial sinus, I have called them sinus *a*, *b*, and *c* respectively, though I do not thereby mean to imply that they belong to the same category.

Sinus *c* is the thin-walled ampulla, into which both stone canal and pore canal open, and it has no connection whatever with any other cavity. Sinus *a* is the part of the aboral sinus which comes in contact with the ovoid gland, and is flattened out on its external surface. Sinus *b* is the axial sinus proper, which is principally developed round the distal swollen end of the gland, but also extends up on to its sides. These three spaces—sinus *a*, sinus *b*, and sinus *c*—are all quite independent of each other. I have traced them in every well-preserved series which I have examined. As to the structure of the gland itself, I find that it often presented the areolated texture referred to above. This I believe to be entirely due to imperfect preservation. When sufficiently strong osmic acid is used, and precautions taken to ensure its penetration (by opening the animal whilst living), one sees a uniformly staining plasma (figs. 2 *b*, 2 *c*) supported

by a close network of interlacing fibres. Intermingled are cells whose bodies stain slightly differently from the general plasma of the organ. In fig. 2 *d* I have drawn some curious nuclei from the ovoid gland of another adult, which seem to me to point at direct cell division. In the extension of the organ towards the nerve-ring the plasma gradually disappears, and it takes on the form of the ordinary connective tissue; but there seems to me to be no reason to regard the spaces in this as in any special sense lacunæ. In the part which is enclosed by the sinus *a* some cells are seen with larger and better defined bodies than in other portions of the gland. These are Hamann's "Urkeimzellen," primitive germ-cells, of which the genital rachis is also composed. Their meaning will be understood when the genital rachis is treated of.

II. Development.—Fig. 3 represents a section (in the standard direction) through an embryo about .2 mm. in diameter. The stone canal is seen lying in the middle of a mass of cells which take the place later occupied by the cœlom; the thickening on the inner side of the canal is an indication of the presence already of the ampulla. Unfortunately the other sections of this series are somewhat broken in this place, and in my other series of the same stage the stain was not good enough to give a clear figure of this cavity. I have no doubt, however, that it exists at this stage.<sup>1</sup>

Russo (17) has mistaken the mass of cells filling the cœlom for the rudiment of the ovoid gland, but the next stage (which I have obtained at least half a dozen times) clearly shows his error. Figs. 4 *a*, *b*, *c*, represent three consecutive sections  $3\frac{1}{4}\mu$  thick through a slightly older embryo (the size is not an exact guide to age). As these three sections comprise the whole stone canal and surrounding rudiment of the gland, the importance of dealing only with perfect series of very thin sections will at once be perceived.

A single layer of nuclei (*ps.*) lining the cœlom, which therefore can be called peritoneal, can be seen in fig. 4 *b* covering

<sup>1</sup> Since writing the above I have seen the Ampulla not only in embryos of this age, but also in bilateral larvæ.

the stone canal. This is the first rudiment of the ovoid gland. The cœlom can be seen to run into a chink at the distal end of the stone canal; a single thread of plasma stretches across it. This chink is the commencement of the axial sinus (sinus *b*), which is thus a diverticulum of the cœlom. The ampulla (sinus *c*) is seen to be quite distinct, and by comparing figs. 4*b* and 4*c* may be seen to communicate with *m. p.*, the madreporic pore.

In fig. 5*a*, and still more distinctly in fig. 5*b*, we see an increase in the number of nuclei forming the rudiment of the ovoid gland. At the point where a mesenteric bridle goes off to the stomach they form more than one layer, and show the characteristic staining properties of the primitive germ-cells. The axial sinus is clearly seen, and though its lumen is the merest slit, its continuity with the cœlom can easily be traced by its walls.

In the next stage (figs. 6*a*, *b*, *c*) the multiplication of the nuclei forming the ovoid gland is very marked, and they project as a lobe which encloses under it a nook, so to speak, of the cœlom. This is the first rudiment of the aboral sinus, which, like the axial sinus, is an involution of the cœlom, but quite a distinct one, though of course both at this stage open freely into the cœlom.

The next and most important stage is represented in figs. 7*a*, *b*, *c*. Here the ovoid gland has increased in size, and has grown round the stone canal, so that in the upper part of the section it appears both external (i. e. towards the mouth) as well as internal to it. In the dorsal portion of the gland the nuclei are spaced widely, and the characteristic plasma is beginning to appear. In the ventral portion the nuclei are very large, and are, in fact, becoming the primitive genital cells, the "Urkeimzellen." Sinus *b* is now distinctly closed off by a double membrane from sinus *a*, which opens freely into the cœlom. Figs. 7*b* and 7*c* show, however, that sinus *a* is prolonged laterally as an involution, and ends in a solid knob of cells. This is the beginning of the lateral outgrowth of the aboral sinus. It is remarkable that it takes place only

on one side of the ovoid gland; and this side, as shown by comparison of vertical sections transverse to the axis of the stone canal, is the right, if we suppose the animal to be placed with its mouth down and the madreporite posterior.

That the interpretation given to these rudiments is the right one is convincingly shown by the next stage (figs. 9 *a*, *b*). Here both axial and aboral sinuses are shut off from the cœlom and from one another. The Urkeimzellen are more distinct, and one sees also smaller interstitial cells amongst them. In this stage also I have been able to detect a trace of the characteristic fibres of the adult gland. In fig. 9 *b* one sees an unmistakable rachis (compare fig. 11) constricted off from the swollen ventral part of the ovoid gland; and yet, traced forward for a section or two, this ends in a similar knob of cells to that represented in fig. 8 *c*. This will, I hope, convince every one that the aboral sinus grows out from the involution at the base of the ovoid gland. These intermediate stages are, however, exceedingly difficult to find; and in the majority of cases when one seeks them one finds in embryos of the same size either that the rachis is not formed, or that it is formed the whole way round. I have, however, succeeded in getting about half a dozen specimens with a rudimentary rachis, though this was in all cases very short.

I have said that the aboral sinus extends laterally as a tubular involution, and of course the genital rachis is an outgrowth (as seen from figs. 9 *a*, *b*) of the similar part of the ovoid gland. If we now compare fig. 10 (which is a section in a plane somewhat oblique to the standard direction) we see the perfect continuity of the primitive germ-cells in the genital rachis with those in the ovoid gland. At the same time we notice a very interesting change in their form. From being spherical in the gland their bodies in the rachis become long and fusiform, and overlap each other, and even show irregularities of outline, which might be termed pseudopodia. Their nuclei at the same time change from a spherical to an oval shape.

These facts, I think, strongly support Hamann's idea that



the primitive germ-cells actually migrate, and I should be inclined to suggest that their place of proliferation continues to be where it is undoubtedly at first, viz. in the base of the ovoid gland. This wandering of the Urkeimzellen is also suggested by the observation which I have made, that when the rachis is complete there is great variation in the position of the primitive germ-cells. Sometimes there are a large number close to the ovoid gland and sometimes very few, and once just close to it the aboral sinus was quite empty.

The last stage in the development of the ovoid gland is shown in fig. 11. Here we see how the axial sinus, sinus *b*, extends laterally so as to enwrap the gland. This is a condition of things which seems to occur sometimes sooner and sometimes later.

To demonstrate this, clear and accurate longitudinal sections are required, but indeed this holds for all these sinuses. Very often, in spite of all precautions, one finds their lumen quite obliterated, but when one succeeds in preventing this their relations are very evident.

Before leaving the discussion of fig. 11 I wish to call attention to the curious space *sk*. This I have called a shrinkage space, because it is due to the different behaviour of the great interradial muscle, *mi.*, to the alcohol and fixing reagents from that of the neighbouring tissues. I mention it specially because I have reason to believe that it has been mistaken for part of the axial sinus by Hamann (7), and given rise to his idea that the axial sinus communicates with the sinus lying dorsal to the nerve-cord, a communication of which I can find no trace in any of my sections. Of course it may be different in the species which Hamann examined. This shrinkage space is quite easy to distinguish from the various sinuses described, as it has no endothelial membrane for its boundary as they all have.

Fig. 8 is a section from an individual slightly younger than the one from which fig. 11 is taken; it is interesting as showing the opening of the ampulla, both into the pore canal and into the stone canal; it also shows very distinctly the strong

double membrane which separates the aboral from the axial sinus.

### Hæmal System.

Before proceeding to describe the development of the genital organs it will be well to detail my observations on the hæmal system, as the composition of the genital rachis is connected with this subject. The view (accepted from Ludwig [11] and Hamann [7]) which is commonly taught in text-books is that there is a true hæmal system of vessels filled in preserved specimens with a deeply staining clot. The aboral sinus is said to enclose one of them, which in its turn surrounds the genital rachis. Another ring-shaped blood-vessel is said to lie close to the dorsal surface of the nerve-ring, and to send branches along the mid-dorsal line of the radial nerves. Finally the ovoid gland has been described as a plexus of vessels connecting these two rings.

In *Amphiura squamata* conditions are as follow:—A section of the genital rachis shows no trace of a blood-vessel. In the centre one sees the characteristic primitive germ-cells with large oval nucleus, and well marked body which also stains well. Usually not more than two of these are seen in one section of the rachis. Associated with them are a number of smaller interstitial cells. These form a kind of epithelium over the surface of the rachis which is turned towards the sinus. The outer wall of the latter (i. e. the wall projecting into the cœlom) is covered with the ordinary peritoneal epithelium. The formation of these interstitial cells can be seen in figs. 7 *a* and 9 *a* proceeding contemporaneously with that of the primitive germ-cells. There is no particle of the section which is not accounted for by the nucleus or plasma of some cell.

That the ovoid gland is no network of lacunæ I have already pointed out. In figs. 7 *a*, 9 *a*, and 11 this organ can be seen to send out a prolongation which extends on to the upper and outer surface of the nerve-ring. This prolongation becomes thinner and thinner as it proceeds, but there is no trace of any

swelling of this to form a blood-vessel, and it can only be traced in the few sections of the nerve-ring which also contain the ovoid gland.

As to radial blood-vessels—in many sections of the radial nerve-cord—there does appear at first sight to be a small round structure, in the mid-dorsal line, between two masses of ganglion-cells. But if one uses careful double staining and examines successive sections, one sees that it is often absent—as, for instance, in fig. 21. There the ganglion-cells with nuclei and plasma cover the whole dorsal surface of the cord. Further, when one looks closely at the sections where there is an appearance of a blood-vessel (cf. fig. 22) one sees that the nuclei of its wall are exactly like the ganglion nuclei; that its clot stains almost if not quite the same as the plasma of the surrounding cells. It is limited by no cell layer from the nerve-fibres below, and its boundary towards them is often jagged and uneven, and the angles of this outline run out into vertical fibres, so as to leave no doubt in my mind that the so-called blood-vessel is merely composed of the cell plasma of two or three rather larger dorsal ganglion-cells which are prolonged into these vertical fibres. A remarkable confirmation of this view is obtained by the study of specimens which have remained too long in osmic acid (*vi. d.*, fig. 23). Here the mass of nerve-fibres is strongly shrunk and its shape altered, so that its dorsal outline is far less convex. At the sides it is more or less wrenched away from the dorsal ganglion-cells, leaving an artificial space; but in the middle one or two adhere, and produce the appearance of a blood-vessel. As to the so-called branches of the hæmal system which go to the alimentary canal, these seem to me to be nothing more than mesenteric bridles; one very marked one is inserted just at the base of the ovoid gland, and in some young specimens there appears to be a prolongation of the peculiar tissue of the gland along it. In adults its relations are obscured by the great extension of the genital bursæ.

### Genital Organs.

The formation of the genital organs need not detain us long, as it is very simple. *Amphiura squamata* is hermaphrodite, and the general disposition of the genitalia has been described when speaking of the adult ovoid gland.

The ovaries appear first as small swellings of the genital rachis (compare figs. 16 *a* and *b*). The rachis here lies in the sinus in such a way that it touches the wall of the bursa from the first. The latter is here very thin, and one can detect a small involution towards the ovary. Here of course, when fully developed, is the point of discharge of the organ. The further history of the ovary merely consists in the increase of the number of the primitive germ-cells and of the subsidiary cells. Finally, one or two primitive germ-cells get the upper hand and form the fully developed ova. Of these there is usually only one in an adult ovary; when it is discharged one of the undeveloped primitive germ-cells takes its place.

Fig. 17 shows the passage of the young ovary into the rachis, and fig. 18 shows the ovary of a small adult.

When the ovary commences to form, the branch of the rachis leading round the bursa into the radial testicular chamber is undeveloped. Its formation is shown in fig. 12.

The first stage in the development of the testis (fig. 13) is indistinguishable from that of the ovary, viz. a solid mass of cells, except that these appear to consist more exclusively of Urkeimzellen. Afterwards a lumen forms as the rudiment increases in size (fig. 14), as sometimes occurs in old ovaries when more than one egg comes to maturity at a time. The Urkeimzellen are finally confined to one or two peripheral layers, and the centre is occupied by the products of their division. In neither the ovary nor testis did I see the least trace of a matrix of plasma and fibres, such as Cuénot (4) has described. Into the maturation of the sexual products it is not my purpose to enter. I only call attention to the following fact. Cuénot (4) states that in the testis the central Urkeimzellen are destroyed. I have seen no trace of this;

the lumen appears to me to come in consequence of the increasing periphery of the organ. It is possible, however, that some of the internal primitive germ-cells divide completely to form spermatozoa, and leave no part to regenerate the mother-cell. Young testes are often quite a solid mass of spermatozoa and sperm mother-cells, and no trace of degenerate cells is ever visible.

The genital bursæ originate late as invaginations of ectoderm (Russo, 16). There is, however, a very curious point about their development hitherto unnoticed. The first sign of their appearance is an increase in size and number of the peritoneal cells (fig. 19). Afterwards the ectodermal invagination is apparent (fig. 20). This first rudiment of the bursa is often very like a portion of the genital rachis; and as it is found at a stage when this is imperfectly or not at all formed, it is apt to lead to confusion. The best methods of distinction are of course the absence of a sinus, and its non-persistence on succeeding sections. When looking for specimens with a rudimentary rachis, one must carefully distinguish this rudiment of the bursa.

#### Literature consulted.

##### I. Ovoid Gland.—“Hæmal and Perihæmal Systems.”

In discussing this subject I think it neither necessary nor profitable to go back beyond the time of Ludwig, as before his time the ovoid gland was either not recognised or confounded with a Polian vesicle; whilst any space that happened to be seen in cross-section was called indiscriminately a blood-vessel. Ludwig (10, 11) not only distinguished the ovoid gland and homologised it with the organ occupying a similar position in other Echinoderms, but discovered the ampulla and distinguished it from the axial sinus; found the aboral sinus with its contained blood-vessel and rachis, and the relation of these to the genital organs. He also described an oral blood-ring and radial blood-vessels. The ovoid gland he regarded as a plexus of vessels uniting the oral and aboral blood-rings.

Like every student of Echinoderms, I cherish a great respect for the judgment of Ludwig; at the same time I must express regret at what seems to me to be the roughness of his methods. His figures are most diagrammatic; his distinction of the ampulla from the axial sinus is, by his own confession, mainly founded on one lucky section; and his figures of the blood-vessels are such as to render it impossible to conclude anything as to the histological nature of what he saw. Of course, at the time when the work was done the modern technique was undeveloped.

The work of Christo-Apostolides (1) was conducted with such crude methods, and contains results so contradictory of every one else, that its discussion would, I think, be mere waste of space. Hamann (7) has given a valuable paper on the Ophiurideæ; he follows Ludwig's interpretations, but gives far better figures. But he himself thinks it necessary to apologise for the imperfect preservation of many of his specimens. His results are chiefly founded on Ophioglypha albida; in venturing to criticise them I do so with some reserve, as I have only studied *Amphiura squamata*, but I cannot help thinking that my results throw some light on the appearances described by Hamann and others. Hamann figures the ovoid gland enclosed in a great sinus, which communicates with the perihæmal ring canal. I suspect that he has confused shrinkage spaces with part of the axial sinus. The ovoid gland he found to be lacunar when he used  $\frac{1}{2}$  per cent. osmic acid. I have already pointed out the great care which must be taken to ensure the due penetration of this fluid; when I used weak osmic, and left the animals only a short time in it, I got the ovoid gland very "maschig," the plasma being, in fact, macerated out from the supporting fibres. As to the blood-vessels, I call attention especially to the following passages:—"Die Wandung ist eine dünne Membran;" "Dieser Membran liegen aussen ovale Zellkerner auf;" "Irgend welche Zellschubstanz ist nicht Vorhanden;" "Die Blutflüssigkeit stellt eine geronne Masse dar welche sich mit neutraler Karminlösung helbrosa färbt." Now it seems pos-

sible to me that the missing cell plasma of the oval nuclei which are on the wall of the blood-vessel is to be found in the blood fluid; for this latter stains brightly, and always quite fills the vessel. The aboral ring has, according to Hamann, a different constitution. Its wall consists of well-marked cells, and there are scattered cells in the "fluid." I believe the suggestion has been made, though I cannot find the reference, that the aboral blood-ring results from a degeneration of the rachis. I have myself seen a structure like what Hamann describes in the large non-viviparous species, *Amphiura Chiajii*; which has, like most Ophiurids, a special breeding season. *Amphiura squamata*, on the other hand, breeds all the year round; and hence one can understand why there should be no degeneration in its rachis. Why, however, the degenerate part of a rachis should be called a blood-vessel I fail to see.

Köhler (9) has examined *Ophioglypha texturata*, and has arrived at very curious results. I must, however, protest against the practice of painting in colours the blood-vessels in figures professing to give histological details. This mixing of diagram and figure seems to me quite to beg the question. Köhler fails to find the aboral sinus, but sees two prolongations of the ovoid gland attaching themselves to the sides of the madreporic plate. This I believe to be due to a misconception of a section like my fig. 11, in which the gland is cut tangentially, and the boundaries of the axial sinus might simulate prolongations such as he describes. The enormous shrinkage cavity one sees in his figure, and his failure to detect the proper relations of the aboral part of the gland, point, in my mind, again to imperfect preservation. The oral blood-ring he finds to be constituted of a mass applied to the dorsal and outer wall of the perihæmal canal, consisting of an irregular meshwork of fibres with cells and brown granules. This is certainly a curious structure to call a blood-vessel, especially when it is remembered that, excepting the brown granules, this is exactly the appearance of the ordinary decalcified tissue of an Ophiurid. The only reason Köhler has for

singling out this as a blood-vessel would appear to be that when he forced an injection into the mass of the ovoid gland he got the colouring matter here. When one thinks of the thin and non-resistant nature of the boundary walls of sinuses, especially in cases of poor preservation, and the little firm tissue (other than lime) there is in the body-wall of Ophiurids, one will not be inclined to place much dependence on results obtained by injection. The radial blood-vessels Köhler finds, consist of fibres, cells, and pigment; and what strong distinguishing mark there is between them and the dorsal ganglion-cells of the nerve-cord appears neither from Köhler's figures nor description.

Cuénot, in his earlier work (4), denies the existence of blood-vessels, and traces cavities lined with cubical epithelium in the gut-wall communicating with the axial sinus. He has also failed to find the Urkeimzellen in the pseudo-heart, and concludes that these, when they occur in the rachis, are due to special formation in situ. The spaces he has found are very possibly mucus-cells cut obliquely; such are greatly developed in the ventral wall of the stomach of *Amphiura squamata*. His failure to trace the primitive germ-cells into the ovoid gland is due to want of study of young specimens.

In his later work on general Echinoderm morphology (6) he finds one large axial sinus, into which stone canal and pore canal open, confusing thus together, from want of study of good series, ampulla and axial and aboral sinuses. He now accepts Köhler's account of the hæmal system.

As to the development of the ovoid gland in Echinoderms in general, most of the notices I have been able to collect are very scanty, and evidently based on one or two observations only.

Thus in *Asterina gibbosa* Ludwig (12) finds that it forms as a split in the mesentery containing the stone canal; in *Asterias hyadesi* Perrier (13) finds that it arises as a conical process of the peritoneal lining of the stomach, which grows down alongside the wall of the axial sinus, and becomes later invaginated into its interior. It contains a number of "corps



vitellins," which afterwards become the corpuscles of the body-cavity.

In Echinoids Prouho (15) describes the rudiment of the gland as an "amas cellule allongé" at the side of the stone canal. Cuénot (6), in *Amphiura squamata*, finds it arise as a thickening of the wall of the axial sinus when the embryo has attained a diameter of 700  $\mu$ ! Russo (16), in the same form, as a cumulus of cells when the embryo has attained its pentagonal form; and Apostolides (1) as a small swelling of the stone canal.

All these statements appear to me to be based on a few casual observations; but I cannot raise too strong a protest against the superficial investigations on which the last three writers have based a history of this organ. Since Cuénot knows nothing of the origin of the sinuses, it is evident how entirely wrong he must be.

The case is very different with the interesting observation of Perrier (14) and Bury (2) on the dorsal organ of Crinoids. This organ, in spite of Cuénot's objections, I regard as the homologue of the ovoid gland. Cuénot's first objection is that the ampulla of the primitive stone canal in Crinoids disappears, whereas in Ophiurids it surrounds the gland. As a matter of fact it has precisely similar relations in both groups. His second objection is that in Crinoids the genital rachis comes off from the oral and not the aboral end of the gland, as in Ophiurids. Taking Asterids for a moment, where the madreporite has a dorsal position, we find that the genital rachis comes off from not quite the aboral end, but there is a portion of the gland beyond it, and this may correspond to the main mass of the organ in Crinoids. The same thing is true of Ophiurids, only here the madreporite is brought round to the ventral side.

As, however, to the general homology of the two organs the observations of Bury and Perrier leave us in no doubt whatever. According to the first observer the dorsal organ arises as a cord of elongated cells; since these lie in the concavity of a prolongation of the right cœlomic sac, which is crescentic in

cross-section, they may be regarded as peritoneal. This prolongation becomes divided longitudinally into five cavities, and these form the beginning of the chambered organ. Later the axial organ grows up under the mesentery of the stomach with an axial cord of Urkeimzellen. Bury finds that here, as in Ophiurids (3), the ampulla of the stone canal represents an anterior cœlomic pouch.

Perrier finds that the dorsal organ is a thickening of one of the layers of the right peritoneal sac. When the dome of the calyx opens it is ovoid, and formed of large pyriform cells with a fibrous membrane. According to Perrier, diverticula from secondary madreporic pores (entonnoirs vibratiles) form vessels around the dorsal organ. If we accept Bury's view, and make allowance for the great divergence of type between Crinoids and Ophiurids, we might regard the sinuses of Ophiurids as being equivalent to the chambered organ of Crinoids, both being diverticula of the cœlom.

II. Genital Organs.—Hamann (8) describes a genital rachis with Urkeimzellen in Asterids, Ophiurids, Echinoids, and Crinoids. He proves that the genital tubes are outgrowths of the rachis in Crinoids, Asterids, and Echinoids, and suspects it in Ophiurids. Cuénot (5) has also asserted this origin for the gonads in Asterids. He says a septum forms which closes the sinus around the genital bud from the aboral sinus, and in this the external opening is formed. Of the development of the gonads in Ophiurids he merely asserts that it is precisely similar; but I can assert that no such septum is formed in them. Cuénot also asserts that the genital rachis is an outgrowth of the pseudo-heart in Asterids; but this is a mere guess, based on the similarity of the cells in both organs. Between a stage where there is neither rachis nor aboral sinus, and one in which both are completely formed, he finds no intermediate phase. His assertion that the ordinary cells of the ovoid gland mature into Urkeimzellen finds no support from my observations, which show that the portion of the gland destined to form the primitive germ-cells is specialised from the very first.

Prouho (15) finds the genital rachis arises as a bud close to but independently of the pseudo-heart. Its further history is similar to that in Ophiurids. I think his statement of the independent origin of the rachis and ovoid gland requires confirmation. Russo (17) has made the strange error of saying that it results from Ludwig's and Hamann's researches that the genital organs, like the genital bursæ, are of ectodermic origin.

### Summary and General Conclusions.

The most important results detailed in this paper are as follows:

1. The primitive germinal cells are peritoneal.
2. The ovoid gland is a solid organ, which develops from a portion of the rudiment which gives rise to the primitive germinal cells.
3. The axial and aboral sinuses are involutions of the cœlom, and have no connection with the ampulla of the stone canal or each other.
4. The genital rachis is an outgrowth from the ovoid gland into the aboral sinus, the formation of sinus and rachis proceeding together.
5. There is no evidence of the existence of Ludwig's hæmal system in *Amphiura squamata*.
6. Both kinds of cells, germinal and interstitial, which are found in the genital rachis, are formed in the ovoid gland.
7. The germinal cells are formed from peritoneal cells directly; there is no evidence of the transformation of the special cells of the ovoid gland into Urkeimzellen.

The conclusions which I draw are these: that Echinoderms agree with other Cœlomata in the origin of their genital cells. These latter have at first an unsymmetrical position in Echinoderms, and afterwards take on a radially symmetrical disposition in correspondence with the secondarily acquired radial form of the body. The origin of these cells adjacent

to the stone canal suggests a comparison of the origin of the genital cells near the nephridia in many Annelids, but the homology of the stone canal with a nephridium has yet to be proved.

In conclusion I have to express my warmest thanks to Dr. H. Eisig and Dr. P. Mayer for many valuable suggestions, especially to the latter for his invaluable assistance with technique.

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## EXPLANATION OF PLATES XVI, XVII, &amp; XVIII,

Illustrating Mr. E. W. MacBride's paper "On the Development of the Genital Organs, &c., of *Amphiura squamata*."

*List of Abbreviations employed.*

C. Cœlom. *gen. b.* Genital bursa. *gen. r.* Genital rachis. *h. r.* Köhler's "hæmal" ring. *m. p.* Madreporic pore. *msch.* Mesenchyme-cells filling the cœlom. *musc. bucc.* External muscles of mouth. *musc. int.* Interradial muscle of disc. *musc. r.* Muscles of the arm. *ov. g.* Ovoid gland. *nerv. rg.* Nerve-ring. *p. c.* Pore canal. *rad. nerv.* Radial nerve. *sinus a.* Aboral sinus. *sinus b.* Axial sinus. *sinus c.* Ampulla of the stone canal. *sinus epin.* Epineural sinus. *sinus rad. perih.* Radial perihæmal sinus. *sinus perist.* Peristomal sinus. *sk.* Shrinkage space. *st. c.* stone canal. *w. v. r.* Water vascular ring.

Figs. 2 E and 6 D are diagrams. The outlines of all the rest have been drawn with the camera lucida, and except where otherwise stated are magnified 340 diameters, and taken from sections parallel to the axis of the stone canal of specimens preserved in osmic acid followed by Müller's fluid.

FIG. 1.—From an individual 86 mm. in diameter. Magnified 130 diameters. Osmic alone. *sinus rad. perih.* Radial perihæmal sinus. *sinus ep. n.* Epineural sinus. *sinus perist.* Circumoral sinus.

FIG. 2 A.—Section of ovoid gland and surrounding structures of an adult. *gen. r.* Portion of genital rachis where it passes into ovoid gland. *sk.* Shrink

age space due to action of preserving fluids on great interradial muscle. *h. r.* Pedicle of ovoid gland (= Köhler's hæmal ring?).

FIG. 2B.—Another section of ovoid gland from the same series. *st. c.* Proximal parts of stone canal.

FIG. 2C.—Horizontal section of ovoid gland of another adult. *sinus b.* Transverse section of the canal sinus.

FIG. 2D.—Nuclei suggesting direct division from another adult organ.

FIG. 2E.—Diagram of relation of gland and surrounding sinuses in the adult. *m. p.* Madreporic pore.

FIG. 3.—From an individual about .2 mm. in diameter. *msch.* Mesenchyme filling ventral portion of the cœlom.

FIGS. 4A, B, C.—Three consecutive sections from a somewhat older individual than Fig. 3. *m. p.* Madreporic pore. *ov. g.* First rudiment of the ovoid gland.

FIGS. 5A, B.—Two sections from a series through an individual about .25 mm. in diameter. *gen. r.* First appearance of primitive germ-cells. *sinus b.* A nook of the cœlom, afterwards becoming the axial sinus.

FIGS. 6A, B, C.—Three sections from a series through an individual .3 mm. in diameter. *sinus b.* Axial sinus still communicating with cœlom though its lumen is obliterated. *sinus a.* A nook of the cœlom, afterwards becoming aboral sinus.

FIG. 6D.—Diagram of relations of the rudiments of axial and aboral sinuses to each other and to the incipient ovoid gland.

FIGS. 7A, B, C.—Three sections from a series through an individual .48 mm. in diameter. *gen. r.* Solid knob in which incipient aboral sinus and genital rachis end. *h. r.* Prolongation of the ovoid gland over the dorsal surface of the nerve-ring.

FIG. 8.—Section of an individual .83 mm. in diameter. Osmic alone. *sinus a, sinus b.* Sharply separated axial and aboral sinuses.

FIGS. 9A, B.—Two sections from a series through an individual .58 mm. in diameter. *gen. r.* Genital rachis constricted off from ovoid gland.

FIG. 10.—Oblique section of an individual .59 mm. in diameter.

FIG. 11.—Section of an individual .9 mm. in diameter. *x.* Curious branched cell in the axial sinus.

FIG. 12.—Another section from same series as Fig. 11, showing growing branch of rachis. *t.* Position in which testis will be formed.

FIG. 13.—Young testis from an individual about .97 mm. in diameter.

FIG. 14.—More advanced stage of testis. From an individual .9 mm. in diameter.

FIG. 15.—Adult testis.

FIGS. 16A, B.—Two sections from same series as Fig. 1, but magnified 340 diameters. 16A is through the genital rachis; 16B through the incipient ovary.

FIG. 17.—Shows young ovary passing into the genital rachis, from same series as Fig. 14.

FIG. 18.—Adult ovary.

FIG. 19.—First rudiment of genital bursa. From an individual .62 mm. in diameter. Osmic alone.

FIG. 20.—More advanced stage of the bursa. *w. v. b.* Radial water vessel.

FIG. 21.—Section of radial nerve-cord of young adult. *w. v. b.* Radial water vessel.

FIG. 22.—Section of radial nerve-cord of another adult. *w. v. b.* Radial water vessel.

FIG. 23.—Section of radial nerve-cord of adult treated with osmic alone. *w. v. b.* Radial water vessel.





**A New English Genus of Aquatic Oligochæta  
(Sparganophilus) belonging to the Family  
Rhinodrilidæ.**

By

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With Plates XIX, XX.

IN the summer of 1891, during a stay at the village of Goring-on-Thames, I was on the look-out for *Criodrilus*, which hitherto has not been found in England. I looked carefully amongst the roots of waterweeds, and in the mud in which these were growing, and ultimately I believed I was successful, for I found a few worms, some three or four inches in length, agreeing closely, so far as regarded external character, with *C. lacuum*, with the exception that the male pore, which is very conspicuous in the latter worm, was not evident. But on further examination the worms were found to present several internal characters which did not harmonise with those of *Criodrilus*. However, the worms had passed the period of their sexual maturity, so that the generative system was in a degenerate condition, and I was unable to trace the sperm-ducts to a pore. I had therefore to wait till the following summer, when I paid several flying visits to Goring, with finally good results, for I found more of the worms, and this time sexually mature. The genital organs conclusively showed that a new genus was in my hands, belonging not to the family Lumbricidæ, but to the Rhinodrilidæ (*mih*i).

For this new worm I propose the name *Sparganophilus tamesis*. The generic name refers to the fact that all the specimens which I could obtain were found amongst the roots and the lower parts of the leaves of the bur-reed (*Sparganium ramosum*), which grows in black, evil-smelling mud on the banks of the Thames. The worms were all found in a backwater some little distance below Goring, and I could find none elsewhere, though I examined similar spots on the banks both above and below this backwater, as well as in the river near Oxford. Moreover these worms appeared to be limited to an area of about ten yards in length along the bank, for repeated examination of this backwater met with constant failure with the exception of this prescribed area. When first discovered the worms were accompanied by a number of cocoons. This was in September, 1890. In the next year I visited Goring during the months of July and August. In the former month I was quite unsuccessful, but in the latter I found several specimens, all of which, as I have said, were sexually mature. I am inclined to think that, as is the case with *Criodrilus*,<sup>1</sup> these worms spend the greater part of the year in the mud at the bottom of the river, and only come to the banks amongst the roots of *Sparganium* during August and September for the purposes of reproduction.<sup>2</sup>

The cocoon is shown, of natural size, in Pl. XIX, fig. 4; it is a somewhat sausage-shaped body, terminating in a narrow frayed end in one direction, and drawn out to a point at the other, as in *Criodrilus*; the cocoons, thus, differ in shape from those of the earthworms *Lumbricus*, *Allolobophora*, *Perichæta*, which are spherical, but resemble those of *Megascolides* very closely in shape.

<sup>1</sup> Oerley, "Morph. and Biol. Observations on *Criodrilus*," 'Quart. Journ. Micr. Sci.,' xxvii, p. 537.

<sup>2</sup> During August and September of this year, 1892, I have frequently found the cocoons in quantities in the neighbourhood of Oxford, both in the Thames, in the Cherwell, and amongst the roots not only of *Sparganium*, but also of *Sagittaria sagittifolia* and other water plants; I have, however, not come across the worm this year.

I. *Sparganophilus tamesis*, nov. gen., nov. sp.,

is a delicate, pinkish worm, rather narrow for its length of three to four inches. The body-wall is, posteriorly to the clitellum, transparent, and, being provided with a dense network of blood vessels, has a pink colour; but this is complicated by the green colour of the gut, which also shows through. The surface of the body exhibits a lovely violet to peacock-blue iridescence. At the anterior end of the body the pink tint deepens. This is due to the large hearts which exist in the segments here, while the sperm-sacs give rise to a light cream-coloured band immediately in front of the clitellum, which is itself a bright orange. The worm is very strong and active; it feels wiry and firm, almost like a nematode; it wriggles violently and coils itself when handled.

The clitellum is quite distinct in the living animal owing to its colour,<sup>1</sup> and occupies Somites XVI to XXIV, with part of XV and part of XXV; but in spirit specimens it is difficult to determine its limits, though its area is marked by the suppression of intersegmental grooves. Its anterior and posterior boundaries are, even when living, very ill-defined, but near its ventral boundary a translucent band—the tubercula pubertatis—is easily recognisable, extending across Somites XVII to XXII, dorsal of the ventral chætæ. In the preserved specimens a deep groove traverses the dorsal surface of the worm, but in the living state the body is cylindrical, the squareness characteristic of *Criodrilus* not being observable.

The prostomium is small, slightly conical, and not marked off from the peristomium by any groove; this is the condition usual amongst the smaller aquatic Oligochætæ, whereas in the terrestrial forms a groove forms the hinder boundary of the prostomium; this is but feebly marked in the aquatic Lumbricid *Criodrilus*. There is no prostomial pore, but in longitudinal

<sup>1</sup> The accompanying figures, 1, 2, 3, are lithographed from coloured sketches, and some of the points which showed well in them are now indistinct.

sections a small pit is seen at the apex (Pl. XX, fig. 12). A prostomial pore is present in some aquatic Oligochætes, *e. g.* the Enchytræidæ, and Vejdovsky figures one for *Criodrilus*,<sup>1</sup> but both Rosa<sup>2</sup> and Collin<sup>3</sup> deny its presence; and I have been unable to find it on a re-examination of my sections of that worm.

The pygidium (fig. 3) is a large truncated conical somite carrying the dorsal anus at its end; the two præpygidial somites are much shorter than the preceding somite, and these three together are about equal in length to the pygidium. In the majority of specimens the "tail" was regenerated, as is so frequently the case in *Criodrilus*, *Pontoscolex* (= *Urochæta*), *Lumbriculus*, &c.

The chætæ have the usual Lumbricid shape and arrangement in two couples on each side; the distal moiety of the chætæ presents three or four transverse irregular ridges (fig. 5), as in *Rhinodrilus* and several allied forms. In those cases where the chætæ are unworn the point is rather sharply hooked. There is no difference in size and shape between the ordinary and the clitellar chætæ.

#### § The Minute Structure of the Integument.

The general structure of the epidermis is similar to that of *Lumbricus*, &c. The clitellum (fig. 30) is several cells deep, or, more correctly, the club-shaped cells are of several different lengths, some reaching to the circular layer of muscles, others not much further than to the base of the epidermal cells. The clitellum is some ten to twelve times thicker than the ordinary epidermis; and on each side of the ventral surface, just outside the ventral chætæ, becomes still thicker, forming in a transverse section a rounded prominence (fig. 19). This is the tubercula pubertatis, consisting, as I have figured for *Microchæta*,<sup>4</sup> of very long cells, somewhat like the

<sup>1</sup> 'System und Morphol. d. Oligochaeten.'

<sup>2</sup> "Sul *Criodrilus lacuum*," 'Mem. d. Reale Acad. d. Sc.,' Torino, 37.

<sup>3</sup> 'Zeit. f. wiss. Zool.,' 46.

<sup>4</sup> 'Proc. Zool. Soc.,' 1892.

ordinary clitellar cells. Although, superficially, the clitellum appears to cease at this spot, yet transverse sections show that the characteristic cells are continued across the ventral surface, but are only one or two rows deep.

It may be mentioned that in *Rhinodrilus* this clitellum is visibly "complete" in its anterior region, but apparently "incomplete" posteriorly.

In the mature worm, where the clitellum is most fully developed, I could find in sections no lateral chætæ, although the ventral ones are distinct enough; I believe they are, in fact, here absent. But whether they are absorbed or whether they drop out is, I believe, a matter of speculation. I am inclined to think that they drop out. At any rate, in sections of a worm which had passed its maturity, and in which the clitellar cells are degenerating (fig. 20), giving thus the appearance of a subepidermic connective tissue, I find the lateral chætæ very small; they appear to be newly formed, and do not by a long way perforate the body-wall.

## II. The Internal Anatomy.

§ With regard to the alimentary tract little need be said. There is no gizzard, not even a thickening of wall; a fairly sharply marked division occurs between œsophagus and intestine. The latter commences in Somite IX, where the gut suddenly enlarges; and a change in the epithelium, as well as in character of the wall, is noticeable. The œsophagus has a fairly thick wall; the lining epithelium, which is considerably folded, consists of tall, ciliated cells. The wall of the intestine is thinner, the epithelium much lower, less folded, and the cilia shorter. The end of the œsophagus projects, valve-like, into the intestine, and here the change in the epithelium is well seen, the cells of this portion of œsophagus being taller than elsewhere. There is no typhlosole in the intestine, nor calciferous glands to the œsophagus.

The buccal region occupies, as will be seen from the figs. 12, 13, about two somites. The pharynx is short, and pro-

vided with the usual dorsal sac in Somite iv. One of my series of longitudinal sections is of a worm with buccal region everted; the other series shows the buccal region withdrawn. I have thought it worth while to append sketches of these two phases, as I am not aware that such pictures have hitherto been published.<sup>1</sup>

Fig. 12 represents a condition of rest, though the upper lip (*a. a'*) is partially everted. The floor of the buccal region is transversely folded, giving a tongue-like appearance. The lining of this region (fig. 15) consists of large round nuclei embedded in a feebly granular protoplasm. I cannot with certainty detect the outlines of the cells, which are probably cubical. The surface is cuticulated. It appears as if these cells were capable of a certain amount of alteration in shape. The epithelium between the lines "*a* and *a'*" in fig. 12 is flattened with elliptic nuclei as in fig. 14. Now, in the everted condition (fig. 13), not only is the region *a a'* lined by flat cells, but nearly all the everted epithelium is similar to this and graduates near the edges of the orifice into the more cubical character shown in fig. 15.

The true pharynx commences at *c* and *d*, and is lined by tall ciliated epithelium, with granular contents and elongated nuclei. These cells are about three times as long as, and much narrower than, those lining the buccal cavity (see fig. 16).

In fig. 13, representing the everted condition, a dorsal sac is represented, opening close to the external orifice of the everted gut; this sac is a normal feature in the pharynx of earthworms, and is not apparently represented in the state of rest (fig. 12). But this is merely owing to the fact that the latter section is more accurately median, whereas the former is inclined to the median plane, so that the dorsal part of the worm is cut through along a more lateral line than is the ventral region. This dorsal sac opens into the general cavity of the pharynx by a wide mouth along the middle line; this mouth narrows laterally and curves forwards, that is, the aperture of communi-

<sup>1</sup> But see Garman on "Diplocardia," in 'Bull. Illinois State Lab. of Nat. Hist.,' iii, pl. i.

cation is crescentic, with the concavity forwards. This dorsal sac is lined by very tall, narrow, ciliated cells (fig. 17) pressed close against one another; the nuclei are at different levels, though I believe there is only one row of cells; the cells are taller and narrower than those lining the floor of the pharynx.

In many earthworms which I have examined from this point of view the floor of the pharynx is cuticulated (see my paper on "Eminodrilus" in 'Journ. Roy. Micr. Soc.,' 1891, pl. iii, fig. 10; pl. iv, fig. 11), only the dorsal sac-like outgrowth being ciliated.

The œsophagus, as the fig. 13 shows, is nipped by the septa; it is lined by cells similar to those on the floor of the pharynx, but rather shorter and less granular.

This region of the gut is hidden, when viewed from above, by three paired white masses, the salivary glands (*sal. gl.*), which are in Somites IV, V, VI. These have the usual structure which I have described for *Eminodrilus* (loc. cit.), and the anterior ones at least are closely connected to the pharynx, with which they probably communicate.

The lining of the intestine is represented in fig. 18. The cells are much shorter than those of the œsophagus, and most of them are dilated distally, where the protoplasm is modified to form a bright refracting and deeply stained border; beyond this is a light refracting edge, which appears in some of my sections to be a cuticle, but in others exhibits a fine striation. I believe that the intestinal epithelium is, as in other Oligochætes, ciliated, and that owing to the mode of preservation the cells have become fused or otherwise rendered indistinct.

In broken sections the shape of the epithelial cells is well seen, and they are distinctly broader at the outer end; hence, when in situ, there appear gaps between the cells. This I suggest is due to the shrinkage caused by reagents, occurring unequally; the modified striated border shrinking very little, the lower end shrinking much.

§ The nephridia are very distinctly pink in a freshly opened worm, owing to the rich plexus of blood-vessels around

them. Each nephridium is a large organ, almost filling the cavity of the somite; this size is due to the great development of large vesicular cells in which the tube is embedded, as in *Pontodrilus*, *Criodrilus*, *Libyodrilus*, *Tubifex*, and other worms.

The nephridia are absent in the first twelve somites. The first one lies in Somite XIII, and has its funnel in Somite XII; in one specimen, however, I noted a nephridium in this latter somite.

The general character of the nephridium agrees with that which I have described<sup>1</sup> for *Lumbricus* and other worms.

*Sparganophilus* agrees, however, with *Criodrilus* in lacking a muscular duct; the "wide tube" perforates the body-wall (fig. 8, *ne. d.*), as I have figured for *Criodrilus* (*loc. cit.*), and opens in front of the innermost *chæta* (fig. 11, *ne. p.*).

In the structure of the funnel, however, the present worm exhibits a rather more complicated condition than any hitherto figured, in the possession of an extra row of small cubical cells round the margin. As in *Lumbricus*, the funnel consists of a large "central cell" (figs. 31, 32, *c.*) surrounded by a series of "marginals" (*m.*) arranged in a fan-shaped way, and diminishing in size towards each side, where they pass round to form an incomplete ventral lip; outside these marginals are set the cubical "extra-marginals" (*ex. m.*), which appear as a single row of cells when the funnel is seen from in front, but are really three or four rows deep, and passing round to the back of the funnel, graduate into the flat *cœlomic* cells normally present. The arrangement is represented in figs. 31, 32, one of which represents a longitudinal section, the other a transverse section of a funnel.

In many cases I have observed in front of the funnel a large spherical mass (fig. 33), consisting of a number of nuclei—most of them deeply stained, irregular, and highly refracting, others with but little chromatin in them—embedded in a

<sup>1</sup> Benham, "The Nephridia of *Lumbricus*," 'Quart. Journ. Mier. Sci.,' vol. xxxii.



somewhat fibrillated network. The nuclei with little chromatin are chiefly on the surface of the mass, and look as if they had only recently been gathered up; the others are probably dead nuclei destined to undergo degeneration previous to their expulsion by the nephridia. In this mass of "débris" are frequently a number of yellow granules (*y*), perhaps the contents of chloragogen cells which have been collected by the funnel.

### § The Generative System (fig. 11).

The four folded digitate testes have the usual position, the first pair on the anterior septum of Somite *x*, and the second pair in Somite *x**i*. The four ciliated rosettes, which are less folded than in *Lumbricus*, &c., lie in these same somites. Both testes and rosettes are quite free in the cœlom, there being no median sperm-sac. There are two pairs of lobulated sperm-sacs, occupying Somites *x**i* and *x**ii*; those in the latter somite being slightly the larger. They are attached to the anterior septum of each of these somites, so that they are entirely post-septal; there are no median sacs.

The arrangement of these sperm-sacs is thus very different from what obtains in *Criodrilus*, in which these organs are situated as in *Allolobophora*, there being two pairs of pre-septal in addition to the two pairs of post-septal sacs.

Still greater difference is exhibited by the relations of the sperm-duct. Passing from the ciliated rosette, in each case, the duct is as usual slightly coiled behind the septum, forming the epididymis; the sperm-duct then dips into the body-wall, penetrates the muscular coats, and attains a sub-epidermic position, which it retains throughout its extent (figs. 19, 20, 22). This superficial position is unknown in any other earthworm, nor does it occur in any Oligochæte; and if we wish to press the homology between sperm-duct and nephridium we may refer to *Libyodrilus*<sup>1</sup> for a corresponding position of part of the nephridial system, which, however, as Mr.

<sup>1</sup> F. E. Beddard, 'Quart. Journ. Micr. Sci.,' vol. xxxii, Pl. XXXIX, figs. 14 and 16.

Beddard has shown, is not a primary but a secondary condition. As regards the sperm-duct, I would suggest that we have in *Sparganophilus* an explanation of the long duct so usual amongst earthworms; the sperm-duct probably opened externally in the segment following the funnel, just as the oviduct does in all earthworms, and the sperm-duct in *Moniligaster*, and many of the aquatic *Oligochæta*, such as *Naididæ*, *Tubificidæ*, &c. In order to convey the spermatozoa backwards a groove might be imagined to appear, which sinking into the epidermis became a canal. This canal lying, as in *Sparganophilus*, within the epidermis, would extend through any number of segments till it opened to the exterior. Accessory parts, such as atria, would appear later on; the duct sank deeper and deeper till it came to lie in the cœlom, as in the majority of worms. I do not wish to be understood as regarding *Sparganophilus* as a primitive form, but merely suggest that in this particular feature it retains an archaic character.

The position of the duct is shown in fig. 19, where it is seen lying amongst the bases of the deep clitellar cells, dorsad of the ventral chætæ, and immediately outside the tubercula pubertatis. In fig. 20 the structure of the sperm-duct is seen to be normal; the worm, of which this figure represents a portion of a transverse section, had passed its sexual maturity. The ordinary clitellar cells (see fig. 30) appear to have undergone a certain amount of change, the contents have been poured out in forming the cocoon, and an appearance as of a "cutis" is presented by the nuclei scattered in a loose network of fibrils, the shrunken walls of the cells.

In Somite XVIII the duct becomes more superficial (fig. 21) where it lies immediately below the ordinary epidermal cells. At the hinder margin of this somite it reaches the surface, as seen in fig. 22. The male pore is very minute, and there are no accessory organs to call attention to its whereabouts, and it may be very readily overlooked; in the section drawn the terminal portion, for some half a millimetre in extent, was filled with deeply stained spermatozoa—evidently I captured the worm at its most active period—which mark the duct distinctly.

At the pore the columnar epidermal cells dip in slightly to meet the already superficially situated duct.

The structure of the sperm-sac is represented in fig. 23. The cavity is very greatly subdivided by muscular (?) trabeculæ (*trab.*), which diverge from an axial bundle (*ax.*) continuous with the septum. The spaces between the trabeculæ are occupied by developing spermatozoa; the outermost lobules contain usually the younger stages, whilst the more advanced stages occupy the central lacunæ. This arrangement, however, as a glance at the figure will show, is not absolute, young spermatozoa frequently occurring in the outer lobules, whilst sperm-morulæ are found centrally.

#### The Female Organs (fig. 11).

The pair of ovaries lie in Somite XIII; the oviducts have the usual relations, and open on Somite XIV, just within the line of the ventral chætæ; a small ovisac occupies the usual position.

The ovary itself is large, and extends across its segment almost to the hinder septum; its narrow neck is relatively long; its tail, too, consists usually of eight ova in a single row. These ova are not noticeably larger than those of Lumbricids, measuring  $\cdot 3$  mm.

The relation of the ovisac to the 13th somite and to the funnel of the oviduct deserves a description, as it is sometimes inferred that the ovisac has no direct communication with the duct.

I give four drawings from a series of transverse sections through the funnel of the oviduct.

In fig. 24, the first section in the series which cuts the funnel, we see the dorsal and ventral lip with a narrow aperture (*ov. f.*) into Somite XIII.

In fig. 25 (next section in the series) the folding of the funnel is evidenced by the discontinuous edge, a portion of which opens directly into Somite XIII (*ov. f.*); another portion (*ov. f'*), itself folded, communicates solely with the ovisac.

In fig. 26 (two sections further on) the septum separates the

two portions of the funnel, and that opening into the 13th somite (*ov. f.*) is very small; in the second section beyond this it is absent. But that part of the funnel communicating with the ovisac (*ov. f.*) is of much greater extent, and occupies a large part of the outer wall of the ovisac. It is still present in fig. 27, five sections further on, where it lies on the dorsal wall of the ovisac, and does not cease till two sections beyond this, so that it passes through about six more sections than does that part which communicates with Somite XIII. Each section is .1 mm. thick, so that the size of this funnel is about 1 mm. in extent, of which only about .5 mm. communicates with Somite XIII.

There is thus an approach to the condition met with in Eudrilidæ, where the funnel opens entirely into the ovisac.

The ovisac itself is thin-walled and slightly subdivided; in the sac of one side were two ova (fig. 28 represents a portion of the fourth section of the series after fig. 27). Each of these exhibits karyokinesis (see fig. 29, which is drawn from the next following section), in which the spindle with the chromosomes arranged at the equator and the "centrosome" and polar rays at its poles are very well seen. The one sketched was sectioned along the axis of the spindle; the other ovum, lying at its side, was cut at right angles to the axis.

Each of these ova measures .3 mm.—exactly the same diameter as the largest ovum in the ovary; it is surrounded by a thick "vitelline membrane," which in the one sketched was folded at two points, owing, no doubt, to contraction.

These two ova appear to be undergoing changes preliminary to the formation of polar bodies.

I am not aware whether this phenomenon has hitherto been definitely recorded as occurring in the ovisac;<sup>1</sup> but there is little doubt that such is the case, the ova undergoing maturation here just as the spermatozoa attain their complete condition in the sperm-sacs.

<sup>1</sup> Vejdovsky, in his "Entwicklungsgeschichte," finds that the polar bodies in *Rhynchelmis* are formed in the ovisac, while in *Lumbricus* and *Allolobophora* they are not formed till the ova are laid in the cocoon.

There are normally three pairs of spermathecae in Somites VII, VIII, and IX. Each sac is pyriform, with a long duct opening at the anterior margin of its somite in a line with the lateral chaetæ. But the number appears to be subject to variation, as I have notes of three abnormalities amongst the score or so of the worm examined, viz.:

A.	Right side:	spermathecae in	VII, VIII;	left side,	VIII, IX.
B.	„	„	VIII, IX;	„	VIII, IX, X.
C.	„	„	VIII, IX;	„	none.

But in this last case the worm had apparently passed its maturity, as other organs were very small, e. g. sperm-sacs, and it is quite difficult to see the spermathecae in immature worms; they were, for instance, overlooked by Beddard in *Allurus*, probably for this reason.

#### § The Vascular System (figs. 6—10).

It is in the vascular system that *Sparganophilus* differs most remarkably from other forms.

The dorsal vessel, which lies freely above the gut, is broad, constricted at the septa, and runs, as usual, throughout the body. In each of the Somites XI, X, and IX it is specially dilated, and frequently slightly curved (fig. 6). In front of Somite IX the vessel suddenly diminishes in diameter to about a third its previous size, and thence runs with a gradually decreasing diameter to the first somite.

The ventral vessel presents no noticeable feature. Supra-intestinal and subneural vessels are absent.

In each of the Somites II to XI a pair of commissural vessels pass from the dorsal to the ventral vessel. Those of Somites II to VI are small equidiametered vessels, whilst those in Somites VII to XI are much larger, moniliform, and slightly contorted; these are the "lateral hearts" (figs. 6, 9).

In each of the succeeding somites, with the exception of Somites XII and XIII, a pair of dorsal tegumentary or "peripheral" vessels is given off by the dorsal vessel, near the hinder septum, which it perforates in order to pass to the

body-wall (figs. 6, 8); a similar ventral tegumentary vessel joins the ventral vessel in each somite, and has a similar relation to the septum: these two vessels, however, only communicate indirectly in the plexus on the body-wall. In addition two pairs of intestinal vessels pass from the dorsal vessel to the gut wall, and two or three pass from this to the ventral vessel in the "mesentery" which attaches this to the gut (fig. 8).

From the dorsal tegumentary or peripheral vessel of Somite XIV a longitudinal vessel runs forwards on the body-wall (fig. 6), and a similar vessel from the ventral tegumentary of this somite accompanies it. These two longitudinal tegumentary trunks can be traced forwards to about the second somite, where they break up into small branches, entering the capillary plexus on the walls of the pharynx, to which network the dorsal vessel also contributes. These longitudinal trunks lie on the inner surface of the body-wall throughout their course (fig. 9), and give off branches to the body-wall and nephridia in each segment,—behaving, in fact, just as do the posterior metamERICALLY arranged tegumentary vessels given off from the median trunks. They give off no branches to the gut wall. In the body-wall is an elaborate capillary plexus (not reaching into the epidermis), receiving constituents from the above-mentioned tegumentary vessels. The nephridia are marked by their pink colour in the fresh state, owing to a dense plexus of blood-vessels upon them, and even with a hand-lens one can see the dilatations described by Claparède, Lankester, and myself in *Lumbricus* upon the nephridial and other somatic vessels. This is especially noticeable in the clitellar region.

The dorsal vessel has a dark red or rather a brownish-red colour, owing to the chloragogen cells surrounding it combining their brownish tint with the red colour of the blood. The intestine appears beautifully red, owing partly to the feeble development of granules in the chloragogen cells, but chiefly to the presence of a perienteric blood-sinus (figs. 7, 8, 9) instead of the more usual network of capillaries. This sinus

appears to commence with the intestinal region in Somite IX, in front of which a capillary network of the ordinary character exists. The constituents of this network enlarge, the meshes are thereby reduced, and a gradual coalescence and disappearance of the walls gives rise to a sinus. In Somite VIII and partly in Somite VII a plexus appears superposed on the sinus, with which it communicates, the plexus being a very close one and the vessels large. More anteriorly the sinus is absent, and a plexus of capillaries only surrounds the gut.

The blood-supply of the pharynx is derived, as above mentioned, from a network, with which the dorsal and lateral vessels communicate; the commissural vessels do not, as far as I can ascertain, give any branches to this plexus—they run round the œsophagus to the ventral vessel. This pharyngeal plexus is continuous with the œsophageal plexus just described.

The lateral hearts of Somites XI, XII, give off a branch to the sperm-sacs.

The present worm is, then, remarkable on account of (*a*) the perienteric sinus, and (*b*) of the longitudinal tegumentary vessels.

(*a*) The sinus, which is similar to that found in many mud-loving and tube-forming Polychætes—as, for example, Sabellids, Arenicola, &c.—occurs but rarely among the Oligochæta; in fact, outside the family of Enchytræidæ it is practically unknown, or at any rate unrecorded. Vejdovsky, in his ‘System und Morph. d. Oligochaeten,’ represents a transverse section of *Allolobophora cyanea* on pl. xvi, fig. 22, in which a sinus surrounds the intestine; again, in fig. 8 of the same plate, illustrating *Dendrobæna rubida*, a sinus is represented around the gut; but he does not label this, and it may be merely a diagrammatic representation of the ordinary plexus. Again, on pl. xiv, figs. 2 and 9, two transverse sections through *Criodrillus* show a perienteric sinus labelled “*ds.*,” which letters indicate “Gefassschlinge des Magendarmes” according to the explanation of the plate.

In the body of the work I find no specific mention of any sinus, though in reference to *Allurus*, *Dendrobæna*, &c.,

he remarks (p. 115) that important modifications occur in the internal vessels, to which "I shall not now allude further."

Beddard states, on p. 549 of his memoir on *Libyodrilus*, that "the plexus of blood-vessels on the wall of the œsophagus, which lie immediately below the epidermis (*sic*), was nowhere a sinus, although the individual vessels were so close together as to give this appearance"—his figures represent a sinus.

From my own observations, I find that *Criodrilus* is provided with a sinus similar to that of *Sparganophilus*, which, like it, is replaced anteriorly by a plexus; but in the hinder part of the œsophageal region certain portions of the plexus are wider than the rest, so that in section it looks as if one had sections of separate vessels; but closer examination of several sections shows that there is really a continuous sinus. Wiren has described in *Arenicola* a very similar condition of intestinal vascular system, which had, up to his time, been considered and represented as a network.

I find, amongst the *Lumbricidæ*, another genus with a distinct perienteric sinus, namely, *Allurus*; this I find in sections, and by removing a portion of the intestinal wall.

In *Dendrobæna rubida*, however, I am unable to satisfy myself as to whether a sinus or a network exists, though I am inclined to believe the latter.

The condition of a perienteric sinus is, by some zoologists, regarded as more primitive than that of a network, and this opinion appears to rest on the suggestion that the vascular system is directly derived from the blastocœl or segmentation cavity. What amount of embryological evidence exists scarcely suffices to settle the matter in regard to *Oligochætes*. Wilson ('*Journ. of Morphology*,' iii, p. 408), in his memoir on the "Embryology of the Earthworm," states that the first vessel to appear is the subintestinal; this is at first without proper walls, and occupies a place between hypoblast and splanchnic mesoblast; but here and there a cell may be detected in its dorsal wall, and these gradually increase in number till the vessel is provided with its own proper wall. He was unable, after the most careful examination, to detect the precise origin of these



walls. He surmises—and this, I think, is from an a priori view probably correct—that the wall arises from the wandering cells of the mesoblast, and the blood-vessels are probably formed, as in the Vertebrata, as spaces amongst the mesoblast-cells, which then give rise to the wall of vessel.

The suggestion that they represent blastocœl seems as little true as that the cœlom does so; of course, both occupy the position of the blastocœl.

From the point of view of comparative anatomy, too, the existence of a sinus does not seem an archaic one, for it is not in simple or “primitive” Polychætes, for example, that this exists, but in the more evidently modified tubicolous forms belonging to the families Serpulacea, Terebellacea, Telthusida, Chlorhæmida, and others. I say these are not primitive forms, and among many reasons for this view I may point to the character of the excretory system in these families; in place of the metameric repetition of simple and similarly formed nephridia, we find suppression of some and enlargement of others; or a differentiation, again, to form excretory organs and genital ducts. A second character upon which I should rely in support of my suggestion is in the accompanying disappearance, or at least extreme reduction, of the septa.

On the other hand, in such simple forms as *Polygordius* and *Protodrillus*—whether this simplicity be primitive or due to degeneration is a matter for discussion—we find no perienteric sinus, and indeed but little in the way of an enteric vascular system. In the more generalised *Nereis* and its allies, which may perhaps more closely represent a primitive Polychæte—not an ancestor of this group, but an early representative of the group, with all the characteristic features well marked—an elaborate plexus around the gut exists.

In fact, the purpose of a vascular system being to distribute nutriment, &c., its usefulness would evidently be increased if the contained fluid were to take a definite course. This would not be the case in a great sinus, though perhaps interchange of

gas or fluid will be more rapid where this exists than where it is replaced by a network.

(b) With regard to the longitudinal tegumentary vessels arising from the dorsal and ventral vessels in Somite XIV, the only earthworm presenting an arrangement at all like that in *Sparganophilus* is *Criodrilus lacuum*. Rosa describes and figures (fig. 4, "Sul Cr. lac.," in 'Mem. d. R. Acad. d. Sci.,' Torino, xxxviii, 2nd ser.) a single longitudinal branch on each side arising from the commissural vessel connecting dorsal and subneural vessels in Somite XII, and running forwards on the body-wall beyond Somite VII. These "vasi ricorrenti" are applied against the body-wall, along the lateral line, and send no branches to the intestine.

Longitudinal vessels, at first sight similar to those in *Criodrilus* and the present worm, are met with in *Urochæta*, *Megascolex*, *Microchæta*, *Lumbricus*, and others, where they have received the name "intestino-tegumentary." But in reality these are very different, for they are in relation chiefly with the gut wall, from the plexus in which, in the majority of cases, they arise, though in *Lumbricus* the two vessels are branches from the dorsal vessel in Somite X. As Bourne<sup>1</sup> has shown, these longitudinally placed vessels correspond with short vessels occurring in each somite behind XIII, which terminate at each end in a capillary plexus, at one end on body-wall, at the other on gut wall. The intestino-tegumentary vessels likewise arise from network on gut-wall, and send branches to body-wall.

The "intestino-tegumentary" vessels, too, lie in close apposition to the œsophageal wall, whereas the tegumentary vessels of *Criodrilus* and *Sparganophilus* adhere to the body-wall and have no connection with gut-wall. But just as the intestino-tegumentary vessels are modified representatives of the posterior metamERICALLY arranged short vessels, so it would appear that the tegumentary vessels are very elongated representatives of branches to the body-wall, given off by

<sup>1</sup> "On *Megascolex cæruleus*," 'Quart. Journ. Micr. Sci.,' vol. xxxii.

the peripheral or tegumentary vessels in each of the posterior somites.

I may note a peculiar appearance occurring in the larger blood-vessels; the blood-clot has not a smooth surface, but a fringe of needle-like processes set at right angles to general surface of clot, and recalling a crystalline structure (see fig. 18).

### III. The Affinities of *Sparganophilus*.

From the character and extent of the clitellum the genus evidently belongs either to the family *Geoscolicidæ* or to the *Rhinodrilidæ*.<sup>1</sup> The possession of tubercula pubertatis points more directly to the latter, for except in the family *Lumbricidæ* these organs are known only in *Rhinodrilus*, *Hormogaster*, and *Microchæta*.<sup>2</sup> *Anteus* probably is another instance, for both Horst<sup>3</sup> and Perrier<sup>4</sup> describe a band extending along each side of the ventral surface of a certain portion of the clitellum. *Urobænus*, too, will very probably be found to possess these structures, though my specimens were too badly preserved for me to be certain of their existence.

The situation of the generative pore at the hinder margin of Somite XVIII separates the worm from the *Lumbricidæ*, whilst it marks a point of agreement with the genera *Rhinodrilus* and *Hormogaster* so far as concerns the intersegmental position of the pore.

The arrangement of the sperm-sacs and their number refer *Sparganophilus* to the *Rhinodrilidæ*, and several other characters of the family are presented by it.

In one point, however, it differs from the members of this family, viz. in the absence of œsophageal or intestinal diverticula.

*Sparganophilus tamesis*, then, is one of the *Rhino-*

<sup>1</sup> For references to descriptions of the genera here named, see my "Attempt to Classify Earthworms," 'Quart. Journ. Micr. Sci.,' vol. xxxi.

<sup>2</sup> Benham, 'Proc. Zool. Soc.,' 1892.

<sup>3</sup> 'Notes from the Leyden Museum,' xiii, p. 77.

<sup>4</sup> Perrier, 'Nouv. Arch. d. Muséum,' 1872.

drilidæ which, having become aquatic in habit, has undergone certain modifications, which give it a resemblance at first sight to *Criodrilus*, an aquatic Lumbricid; for example, the loss of a gizzard, the disappearance of nephridia from the anterior somites, the vesicular character of the cœlomic epithelial cells surrounding the nephridia, the peculiar modifications in the vascular system—viz. the breaking down of a network on the gut to form a sinus—and the longitudinal tegumentary vessel, and the absence of dorsal pores.

#### SYSTEMATIC.

Family *Rhinodrilidæ*, mihi.

*Sparganophilus*, nov. gen.

Clitellum extensive, occupying nine or ten somites; bounded latero-ventrally by tubercula pubertatis.

Prostomium not marked off from the peristomium.

Male pores inconspicuous, between Somites XVIII and XIX, without accessory organs.

Sperm-sacs, two pairs; no median sac.

Spermathecæ simple; three pairs.

No gizzard nor œsophageal diverticula; no typhlosole.

Vascular System.—The only commissural vessels are situated anteriorly; perienteric blood-sinus; no subneural vessel. A couple of longitudinal tegumentary vessels on each side traverse the anterior somites, and have no connection with the gut wall.

Species *S. tamesis*, n. sp.

Since only a single species is known, it is well-nigh impossible to separate specific from generic characters.

Distribution.—There is but little doubt that the home of the *Rhinodrilidæ* is America, and the occurrence in England of a member of the *Rhinodrilidæ* is very striking. Hitherto only one member of the family has been discovered in Europe, viz. *Hormogaster*, from Italy; the more typical genera, *Anteus*, *Rhinodrilus*, and *Urobenus*, being South American.

*Microchæta* is confined to the south of Africa. *Kynotus*, *Tykonus*, and *Callidrillus*, *Michaelsen*,<sup>1</sup> are also African. *Bilimba*, *Rosa*,<sup>2</sup> is from Burmah; and *Glyphidrillus*, *Horst*,<sup>3</sup> comes from Malay. The habitat of *Brachydrillus* is unfortunately unknown.

The Thames is visited by all sorts of traffic, and it is possible that cocoons may have been brought over with timber; or amongst the roots of some water plants, such as *Anacharis alsinastrum*, from North America, and like it have increased and multiplied in our rivers.

Beddard has recently ('Annals and Mag. of Nat. Hist.,' ser. 6, vol. ix, 1892) suggested that *Anteus* and *Rhinodrillus* are one and the same genus (p. 118), and states that the only points in which the two genera differ are—

- (1) The presence of a greater number of calciferous glands; and
- (2) The presence of an elongated prostomium in *Rhinodrillus*.

He rightly suggests that these characters are without generic importance, but he overlooks the absence of spermathecae<sup>4</sup> in *Anteus*; and it seems to me that till we know from the examination of sections whether sperm-ducts exist (which they probably do, and perhaps, as in *Sparganophilus*, they are in the body-wall), and where they open externally, we shall scarcely be justified in uniting the two genera. The character of the nephridial loop in *Anteus* is very different from that of *Rhinodrillus*. *Michaelsen* ('Arch. f. Naturgesch.,' 1892) has

<sup>1</sup> *Kynotus*, *Michaelsen*, 'Jahrb. d. Hamburg. wiss. Anstalt.,' ix, 1891; and 'Arch. f. Naturgesch.,' 1891; *Rosa*, 'Boll. Mus. Zool. Torino,' vii, 1892. *Tykonus*, 'Arch. f. Naturg.,' 1892.

<sup>2</sup> 'Annal. Mus. Cir. d. Stor. Nat.,' Genova, 1890.

<sup>3</sup> 'Zool. Anzeig.,' 1891.

<sup>4</sup> One or two species of *Allolobophora* are stated to be deprived of their spermathecae; I am not aware at what period of life these species were examined. *Allurus tetraedrus* is usually stated to be deprived of them. I can confirm *Vejdovsky* in stating their existence. I have found three pairs opening dorsally of the lateral setæ.

recently further extended the genus *Anteus* to include *Urobenus*; but it appears to me that the characteristic intestinal cæca in Somite xxvi, as well as the peculiar shape of the œsophageal glands, the pyriform glands, the absence of ornamentation in the chætæ, and other features, are sufficient to separate the two genera: his *Anteus papillifer* is undoubtedly *Urobenus*. I would, therefore, still retain the three genera *Anteus*, *Rhinodrilus*, and *Urobenus* as distinct.

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#### EXPLANATION OF PLATES XIX & XX,

Illustrating Dr. Benham's paper on "A New English Genus of Aquatic Oligochæta (*Sparganophilus tamesis*) belonging to the Family *Rhinodrilidæ*."

FIG. 1.—Dorsal view of *Sparganophilus tamesis*; enlarged twice.

FIG. 2.—Ventral view of the anterior end of the worm; enlarged twice.

FIG. 3.—The hinder end of the worm, dorsal view, to show the elongated pygidium; much enlarged.

FIG. 4.—Two cocoons; natural size.

The figures 1, 2, 3, 4, are lithographed from coloured drawings retained in the author's possession.

FIG. 5.—A chæta. Note the ridges.

FIG. 6.—The worm dissected from above, intended to exhibit chiefly the vascular system. The nephridia are omitted. *Com. v.* One of the commissural vessels, which occur only in the anterior somites. *Dors. v.* Dorsal blood-trunk. *D. teg. v.* One of the tegumentary vessels arising from the dorsal trunk, and repeated metamerically throughout the body behind Somite XIII. Their relations to the septa are not accurately shown (see Figs. 8 and 10). *heart.* One of the five lateral hearts. *Int.* Intestine, commencing in Somite IX. *Long. teg. v.* The longitudinal tegumentary vessels arising from the tegumentary vessels of Somite XIV: that connected with the ventral vessel is in outline. *œs.* Œsophagus. *sal. gl.* One of the three pairs of salivary glands. *spth.* Spermatheca. *V. teg. v.* One of the ventral tegumentary vessels.

FIG. 7.—Longitudinal section through three Somites, XI, XII, XIII, in order to show the perienteric blood-sinus. Only structures occurring in the middle line are shown, and no detail is intended. The figure is sufficiently explained on the plate.

FIG. 8.—A diagrammatic transverse section in the posterior region of the body. On the left side a septum is represented, on the right the cœlom is almost filled by the nephridium. *apert.* Apertures in the septum for the passage of the tegumentary vessels, which originate from the median trunks immediately in front of the septum, and pass through the septum to be distributed to the somite behind. *D. ves.* Dorsal trunk. *Dors. teg. v.* The dorsal tegumentary vessel: that part lying in front of the septum is transversely shaded. *Int.* Intestine, with its perienteric blood-sinus. *l. ch.* Lateral chætæ. *Neph.* Nephridium. *ne. d.* Wide tube of the nephridium perforating the body-wall. *ne. p.* Nephridiopore. *ne. v.* The branch from the tegumentary vessel to the nephridium. *Vent. teg. v.* Ventral tegumentary vessel: its portion lying in front of the septum is outlined by dots. *V. v.* Ventral vessel.

FIG. 9.—Diagrammatic transverse section through one of the anterior somites. The figure is sufficiently explained on the plate. On the left side, the dorsal and ventral longitudinal tegumentary vessels are shown simply cut across; on the right side, the branches from them to the body-wall are indicated. As in other figures, that connected with this ventral vessel is merely outlined, the other being solid.

FIG. 10.—A diagrammatic view of four posterior somites: the worm has been opened along the left side, the body-wall on this side being depressed; the arrow points to the anterior end of the preparation. The tegumentary vessels are here represented in their true relation to the septa, which they perforate. One nephridium (*neph.*) is outlined, and its funnel (*ne. f.*) indicated. *ne. v.* is a cut nephridial vessel.

FIG. 11.—A general view of the generative organs. To some extent it is diagrammatic, in that the chætæ and the sperm-duct are shown as if the body-wall were transparent. In the last three somites, too, the nephridiopores are shown (*ne. p.*). *cil. ros.* The two pairs of ciliated rosettes. *clitell.* The extent of the clitellum. *Epid.* The post-septal coiled part of the sperm-duct, the epididymis. *lat. ch.* Lateral chætæ. *ov.* Ovary. *ov. d.* Oviduct, the funnel of which is shown bending into the ovisac. *sp. sac.* Sperm-sac. *sp. d.* Sperm-duct, which lies in the body-wall (see Fig. 19). *sp. p.* Spermiducal pore. *sph.* Spermatheca. *t.* Testis. *vent. ch.* Ventral chætæ.

FIG. 12.—A longitudinal median section through the anterior end of a specimen in which the buccal region is withdrawn, with the exception of a small portion (*a—a'*) of the upper lip. *cer. g.* Cerebral ganglion. *N. c.* Nerve-cord. *prosl.* Prostomium. *Pit.* Prostomial pit. *sac.* Dorsal sac of

the pharynx, opening by a wide mouth. *sept.* One of the septa: the first one appears to be between Somites II and III. The relative thicknesses of epithelium in various parts are represented. The letters *a, b, c, d*, merely indicate points or regions to be compared with those similarly lettered in Fig. 13.

FIG. 13.—A longitudinal section through the anterior end of a specimen in which the buccal cavity is everted. The series of sections were not quite parallel to the vertical plane, so that the upper portions are really more laterally situated than the lower; hence the sac of the pharynx appears to open by a narrow orifice: this is merely the narrower lateral part of the orifice, which is wider medially. Most of the letterings as in Fig. 12. *sal. gl.* Salivary gland. *oes.* Œsophagus. *long.* The longitudinal muscles of the body-wall. *circ.* The circular muscles. *a, b, c, d*, indicate regions for comparison with their position in Fig. 12.

FIG. 14.—A portion of the epithelium at *a* in Figs. 12 and 13.

FIG. 15.—A portion of the epithelium of the buccal cavity between *b—c* in Fig. 12.

FIG. 16.—A portion of the epithelium from the floor of the pharynx behind *c* in Fig. 12.

FIG. 17.—A portion of the epithelium of the roof of the sac of the pharynx behind *d* in Fig. 12.

FIG. 18.—A portion of the wall of the intestine where the septum (*sept.*) nips it, as at *a* in Fig. 7. *Int. epith.* Intestinal epithelium, the details in which are represented only on the left. Each cell has a dense, deeply staining border, represented in the figure by the darker line; and the light band outside this is probably caused by closely pressed cilia. *circ. mus., lg. m.* The muscular coats of the intestine. The blood-clot in the perienteric blood-sinus exhibits a peculiar fringing of its outer border.

FIG. 19.—The ventral half of a transverse section through Somite *xvi*, in order to show the epidermic position of the sperm-duct on each side—immediately outside the tubercula pubertatis (*tub. pub.*). *vent. ch.* Ventral chætæ. *cl.* Clitellum. *cl'.* The thin extension of the clitellum across the ventral surface.

FIG. 20.—A portion of a transverse section more highly magnified, showing the structure of the sperm-duct. The specimen of which this is a section had passed its sexual maturity. The epidermis (*ep.*) is evident, the rounded nuclei indicating rather short cells whose outlines are not evident. Below is a peculiar tissue—due, I believe, to degenerate clitellar cells (*cl. deg.*). *b. v.* Blood-vessels in this region. *circ.* Circular muscles. *long.* Longitudinal muscles.

FIG. 21.—A portion of a transverse section in the same series as that of



Fig. 19. It passes through the 18th somite behind the chætæ, close to the spermiducal pore. The sperm-duct is quite superficial. *tub. pub.* Tubercula pubertatis.

FIG. 22.—Section through the male pore, from the same series as Figs. 19 and 21. *sp. d.* Sperm-duct, filled with spermatozoa. *ep.* Ordinary epidermis, dipping in to meet the wall of the duct. *b. v.* Blood-vessels. *cl. c.* Clitellar cells.

FIG. 23.—A sperm-sac in longitudinal section, under a low power. *sept.* Septum. *ax.* Axial group of muscle- (?) fibres, traversing the sperm-sac for some distance. *trab.* Trabeculæ of the same tissue; various stages in the development of the spermatozoa are indicated.

FIGS. 24—27 represent selected sections from a series through the oviducal funnel. XIII, XIV, indicate the somites. *sept.* The intervening septum. *Int.* Intestine.

Fig. 24 passes through the opening of the funnel (*ov. f.*) into Somite XIII.

Fig. 25. The next section of the series shows the folding of the funnel, and its bending over into the ovisac. *ov. f.* That part of the funnel communicating with Somite XIII, and which is cut along its edge. *ov. f'.* That part opening into the ovisac.

Fig. 26. Two sections further on: the opening of the ovisac into Somite XIII is past. The funnel (*ov. f'.*) dips into the sac and lines one wall.

Fig. 27. The fifth section beyond the last; still shows a small portion of the funnel in the ovisac.

FIG. 28.—A section through the ovisac two sections further on than Fig. 27. A couple of ova are seen: each exhibits a karyokinetic figure.

FIG. 29.—One of the ova represented in Fig. 28, much more magnified, showing the nuclear spindle, chromosomes, and cytasters. It is probably about to form directive corpuscles. The irregularity in the vitelline membrane is due to reagents.

FIG. 30.—A portion of a section through the clitellum.

FIG. 31.—A longitudinal section of a nephridial funnel. *c.* The nucleus of the central cell. *c. ep.* Flat cœlomic epithelium covering the back of the funnel. *m.* Marginal cells. *ex. m.* Extra-marginal cells.

FIG. 32.—A transverse section of a nephridial funnel. *c.* Central cell. *m.* Marginal cells. *ex. m.* Extra-marginal cells. *c. ep.* Flat cœlomic epithelium.

FIG. 33 represents a section through a spherical mass of cells lying in front of a nephridial funnel (*neph. f.*). *y.* Yellow granules embedded in the mass.



**On the Relationships and Rôle of the Archoplasm during Mitosis in the Larval Salamander.**

By

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With Plate **XXI.**

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IN the thirty-seventh volume of the 'Archiv für mikroskopische Anatomie' F. Hermann figured and described certain bodies existing in the dividing spermatocytes of the salamander and Proteus in these words: "Ausserhalb der deutlich sichtbaren Kernmembran liegt nun diesen Kernen ungefähr in der Form eines flachen Brodlaibes eine Scheibe körnigen Protoplasmas an, die durch ihre dunkler Färbung deutlich sichtbar wird." These archoplasmic bodies, as he named them, are apparently homologous, on the one hand, with the "sphères-attractives" of van Beneden (described as arising simultaneously), and on the other with that remarkable structure of which Platner has said, "Der in dem Protoplasma vieler Zellen sich findende sogenannte Nebenkern<sup>1</sup> hat in neuerer Zeit durch die Untersuchungen von Nussbaum, Gaule, Masanori Ogata und Andern ein immer grösseres Interesse erregt."

The great rôle which Platner ascribed to these bodies in the

<sup>1</sup> The term Nebenkern has been applied to a great variety of structures by as many authors, but as the majority of these descriptions relate to bodies either parasitic or obviously different from the above, I have abstained from any detailed reference to them.

divisional metamorphosis in the cells constituting the spermatocytes of *Helix*, renders their homology with similar structures forthcoming in the cells of Vertebrates, of paramount importance to those desirous of embracing under some more general formula the numerous as well as heterogeneous life-histories which constitute our knowledge of this subject.

No one, so far as I am aware, has instituted any close inquiry into the specific relationships existing between these various "archoplasms," "sphères-attractives," and the apparently often similar "Nebenkerns."

It is not, for example, generally recognised that if the archoplasm, as figured by Hermann, has the relationships he described in his work,<sup>1</sup> or is equivalent to that apparently similar outer portion of the "sphère-attractive" of van Beneden and Boveri, the sphère, as it appears in a variety of tissue-cells described in Flemming's works, differs in essential parts from theirs.

In Flemming's figures it is never represented as composed of more than a simple radiation related to one or two central bodies, with or without that immediate lighter zone, the "medullary corpuscle" of van Beneden. The whole "sphère-attractive" of van Beneden and Boveri, however, always consists of three distinct parts, an outer archoplasmic portion and inner medullary corpuscle enclosing one or two central bodies, while there is often present a prominent external radiation of the whole cell-mass. Our knowledge of the specific relationships between these various zones, bodies, radiations, and the similar parts in the archoplasm ("Nebenkern") is in a most unsatisfactory condition.

It is not apparent whether the radiation about the central bodies of Flemming<sup>2</sup> in tissue-cells and leucocytes is equivalent to the archoplasmic portion of van Beneden's sphère, or to its entirely external radiation.

<sup>1</sup> 'Archiv für mikroskopische Anatomie,' vol. xxxvii, p. 575.

<sup>2</sup> See Flemming on the Leukocytes and the Attraktionsphären of the cell, in the 37th volume of the 'Archiv für mikroskopische Anatomie' on 'Taf. xiv, pp. 274—287, and figures.

It is not clear whether the archoplasm is more especially related to reproductive cells, or is a normal constituent of the resting sphere, though often masked by individual specialisation.

It is not known whether the immediate relationship existing, according to Platner, between the disappearance of the "Nebenkern" (archoplasm of Boveri and van Beneden) and the generation of the spindle, is found elsewhere than in the cells of *Helix*;<sup>1</sup> although the last results of Hermann, in his work on the spermatocytes already referred to, is, at any rate, not antagonistic to a belief in its existence.

A series of observations on the conditions of these various bodies and zones in several tissues of the larval salamander, most notably the undifferentiated genital ridge and the leucocytes, have not only enabled me to arrive at definite conclusions respecting the above relationship of archoplasm and spindle, but, by the powers of the beautiful process of research inaugurated by Hermann, have thrown considerable light on the foregoing confusions.

In salamander larvæ, taken while living from the parent, fixed with the platinum chloride solution, reduced with "Rohen Holzessig," cut and examined without further preparation, after the manner of Hermann, the archoplasm ("Nebenkern," "sphère-attractive") was beautifully differentiated in the cells constituting the embryonic genital ridge (figs. 1, 3, 4, 7, 8, 16) as a pale grey round or oval mass, as sharply circumscribed as, and often not much smaller than the nucleus itself (figs. 5, 7, 4, 8).

When most conspicuous, however, the archoplasm is relatively small (figs. 13, 16, 14), and in this condition presents, even with the highest power, only doubtful suggestions of "medullary zone" or central body, and there are good grounds for believing that in some conditions of the cell<sup>2</sup>

<sup>1</sup> See Platner's second paper "Zur Bildung der Geschlechtsprodukte bei den Pulmonaten," 'Archiv. mikr. Anat.,' Bd. xxvi, p. 604.

<sup>2</sup> *Infra*, pp. 194, 195.

those appearances apparently indicative of such structures were absolutely illusory.

The definite nature of the whole archoplasmic structure, however, in this undifferentiated tissue will, on comparison with that figured and described by Hermann and Meves,<sup>1</sup> be obvious at once.

Whether this difference finds an explanation in the much younger condition of my material<sup>2</sup> or in some happy manipulative chance I can offer no direct opinion, but incline rather to the belief that all those cells figured by Hermann were taken during a phase of structural metamorphosis when the body, though extremely large, is most difficult to differentiate as a concrete whole, growth being always inversely proportional to distinctness, as in figs. 13—16, 2, 3, 4, 11, 10.

Notwithstanding this it is possible, however, by appropriate preservation and staining (see below), to determine that all the resting cells of the genital ridge present distinctly bounded archoplasmic figures—often, it is true, ovoid (fig. 7), elongated (fig. 9), or bent like a German sausage round the nuclei, to which they may or may not be closely applied.<sup>3</sup>

The extreme pallor of the archoplasm when large and expanded, as it is towards the advent of mitosis, calls for special manipulation, as I have just stated. I have been most successful in the use of a combination of Flemming's triple stain with the reduction process of Hermann, or by staining with hæmatoxylin after such reduction.

The sections were stained very black, and washed out with acid alcohol.

When we have become assured of the presence of an archoplasmic body, it is often possible, in this condition of the

<sup>1</sup> 'Anat. Anzeiger,' 1891, vi, "Ueber amitotische Kernteilung in den Spermatogonien des Salamanders und Verhalten der Attraktionssphäre bei derselben.

<sup>2</sup> Hermann's results were obtained from spermatocytes of salamander at the end of the summer.

<sup>3</sup> Cf. Meves' description of the "Spermatogonien," loc. cit.

cell, to discern its contour when the tissue has been treated by Hermann's method alone.

By whatever means it has been brought into view, there is always presented in this particular phase of cell life one or two central bodies (figs. 3, 4), immediately surrounded by the light zone, "medullary corpuscle" of van Beneden (figs. 3, *b*, 4), across which can be traced a few broad radial bands, putting the central body (or bodies) in connection with a large and pale granulous sphere, the archoplasm (fig. 3, *c*), the radiation of whose granules is centred to the "medullary zone" as a whole, and not directly towards the central body, as in the "spheres" of van Beneden.

The further relation of these constituent parts and the general protoplasmic radiation of the cell are identical with that obtaining in the segmentation spheres of *Ascaris*.

As I have already said, all these parts are never visible at once in any attraction-sphere of Flemming; but it may be borne in mind, from what has gone before, that the archoplasm, prior to the onset of mitosis, is extremely difficult of differentiation.

Further, in this condition the central bodies and their immediate zone (medullary corpuscle) are far more easy of diagnosis than the archoplasm is itself, as in fig. 2.

And it is no less certain that this condition of things is presented by far the greater number of the cells in the genital ridge (of the salamander), and I believe elsewhere, owing to its long duration.

All these considerations may perhaps, to some extent, account for the conspicuous absence of description of anything clearly comparable to the archoplasm (outer portion of the "sphère-attractive"), or the "Nebenkernel" in any of Flemming's magnificent researches.

There is, however, in this author's second paper in the thirty-seventh volume of the 'Archiv' (his figs. 25 and 26) a delineation at least very suggestive of an archoplasmic body, and in the latter figure it occupies a very remarkable position, as the sequel will show.

The term "Nebenkern," as I have before incidentally mentioned, has been applied by a variety of authors indiscriminately to all manner of foreign particles, from parasitic bacteria and fungi, to globules of purely manipulative origin. And the confusion thus arising has been so much deepened by the involved karyokinetic phenomena in the tissue-cells of adult animals as to make investigators, at least for the present, wary of associating any variable structure with well-ascertained bodies such as the central corpuscles and their radiation. And it is probable that Flemming, while dealing with such tissue, has through his habitual caution figured only that of whose nature he was absolutely certain.

Notwithstanding the apparently intimate relation we have already traced between the archoplasm in the genital ridge of the salamander and the "sphère-attractive" of van Beneden and Boveri (the homology between the first and the "Nebenkern" of Platner needs no discussion), certain difficulties remain as yet unexplained.

In Hermann's figures of the archoplasm of the spermatocytes there is no "medullary zone," and, as he goes on to say, "eine sichere Diagnose eines Polkörperchens ungemein erschwert."

The description I have given above, where all these parts were present in the embryonic genital ridge—that is, in the tissue which directly gives rise to the spermatocytes—shows that this difficulty probably arises merely from structural changes during maturation.

Again, as Hermann himself points out, the "sphère-attractive" of van Beneden is duplicated, whereas the archoplasm in the cells constituting the spermatocytes is invariably single. It should, however, be borne in mind that the "sphère-attractive" in some of Boveri's figures (27, 71, 73, 74) is certainly not duplicated;<sup>1</sup> whilst I have found besides several traces of such division of the archoplasm ("sphère-attractive") in the genital ridge of the salamander—one undoubted example (fig. 6).

<sup>1</sup> T. Boveri, "Zellenstudien," 'Jenaische Zeitschrift für Medicin,' Bd. xxii, p. 685.



I trust, then, that in the above I have made it clear how certain objections to a complete structural homology between the "sphère-attractive" of van Beneden and the archoplasmic bodies in the spermatocytes of *Helix* and *Amphibia*, are removed by the observations I have recorded in the undifferentiated genital ridge of the salamander; and how the difference existing between the spheres described in these, and those from various types of cells by Flemming, may in part result from the archoplasm being difficult to put "en évidence," in the prevailing condition of the resting cells. I now pass on to a confirmation and extension of the above results, obtained by the discovery of bodies strictly comparable to the archoplasm ("Nebenkernel") in the leucocytes of the same larval salamander.

So far as I am aware no such bodies have ever been described in any leucocytes before.

The able researches of Flemming on this subject<sup>1</sup> show the relatively large central body (always single in his figures) as related to a marked and simple radiation, extending through but a fraction of the granular cell-mass, the archoplasm as well as the "medullary corpuscle" of van Beneden being entirely absent.

In fig. 23 I have copied two of Flemming's leucocytes, in order to facilitate a comparison between the spheres represented there, and those of my figs. 17—19. The remarks I have already made respecting the extreme difficulty with which the archoplasm is differentiated during certain phases of its life apply here as elsewhere, only more so; for the dark nature of these elements renders the coloration obtained from a combination of Flemming's and Hermann's methods (p. 184) only successful under exceptional circumstances, and then only by dint of an objectionably bright light and small diaphragm.

The use of hæmatoxylin is preferable to the triple orange stain, but I have found the simple reduction process of Hermann peculiarly adapted to this portion of the work.

In leucocytes thus treated there appears a dense spherical

<sup>1</sup> 'Archiv für mikroskopische Anatomie,' Bd. xxxvii, pp. 249—297.

mass, obviously homologous to the archoplasm ("Neben-kern"), concentrically gathered about a very distinct pale zone, the "medullary corpuscle" of van Beneden, which encloses one or two large and beautifully defined central bodies (figs. 17—20).

A delicate radiation spreads from the whole sphere to the periphery of the cell. This is not concentric with the radii of the archoplasm, nor are these latter centred towards the enclosed body or bodies, but to the "medullary corpuscle" as a whole.

Thus it is seen that the radial conditions apparent in the spheres of *Ascaris*, *Helix*, and the undifferentiated genital ridge of the salamander, repeat themselves in the leucocytes of the last.

In certain leucocytes I have often observed the archoplasm expanded like a fan, whose apex is usually turned towards the nuclear elements, and crowned by a distinct and stained central body from which radiations pass in all directions (fig. 20).

This condition appears to me to be strictly analogous to that in figs. 13, 14. Whatever method may have been used with respect to the leucocytes, in the majority the archoplasm is with difficulty or not at all forthcoming, the central body or bodies usually appearing related to a simple radiation extending at once from them to the circumference, the condition being closely similar to that I have represented in the cells of the genital ridge in fig. 22; and both appear to present structural relationships identical with those figured by Bürger in the cell-bodies of the Nemertian "Leibesflüssigkeit."<sup>1</sup>

From these differences of appearance in the archoplasm it is in the highest degree probable that the leucocytes present a similar archoplasmic metamorphosis to that I have alluded to, and shall presently describe in detail, in the cells constituting the genital ridge, and which is so conspicuous, according to Platner, in the spermatocytes of *Helix*. The existence of the "Neben-kern" (archoplasm) in the cells of the embryonic

<sup>1</sup> 'Anatomischer Anzeiger,' 1891, p. 484.

genital ridge of the salamander, while yet undifferentiated to form either ova or spermatozoa, shows that this structure cannot bear any special relation to the spermatocytes; while its occurrence, as I have shown, in cells at once so widely different from these, and primitive, as the leucocytes, exclude it from any peculiar relation with the reproductive elements at all, and speaks volumes for its probable existence in all the intermediate tissue forms.

From the similar appearance and relationships of the archoplasm ("Nebenkern" of Platner) in Vertebrates and Invertebrates alike, and from the wide distribution and appearance of this structure wherever the conditions favour the elucidation of the sphere, I confess I see no alternative but to regard the archoplasm as a normal accompaniment of the period of comparative repose that marks the resting cell.

The foregoing comparison between the spheres and their constituent parts in these various animal cells, might appear pedantic, and in the present state of our knowledge unnecessary, if it were not that some of these parts are probably, as we have seen, the fleeting expression of metamorphic phenomena; while others, such as the central bodies, though dividing, retain their characteristics unimpaired.

It will have become obvious that the archoplasm ("Nebenkern" of van Beneden), when considered independently of its enclosed zone or central body, undergoes a cycle of changes of form and size, each corresponding more or less closely with changes proceeding in the nucleus itself, on its passage from a condition of complete repose to one of active mitosis.

It should be borne in mind, however, while discussing this question, that the successive archoplasmic phases by no means invariably keep pace with the corresponding nuclear metamorphoses.

For example, as Flemming has pointed out,<sup>1</sup> so marked a feature as the divarication of the central bodies, and the

<sup>1</sup> "Attraktionssphären und centralkörper in Gewebszellen und Wanderzellen," 'Anatomischer Anzeiger,' 1891, pp. 79, 80.

appearance of an initial spindle, is not by any means necessarily accompanied by any specific condition of the nucleus, which may present the aspect of repose or active looping of its constituent chromatin elements (cf. figs. 10, 22, 11).

I have often observed in the genital ridge of the salamander the co-existence of a nearly full-sized spindle and a resting nucleus (figs. 11, 22); and this peculiar retardation of the looping of the chromatin, and ultimate disruption of the nuclear membrane, presents many points of analogy, and may be directly related, to the peculiar conditions Hermann described as existing in the older spermatocytes. During any given mitosis final equilibration is always reached by the nucleus prior to that of the archoplasm and its related constituents (figs. 16, 13, 14).

In attempting to follow this cycle and its meaning, I have chiefly concerned myself as heretofore with the cells constituting the embryonic genital ridge of the salamander. And from what experience I have had with other tissues, I am inclined to the belief that the conditions passed through elsewhere, will be found to closely resemble those met with in these.

In these cells of the genital ridge the archoplasm is always most condensed and conspicuous, as I have said, in those elements that have just completed their division, and whose nuclei present the well-known horseshoe shape. These horseshoe nuclei are represented by previous authors<sup>1</sup> with their concavities looking directly away from one another, and with the cornua of the nuclear figures in the plane of the paper.

In the cells under examination I have never found this to be the case, the planes containing the nuclear cornua being parallel, and quite or nearly normal to an axis passing through the extremities of the enclosed spindle and the central bodies. These relationships existing between the planes of the daughter-nuclei and the spindle axis are represented in fig. 24.

I have laid some stress on this point, as it is doubtful if the

<sup>1</sup> "Neue Beiträge zur Kenntniss der Zelle," Flemming, 'Archiv für mikr. Anat.,' Bd. xxxvii.

following description of the archoplasmic metamorphosis during mitosis will otherwise be intelligible. Although, as I have more than once remarked, the archoplasm is most conspicuous immediately after the division of the cell, it will, for reasons that will make themselves sufficiently obvious in the sequel, be better to begin with that expanded archoplasmic figure characteristic of the period immediately prior to the onset of mitosis (figs. 1, 3, 4).

At this period, as we have seen, the sphere is built up of its full complement of parts (central bodies, zone, and archoplasm), as in the spheres of *Ascaris*; and to the external surface of the archoplasm there is usually related a fine radiation of the peripheral cell protoplasm (figs. 3, 7, 8).

A slight concavity presents itself on that side of the nucleus facing the archoplasm, and the chromatin usually presents signs of active metamorphosis. In elements a trifle more advanced, the central body is already divided (fig. 9), and the two halves now recede from one another through the archoplasm, the intervening portion acquiring a fibrillated appearance—the initial spindle of Hermann (fig. 9, *a*).

Simultaneously with this divarication of the central bodies, the archoplasm elongates in the direction of their motion until it assumes the pointed ovoid form represented in fig. 9.

The central bodies continue to recede from one another until they occupy the polar extremities of the archoplasm, the fibrillated appearance of the intervening portion creeping over a greater and a greater area, until it is co-extensive with the contour of the whole mass (figs. 10, 11), when the archoplasm presents the appearance of a full-sized spindle.

During all these changes a corresponding disturbance is apparent in the exterior radiation, its fibres showing a marked tendency to follow the central bodies as foci while en route to the polar extremities of the archoplasm, until simultaneously with their arrival in that position they assume the characteristics of the well-known astral radiations.

At this juncture the nucleus may or may not have lost its membrane and become looped, but it invariably shows a

marked concavity (fig. 22) on the side opposite the archoplasm, now elongated in the form of a spindle. The nucleus also has become elongated, so that it presents an initial form corresponding to the final horseshoe outline of the daughter-nuclei. The plane of this initial horseshoe is conspicuously at right angles to that of the archoplasmic axis, which at this period is also bent, so that the two structures interlock after the manner of one horseshoe hanging in the concavity of another. The chromatin is now looped across the longer axis of the nucleus, as in the final condition (figs. 21, 13); the nuclear membrane, becoming wavy and indented, as described in the spermatocytes by Hermann, finally disappears, the chromatin elements remaining free in the cell-mass.

Prior to this disruption of the nuclear membrane, the radiations from the central bodies become connected with the individual chromatic elements. But the question whether they are extra-nuclear structures and push inwards from without (as suggested by Strassburger and Watase<sup>1</sup>), or are continued at the expense of the intra-nuclear substance from within, must remain for the cells here described an open one.

These astral radiations are completely outside the archoplasmic spindle (if I may use the term), and, as Hermann says, they invest it like a mantle.

The free ends of the loops of chromatin stand stiffly out at right angles to the inner spindle-fibres (the central spindle-fibres of Hermann). They usually, however, do not complete the circle, the space left being probably the representative of the side of the cell destitute of nuclear elements in Hermann's figures of the spermatocytes.

All these chromatin bodies are absolutely outside the spindle, and I can obtain no evidence from the cells of the above embryonic ridge that any of the spindle-fibres are formed from the intra-nuclear protoplasm at any time.

In some cases the spindle is apparently not continuous from end to end, the fibres presenting an appearance somewhat

<sup>1</sup> 'Studies on Cephalopods: Cleavage of the Ovum,' S. Watase, 'Journ. Morph.'

resembling the duplicated conical figure described by van Beneden,<sup>1</sup> and therein supporting the views advocated by Watase.<sup>2</sup>

This appearance is precisely what would be produced by the evolution of halves of the spindle from a duplicated archoplasmic mass such as is represented in fig. 6, and I am inclined to believe that it may have a most important bearing on the curious "oblique division" described by Flemming.<sup>3</sup>

This subject, however, requires much further investigation.

From the above description of the central bodies, and the formation of the spindle, it appears that the latter structure is formed entirely from the intervening archoplasm, and from nothing else.

The astral radiations, as Hermann has pointed out, are to be regarded as the medium by which the chromatin fibres are dragged along the central archoplasmic spindle on which they slide.

So far, the karyokinetic phenomena appertaining to the cells constituting the embryonic genital ridge of the salamander are only so many confirmations and extensions of those Platner described as presented by the spermatocytes of *Helix*. From this point onward, to that at which the daughter-nuclei begin to collect about the poles of the di-astral figure, and an annulus forms about the cell corresponding to the point of disruption of many of the spindle-fibres to which I have alluded, the metamorphosis is perfectly normal. Afterwards the spindle-fibres show a strong and increasing tendency to become concentrated about the intermediate body of Flemming.<sup>4</sup>

While the chromatin is gathering itself together, as in the preceding diagram, fig. 24, the central bodies occupy the

<sup>1</sup> "Nouvelles recherches sur la fécondation et la division mitosique chez l'Ascaride Mégalocéphale," 'Bull. Acad. Belg.,' 3 sér., t. xiv, No. 8, 1887.

<sup>2</sup> Loc. cit., p. 14; cf. also Wood's 'Hall Lectures,' 1891.

<sup>3</sup> 'Archiv für mikr. Anat.,' Bd. xxxvii, pp. 735-744.

<sup>4</sup> Op. cit. I have never seen more than one of these bodies in the cell of the undifferentiated genital ridge of the salamander, and only one is figured by Flemming in the spermatocytes (fig. 14).

apices of the conical spindle figure, round which the chromatin elements lie.

Fine protoplasmic fibrillæ complete the space between these elements and the apices, passing through a well-marked lighter zone in their immediate proximity (the "medullary corpuscle" of van Beneden).

The present condition of the cell is most favorable for the study of this "medullary zone" and central body. The zone (fig. 3, *c*) presents a somewhat irregular contour, which appears to correspond exactly in diameter to that region in which the individual fibres of the astral radiation are compressed together into a nearly homogeneous sphere, its size naturally being directly related to their specific diameter (fig. 3, *c*).

In the phases immediately succeeding this, the centring of the spindle-fibres about the intermediate body becomes more and more marked, until, for a more or less considerable pyramidal space on either side the division plane, they are completely fused (figs. 14, 15). This fusion presents the appearance of a refractive dusky spot, which, growing at the expense of the remaining spindle-fibres, spreads outwards as a hollow sphere, whose optical section presents a pair of cornua (figs. 14, 15), and from this time onward it is undistinguishable from, and presents the characteristics of, the archoplasm.

This relation of the archoplasm to the spindle, and its final regeneration from the spindle-fibres, is precisely what Platner described as obtaining in the spermatocytes of *Helix*.

While the archoplasm is thus regenerating itself on either side of the division plane, the central bodies at the apices of the whole spindle figure begin to approximate once more, while the nuclei apparently recede until the bodies are lost in their dark granulation. Hitherto I have been unable to satisfy myself of their presence in this situation, for the axial bay or perforation in which they ought to exist is filled by astral radiations, which present the appearance of having been sucked in after them (figs. 13 and 21). But it cannot be doubted that they do pass this spot, as they reappear immediately, creeping up the cones of fibres which remain



directed towards the concavities of the horseshoe-shaped daughter-nuclei (figs. 14, *a*, 16, *a*).

So soon as the central bodies have reached the archoplasm and become stationary within it (figs. 14, *b*, 15) that structure steadily grows, becoming fainter and fainter until it has attained the gigantic size represented in figs. 1, 3, 4, 8. A "medullary zone" makes itself apparent about the central bodies, and we are brought back again to that condition of the resting cell from which we started.

I have not arrived at the same exact conclusions respecting the archoplasmic evolutions in the leucocytes, partly owing to their small size and peculiar granulation, and possibly to some actual difference in the appearance of the spindle and its associated parts. Nevertheless, I have seen indications of the archoplasm in these cells being drawn out to the lenticular form described in those of the genital ridge. Their central bodies often exist duplicated (fig. 17), and between these bodies stretches that dusky band (fig. 17, *a*) which we have seen in other cells to represent the embryonic spindle.

Moreover, from such arrangements of the chromatin as are figured by Flemming in his paper on the leucocyte (op. cit., fig. 2, *b*), there is little room left for doubt as to the existence of a spindle, although direct evidence of its presence cannot always be obtained.

Again, the fan-shaped archoplasms in the leucocytes, such as fig. 20, often present relationships in recently divided elements apparently analogous to the conditions represented in figs. 13—16), i. e. they are the collecting fibres of a spindle figure stretching between two separating elements.

The conclusions of the whole of this part of the inquiry, then, appear to be (i) that with respect to the cells constituting the undifferentiated genital ridge of the Vertebrate (salamander), Platner's generalisation concerning the spermato-cytes of the Invertebrate (*Helix*) that "zwischen Knäuelgerüst, spindelfasern und Nebenkern ein genetischer Zusammenhang existirt," is wonderfully borne out; (ii) that the archoplasm is an accompaniment of the attraction-sphere in

the leucocytes of the larval salamander, exhibiting a metamorphosis, the known phases of which have been seen to closely correspond with those in the larger and more easily elucidated elements. Lastly, all the cells I have described are little differentiated (or, at any rate, their divisional phenomena are not complicated by the presence of secondary structures arising during the development of adult tissues), and the ease with which the archoplasm (Nebenkern of Platner) is discernible in such elements, has, I believe, been the sole cause of its association more particularly with the reproductive ones, when, in reality, it would appear to be an essential factor in a type of indirect division wide-spread among the tissues of Vertebrates and Invertebrates alike.

In conclusion I must thank Professor Howes for his kindness in allowing me the use of the Huxley laboratory, and for many valuable suggestions during the progress of the work.

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### DESCRIPTION OF PLATE XXI,

Illustrating Mr. John E. S. Moore's paper "On the Relationships and Rôle of the Archoplasm during Mitosis in the Larval Salamander."

FIG. 1.—Resting cell from the undifferentiated genital ridge of the salamander, showing lobose archoplasm and central bodies.

FIG. 2.—Ditto, showing central body; the archoplasm undifferentiated.

FIG. 3.—Ditto, showing (*a*) central body, (*b*) medullary zone, (*c*) archoplasm, (*d*) the external radiation of the cell-mass. Hermann's treatment and hæmatoxylin.

FIG. 4.—Ditto, Hermann's treatment and triple orange stain.

FIG. 5.—Ditto, Hermann's treatment alone.

FIG. 6.—Ditto, showing duplicated archoplasm. Hermann's treatment alone.

FIG. 7.—Ditto.

FIG. 8.—Two resting cells which have recently completed their division, showing the relative position of the archoplasms and their external radiation.

FIG. 9.—Cell from the genital ridge, showing the central bodies receding from one another through the mass of the archoplasm, and the intra-fibrillated portion (*a*).

FIG. 10.—Ditto, showing the central bodies at the extremities of the pointed archoplasm.

FIG. 11.—Ditto, Hermann's treatment and hæmatoxylin.

FIG. 12.—Recently divided cells from the genital ridge, showing intermediate body of Flemming (*a*), and the spindle-fibres radiating on either side of this.

FIG. 13.—Ditto, showing regenerated archoplasm on each side of the division plane. Hermann's treatment and Flemming's triple stain.

FIG. 14.—Ditto, ditto, showing central body (*a*) entering into secondary connection with regenerated archoplasm.

FIG. 15.—Ditto.

FIG. 16.—Two recently divided cells of the genital ridge, showing regenerated archoplasms, and relation of the central body (*a*).

FIGS. 17—19.—Leucocytes, showing archoplasm, medullary zone, and central body. The latter is divided in Fig. 17, and the two portions are connected by a dusky bridge (*a*). Hermann's method and hæmatoxylin.

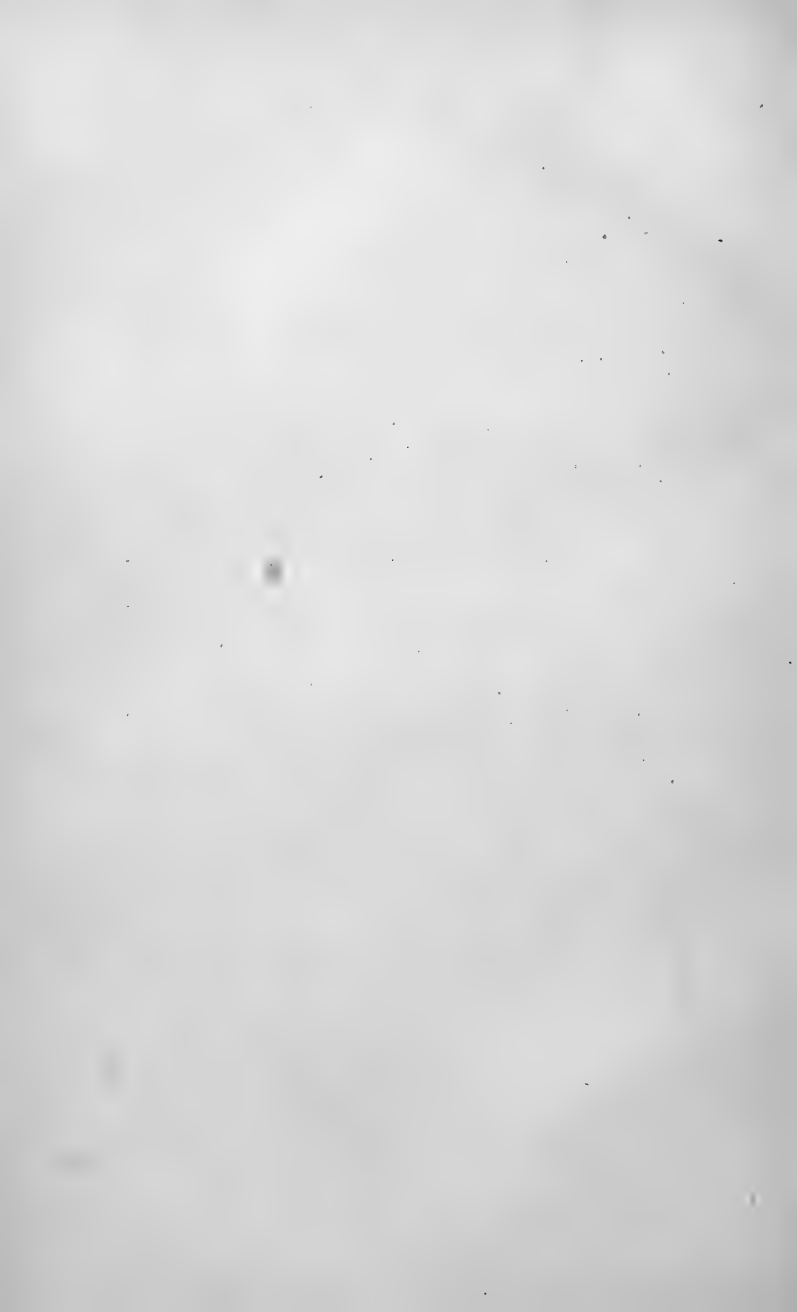
FIG. 20.—Ditto, showing central body, radiation, and fan-shaped archoplasm.

FIG. 21.—Cell from the embryonic genital ridge, showing the annular form of the daughter-nucleus, and the relation of the central body and its radiation within the annular apertures.

FIG. 22.—Ditto, showing the interlocked condition of the archoplasmic spindle and nucleus.

FIG. 23.—Two leucocytes with attraction-spheres, after Flemming.

FIG. 24.—Diagram showing the relation of the nuclei and the spindle.



## On the Occurrence of Embryonic Fission in Cyclostomatous Polyzoa.

By

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With Plates XXII, XXIII & XXIV.

THE results of the present paper have formed the subject of a preliminary communication made to the Cambridge Philosophical Society (16). The case of embryonic fission which I have now to describe in greater detail appears to me, on the assumption that my explanation of the observed facts is the correct one, to be without parallel in the animal kingdom.

My observations refer entirely to the genus *Crisia*, and in particular to a form common at Plymouth, which I have described as a new species under the name *C. ramosa* (17). The general results may be stated as follows:—

(i) The ovicell, which is morphologically equivalent to a zoëcium, develops at the growing-point in the same way as an ordinary zoëcium.

(ii) A polypide-bud is found in the young ovicell, consisting of tentacle-sheath and a part which represents the alimentary canal of a polypide.

(iii) Small egg-cells are present in various parts of some of the growing-points. One of these acquires a close relation to the potential alimentary canal of the ovicell-polypide.

(iv) This potential alimentary canal grows round the ovum, losing its previous form, and becoming a compact multi-

nucleated follicle surrounding the egg, which at first lies in an excentric cavity in the follicle.

(v) The ovum segments<sup>1</sup> and the blastomeres may, in early stages, be completely separated from one another. The relations of the segmenting egg to its follicle are similar to those described by Salensky (28) in *Salpa* (cf. Salensky's figs. 12, 13, on pl. x).

(vi) The ovicell is meanwhile maturing, and by the end of the segmentation of the ovum has been shifted to some distance from the growing-point by the superposition of new zoœcia above it. Its non-calcified aperture, which, at an earlier stage, formed the wide end of a large funnel, has become constricted, and has grown out into a long tubular orifice.

(vii) At the end of segmentation, the embryo consists of a small mass of undifferentiated cells, lying near the distal end of the follicle, which has increased largely in size, and now forms a spherical knob projecting freely into the interior of a spacious tentacle-sheath. A complicated arrangement of cells connected with the aperture has meanwhile been formed.

(viii) The follicle becomes vacuolated, and is soon transformed into a nucleated protoplasmic reticulum. The tentacle-sheath loses its distinctness.

(ix) The number of blastomeres increases, cell-limits being indistinguishable at this, as at all other stages, excepting the very earliest.

(x) The embryo, having thus considerably increased in size, although remaining a solid mass, without differentiation of organs, grows out into several finger-shaped processes, which are generally directed towards the distal end of the ovicell.

(xi) The finger-shaped processes are divided up by a series of transverse constrictions into rounded masses of cells, each of which becomes a complete larva.

(xii) This process of embryo-formation continues during the whole functional period of the life of the ovicell, and is still actively proceeding at a stage when many of the embryos are mature, or nearly mature. The number of (secondary) embryos

<sup>1</sup> The occurrence of a process of fertilisation was not made out.

present in an ovicell at any one time may exceed one hundred, and these have all been produced by budding from the above-described "primary embryo."

(xiii) Each of the "secondary embryos" acquires its well-known two-layered condition at the time of its separation from the budding mass of embryonic cells. It develops in a vacuole of the protoplasmic reticulum, which presumably supplies it with nutriment since the embryo rapidly increases in size, becoming ciliated externally, and ultimately escaping through the tubular aperture of the ovicell as a characteristic Cyclostome larva.

Taking the above history into consideration, it is not surprising that, as is actually the case, the Cyclostome larva differs considerably in structure from that of other marine Polyzoa. This history also explains the fact that no observer has ever succeeded in giving an account of any process corresponding to egg-cleavage in Cyclostomata.

The protoplasmic mass surrounding the embryos has been figured by Smitt (34),<sup>1</sup> who has alluded to the yellow colour so characteristic of the contents of the ovicell. This colour is contained principally in the protoplasmic reticulum, although the embryos themselves have a yellowish colour.

The first satisfactory account of the Cyclostome larva was, however, given by Barrois (1), who calls special attention to the fact that no previous observer had been able to discover "genital products" in any Cyclostome, and adds, "Je n'ai pour ma part encore réussi qu'à suivre les morulas jusqu'à des stades composés d'un nombre d'éléments de moins en moins nombreux et plus volumineux, sans réussir encore à constater d'une manière bien certaine la présence de l'œuf;" although supposing that the Cyclostomes do not really differ from other Polyzoa in this respect.<sup>2</sup> Barrois' failure to understand the early development of the embryos is readily explained if my own account be correct; and it is not surprising, con-

<sup>1</sup> See his pl. iv, fig. 2.

<sup>2</sup> L. c., pp. 58, 59, note.

sidering the great difficulty of making out anything of the nature of the early stages except by means of sections.

Barrois expressly states that the earliest stage to which he succeeded in tracing his morulas with certainty is that represented in his pl. iii, fig. 3. This stage exactly corresponds with the condition at which I have found the embryos to be constricted off from the budding primary embryo (cf. Pl. XXIII, fig. 11). Barrois was, however, once successful in finding a cell, the egg nature of which he considers uncertain (his pl. iii, fig. 1); and in another case in finding what may have been an egg divided into two blastomeres. It is not easy to say whether the former cell was really an egg, or whether it was merely one of the giant-cells described below.

The rest of Barrois' account contains an erroneous history of the later stages, which he himself was the first to correct (2). I am compelled to doubt altogether Barrois' account here given (not accompanied by any figures) of the supposed occurrence of a process of segmentation of the egg, accompanied by the formation of an epibolic gastrula. In a later paper (3) Barrois figures quite accurately the "morula" at the stage at which it becomes independent (his pl. i, fig. 26), although he wrongly supposes that the inner layer of cells disappears in the later stages (his pl. iii, figs. 29, 30).

Although Metschnikoff (23, pl. xx, figs. 61—64) gives admirable figures of the early embryos of *Discoporella radiata*, the earliest stage observed by that author is the stage at which the "secondary" embryo becomes free from the budding mass of embryonic cells. Ostromnoff (25) is no more fortunate in elucidating the early history of the embryo of *Cyclotomata*.

### I. Development of the Ovicell.

This process, which takes place fundamentally in the same manner in all the species of *Crisia* which I have examined, has been to some extent described by Smitt (34), although most writers have paid little attention to the difference



between the form of the adult ovicell and that of the younger stages of the same organ.

The ovicell is developed at the growing point, and it is here that the early stages in the development of the egg take place. A young internode<sup>1</sup> may be described as an acute-angled isosceles triangle with two sub-equal sides (*AB*, *AC*). Within the triangle a calcareous septum occurs parallel to *AB*, cutting off the oldest zoëcium of the internode from the others. The next septum is parallel to *AC*, and is nearer to the base of the triangle. The formation of septa, alternately parallel to *AB* and *AC*, gives rise to a series of alternate zoëcia, an arrangement characteristic of *Crisia*. The oldest zoëcia are, of course, those nearest to the apex of the triangle, and the central part of the base is the region from which, with continued growth, fresh zoëcia are cut off. It remains to be stated that the growing-point, like the adult internode, is flattened, and that the openings of the zoëcia are lateral, and are directed towards one of the flat surfaces of the branch.

As the internode elongates, its proximal zoëcia acquire their full length, and cease to take part in the formation of the growing-point. Or, explaining this by the former illustration, let the internode grow to twice its former length, the growing point remaining of the same width throughout its growth. By producing the lines of the septa already present it will be seen that if the growing point does not grow wider the older zoëcia will be excluded from it, their growth being completed. It follows that the zoëcia, several of which occur in a young state at the end of the branch, become successively shifted to the edges of the growing-point, preparatory to leaving it altogether.

The growth of the zoëcia and of the ovicells takes place by the apposition of fresh material at the distal end. The proximal end of each unit of the colony is first laid down, and the last-formed portion is the aperture. Thus, by drawing a line transversely at any level across an internode, whether the internode bears an ovicell or not, we obtain an accurate idea of

<sup>1</sup> Compare pl. XXIV, fig. 15.

the condition of the branch when the growing-point was at the level of that line. It follows from the shape of the ovicell, that an ovicell which is half grown will have the form of a wide-mouthed funnel, as shown in the figures of Smitt and others. But although it is easy to recognise a young ovicell at this stage, it is anything but an easy matter to distinguish the ovicell while it is still a sub-median member of the growing-point.

The ovicell is indeed merely a modified zoëcium, as is shown by the method of its development, as well as by its internal structure. Further evidence for this statement is afforded by the occasional occurrence of abnormal units of the colony, intermediate in form between the zoëcia and ovicells (17, pl. xii, fig. 12).

In Pl. XXIV, fig. 19, the proximal portion of the ovicell is already developed. The first, second, and third units of the internode are zoëcia, the fourth being an immature ovicell. The growing-point is formed, on the right side, by the base of a lateral branch, which would have been borne by the fifth member of the internode. There follow, in order from right to left, the fifth unit, the actual growing-point capable of producing fresh zoëcia, the sixth unit, and the ovicell. The last occurs at the left side of the growing-point; but while its proximal end is in the same plane with the zoëcia of the internode, the open end of the funnel is already projecting forwards (i. e. in the direction of that surface of the internode on which the zoëcia open). This condition becomes more prominent at a later stage, so that the ovicell, in its most swollen portion, projects considerably beyond the level of the general surface of the internode.

By referring to pl. xii, fig. 11, of my former paper (17) it will be seen that the zoëcium "5" (in fig. 19) would have formed its aperture at the level of the middle of the ovicell, while "6" would have completed its growth at a very short distance above it.

The young ovicell has, at first sight, the appearance of an open funnel. This is not really its condition, since its end is

closed by a chitinous uncalcified membrane (ectocyst). This is the condition of the ovicell, and of the growing-points generally, at all stages before their growth is completed and the definitive apertures are formed. The funnel, which is, in fig. 19, the most conspicuous part of the ovicell, is consequently merely that part of the ovicell in which calcification has occurred.

In fig. 20 (in which the arrangement of the lateral buds does not correspond with that in fig. 19) the zoëcia have been numbered in such a way as to facilitate comparison with fig. 19. The zoëcium "5" is already complete, while "6" is beginning to free itself from the growing-point. The growth of the ovicell has progressed, the most swollen part is already completed, and the aperture (still closed by a membrane of uncalcified ectocyst) is beginning to constrict.

In fig. 21 the zoëcia "6" and "7" are complete. The aperture of the ovicell is still further constricted, and now consists of a slit-like portion which will soon close completely, and of a wider portion which will become the base of the tubular aperture so characteristic of this species (*C. ramosa*). A comparison of figs. 19—21 with one another will show that the method of the growth of the ovicell has been such as to bring its distal portion on to the front of the branch, while its proximal portion is lateral, and in series with the zoëcia. The base of the tubular aperture thus comes to be situated at about the middle line of the internode.

The valve of the ovicell (17, pl. xii, fig. 10) is formed as a ridge from the back of the ovicell at a stage between figs. 20 and 21. The growth of the ovicell will be completed by the outgrowth of the tubular aperture.

So far as I have been able to make out, the aperture is closed by the uncalcified membrane of ectocyst at all stages of its development, and does not become actually perforated until the escape of the first larva. I am quite unable to say when and how the process of fertilisation is effected.

## II. The Male Sexual Elements.

There can, however, be no doubt of the existence of spermatozoa in Cyclostomes, although I am not aware that they have previously been described.

In *Crisia* I have usually found them in colonies without ovicells<sup>1</sup> (17, p. 145), although they occur in ovicell-bearing colonies in *Idmonea serpens*.

The spermatoblasts occur in masses filling up a large portion of the body-cavity of sexual individuals. The sperm mother-cells in both *Idmonea* and *Crisia* seem to occur in groups of four (Pl. XXII, fig. 4); and the four flagella when first developed appear, under insufficient magnification, as if they belonged to one cell. The mature spermatozoon (fig. 4) possesses an elongated head (measuring about  $\cdot 0064$  mm.), and a long, active flagellum.

In *C. cornuta* it was noticed that a delicate, hyaline layer of endocyst protruded from the aperture of the zoëcium, during the escape of the spermatozoa, in the form of a cone at the apex of which the spermatozoa escaped.

## III. The Origin of the Secondary Embryos.

My observations on this part of the subject have been made almost entirely by means of sections. The ovicells were preserved and decalcified, at one operation, by placing in a mixture of corrosive sublimate, nitric and acetic acids. The most successful staining was obtained with Grenacher's hæmatoxylin or with borax-carmin, in the latter case washing with alcohol containing picric acid.

The free larva of *C. eburnea* is well figured by Barrois (1, pl. iii, fig. 22). It is, roughly speaking, cylindrical in shape, being covered externally by a complete coating of cilia. At one end of the cylinder is an aperture leading into the "sucker," by means of which fixation is effected; and, at the opposite end, is another aperture leading into the so-called

<sup>1</sup> In one case, spermatozoa were found in a colony of *C. cornuta*, which bore a single very young ovicell.

“mantle-cavity.” I have observed no trace of a “pyriform organ.” Barrois (2, p. 142; 3, p. 43, pl. iii, fig. 31) states, however, that he has discovered a rudiment of this structure in the larvæ of *Discopora*.

The internal structure of a young larva may be illustrated by means of fig. 23, a median longitudinal section. The sucker is already well developed, having been formed, as in most other *Ectoproct* larvæ, by a process of ectodermic invagination. Cilia have appeared on the greater part of the external surface, the non-ciliated part of the ectoderm representing the portion which will be later invaginated to form the mantle cavity. The inner layer of cells is still perfectly distinguishable, forming a thin layer, closely applied to the ectoderm, and enclosing a cavity which occupies the whole of the interior of the embryo.

The earlier stages, which alone concern us at present, may be realised by assuming that the volume of the embryo shown in fig. 23 has become largely reduced; and that the sucker has become flattened out. Slightly anterior to the stage of fig. 22, the sucker is much shallower, and opens by a wide aperture in the middle of the “oral” surface. Still earlier, the sucker is a very slight depression of the thickened “oral” ectoderm. The inner layer is at this stage a layer of great tenuity, in which a nucleus is thick enough to form a swelling wherever it occurs. Before this, the embryo is plano-convex, the position of the future sucker being represented by its flat side; and, still earlier, it is rounded in section, the inner layer consisting of a few cells, completely surrounding a central cavity. Between this stage and that shown in fig. 22, the inner layer may be separated, in parts or completely, from the ectoderm; so that it would be impossible to overlook its presence in any well-preserved section.

At the earliest stage at which the embryo is free in the ovi-cell, it consists of a small rounded mass (Pl. XXIII, fig. 11) The outer layer is in the form of a continuous mass of protoplasm, enclosing one layer of nuclei. The inner layer also consists of continuous protoplasm, with a very small number

of nuclei arranged in one row; and it encloses a minute central cavity.

Pl. XXIV, fig. 17, represents a median section, slightly magnified, of an ovicell of *Crisia ramosa*. The ovicell contained in all about 115 embryos, which were embedded in a loose protoplasmic reticulum, filling up most of the cavity of the ovicell. In the older embryos, the conspicuous sucker or "internal sac" is clearly seen; and in some of them, a slit-like space which is the mantle-cavity. The aperture of the latter to the exterior is not shown in any of these embryos. To the left of the ovicell is the structure from which all the embryos have been produced. This structure is labelled "primary embryo;" the evidence that this name implies its real nature being given in the sequel. The primary embryo is produced into several processes; and indications are seen, in at least one case, that the end of the process is being constricted off, as a rounded mass of cells, which is equal in size to the smallest of the embryos found free in the protoplasmic reticulum.

Fig. 11 (Pl. XXIII) is a longitudinal section of a young ovicell, at the period when the formation of "secondary" embryos (i. e. embryos which are developed by budding from the "primary" embryo) has just commenced. The protoplasmic reticulum includes one or two free embryos, the structure of which has already been described. The most conspicuous structure in the section is, however, the large primary embryo, which consists of a dense mass of granular protoplasm containing numerous nuclei, and having an extremely embryonic appearance. This structure is in a state of active growth, as is shown by the occurrence of nuclei with karyokinetic figures. The proximal end of the primary embryo is compact and rounded, and contains centrally a group of nuclei which are distinguished by the activity with which they are undergoing division. The opposite end of the primary embryo is produced into several irregular processes, which show constrictions at intervals. From the ends of two of these processes, embryos have just been constricted off, and

are seen disconnected from the primary embryo. The constrictions indicate the limits of as many future embryos.

The "primary embryo" contains, distally, an irregular cavity. It is difficult to be sure of the exact arrangement of the embryogenic processes; but in some cases at least it is evident that the distal end of the primary embryo has the form of an irregular cup, the processes forming the wall of the cup, from which they become free at their ends. The irregular cavity seen in fig. 11 is part of the cavity of the cup.

Towards the ends of the processes an ectodermic layer becomes clearly differentiated; while, in the centre of each of the swellings indicating a future embryo, a small group of inner-layer cells can, in some cases, be clearly distinguished. The ectoderm of the processes is continuous with the outer nucleated layer of the primary embryo, and with the similar layer immediately lining its distally-placed cavity. The inner-layer cells of the secondary embryos are continuous with the inner nuclei of the more solid, proximal half of the primary embryo. But these nuclei and the protoplasm surrounding them are not throughout clearly differentiated from the outer layer of nuclei. I am, however, inclined to suppose that the somewhat triangular, clear mass of protoplasm at the proximal end of the primary embryo, containing actively dividing nuclei, is the region which gives rise to the inner-layer cells. This region can generally be distinguished with ease in ovicells at this stage.

The primary embryo consists of a mass of embryonic cells (or, rather, nuclei embedded in continuous protoplasm) which are obscurely differentiated into outer and inner cells (or nuclei). The whole function of this embryo is to act as an embryogenic organ, or producer of secondary embryos, and it possesses no structures which can be described as its own organs.

At its proximal end, the primary embryo is budding off nuclei which migrate into the protoplasmic reticulum, where they become indistinguishable from the rest of the nuclei of that reticulum. I have been unable to make out the

significance of this phenomenon, which I have frequently observed.

I am in a position to multiply indefinitely figures showing the important fact that the young larvæ are really produced as buds from a "primary embryo." I consider that I have the clearest possible evidence of the following statements:

i. The larvæ are produced as buds from an embryonic mass of cells found in the young ovicell.

ii. They are produced in no other way than that mentioned under i.

The embryogenic organ is invariably present in all ovicells in which young embryos are found, and in most of the older embryo-containing ovicells as well. It is still active, even at the stage shown in fig. 17. The youngest embryos, free in the reticulum, are invariably identical in structure with the ends of the processes of the primary embryo, and there is not the slightest trace in any of the ovicells, young or old, of the development of larvæ by the ordinary process of the segmentation of an egg.

It might, indeed, be supposed that the bi-nucleated cell shown in the upper part of the reticulum in fig. 11 had the nature of a dividing egg. This supposition is not confirmed by an examination of the actual facts. While the evidence in favour of the origin of the larvæ by a process of budding is unmistakably clear, there are no transitions between such cells as the large one shown in fig. 11 and the young two-layered larvæ. These large cells, which are normally present in the ovicells, are probably of the nature of "giant-cells," similar to those which are found in developing bone. This subject will be considered later; but it may be pointed out that it is possible that the supposed egg-cell figured by Barrois (1, pl. iii, fig. 1) may have been one of these giant-cells.

#### IV. The Development of the Primary Embryo.

Fig. 15 (Pl. XXIV) is a decalcified internode of *C. eburnea*, possessing a very young ovicell. The internode consists of one complete zoëcium, which bears the beginning of a lateral



branch; of a second zoëcium, which is very nearly mature; of the ovicell as the third member of the internode; and of the real growing-point, which contains a young polypide-bud; although the corresponding zoëcium is not yet separated off from the growing-point by a septum.

The ovicell contains a structure which is the exact equivalent of an ordinary polypide-bud. This consists of (1) a thick (proximal) mass of cells, which in a zoëcium would give rise to alimentary canal and tentacles; (2) a thin-walled portion, next to the above, and corresponding to the tentacle-sheath; and (3) a distal portion, indicated by two parallel lines in the sketch, and which is really an invagination of the distal body-wall of the ovicell. This is formed in a precisely similar manner in any young zoëcium, where it develops into the aperture.

Fig. 1 (Pl. XXII) is a nearly median longitudinal section of an ovicell at nearly the same stage as fig. 15. The body-cavity is, as in ordinary zoëcia, largely filled up by funicular tissue, but contains an obvious polypide-bud, the distal portion of which can be clearly distinguished as a tentacle-sheath, similar in all respects to the same structure in an ordinary polypide-bud. The one fact, indeed, which enables this member of the colony to be distinguished as an ovicell is the presence of a relatively large cell, which is closely applied to one wall of the polypide-bud. The latter shows some tendency to give off cells which are growing round the large cell. This has a diameter of about  $\cdot 0176$  mm., and it has a large clear nucleus with one or two nucleoli. Its structure, in fact, reminds one irresistibly of that of an egg; and I believe this cell to be the source from which all the larvæ produced in the ovicell are developed.

“Eggs” of this kind are found in various positions in some of the growing-points. Thus in the particular individual in question there is a second, smaller egg<sup>1</sup> in the same ovicell; and in the next zoëcium there are two eggs<sup>1</sup>, one of which is at the apex of the polypide-bud. The fact that these eggs are commonly found in the growing-points leads me to suppose

<sup>1</sup> Not visible in the particular section figured.

that several are produced in each fertile internode, apparently by a modification of cells of the funicular tissue, and that their further development depends on their entering into definite relation with a polypide-bud. If this association is brought about, it may be assumed that what might at first have developed into a zoëcium becomes an ovicell. In abnormal cases, where several polypide-buds enter into relation with ova, two or more ovicells may be produced in the same internode (17, p. 166; pl. xii, fig. 13). It may further be supposed that the failure to bring about the association between the egg and the polypide-bud results in such abnormalities as that shown in fig. 12 of my former paper, and that this or some other cause, such as the failure to get fertilised, results in the development of the empty ovicells which are so frequently observed.

On decalcifying a number of ovicells, it is soon noticed that many ovicells are either completely empty or are abnormally developed. An ovicell, with complete tubular aperture, may be absolutely devoid of any trace of primary or secondary embryos. In some cases, these empty ovicells are probably the result of degeneration which has set in after the completion of the process of development of free larvæ. After the escape of the last larvæ, the remaining tissues of the ovicells degenerate, and are gradually absorbed. Many of my sections bear out this assertion.

In other cases, however, the degeneration takes place in ovicells which have produced no larvæ. Empty ovicells which are near the growing-points are, probably, generally of this character. It is easy to obtain evidence of the fact that, in such cases, degeneration may set in at various periods—sometimes after the egg has developed to a considerable extent. In some cases, this may be the result of the absence of fertilisation—a process of which I have vainly endeavoured to prove the existence. That fertilisation does actually occur at some period can hardly be doubted, considering the fact that normal spermatozoa are developed in some colonies. In other cases, the degeneration is probably due to the atrophy of the poly-

pides in the zoëcia contiguous to the ovicell. It is well known that the thick calcareous ectocyst of the Cyclostomata is perforated by pores. On decalcifying a colony, and staining what is left, it can be easily shown that all the zoëcia are in organic connection by means of the funicular tissue, which passes through the pores from one zoëcium to another, and from the zoëcia to the ovicell. It can hardly be doubted that the nutriment at the expense of which the larvæ develop is provided by means of the protoplasmic network which thus connects all the individuals of a colony. The ovum is extremely minute, although it gives rise to a massive primary embryo; and this to numerous free larvæ, each of which is very many times larger than the original ovum. This rapid growth—to say nothing of the development of an extensive reticulum of funicular tissue in the ovicell itself—can only depend on the existence of pores by which the ovicell is connected with zoëcia which possess functional polypides.

In fig. 2 the ovum is completely surrounded by the polypide-bud, whose tentacle-sheath has considerably increased in size; while in fig. 3 further alterations of importance have taken place. The tentacle-sheath has grown very much larger; but, so far as this structure and the invagination which forms the aperture are concerned, the ovicell still resembles an ordinary zoëcium. The proximal part of the polypide-bud, which in the younger ovicell was practically indistinguishable from the corresponding structure in an ordinary ovicell, has now become much modified. The egg is now completely surrounded by it; and the polypide-bud has in fact transformed itself into a round mass of cells which may be termed the "follicle." The ovum lies partly surrounded by a cavity in this follicle.

The fact that the distal endocyst is not in contact with the ectocyst is probably due to shrinkage brought about during decalcification. The side-walls of the zoëcium are of course calcified (*cf.* fig. 19), while the distal ectocyst forms an uncalcified membrane stretching across the mouth of the funnel formed by the ovicell.

It is presumably at this stage that fertilisation takes place; but I have in vain looked for any evidence of perforation in the terminal membrane of the ovicell, or for traces of spermatozoa inside the tentacle-sheath. This fact is not really surprising when it is remembered that the finer details of the highly calcified ovicell of *Crisia* can hardly be examined except by means of sections; and that the spermatozoa are very minute.

In fig. 5 the whole ovicell has considerably increased in length. Its irregular form is of course due to shrinkage caused by the action of reagents. The ectocyst is not represented in the figure. The ovicell was probably at about the stage represented in fig. 21.

The valve (*cf.* pl. xii, fig. 10, of my former paper) is now developed as a fold of the ectoderm on the back wall of the ovicell. The aperture has no longer any obvious opening to the exterior; and the tentacle-sheath has increased in size, its walls having become very thin, except at its distal end, which is considerably thickened.

The follicle is slightly larger than before, and its nuclei have obviously increased in number. In place of the egg found in the preceding stage, there are now three egg-like cells, which are not in contact with one another; and which I regard as blastomeres. Remains of the follicle-cavity are still present.

Although I have no direct evidence that the "blastomeres" are really derived from the egg, their subsequent history leaves room for little doubt on this point. The details of the formation of the primary embryo in *Crisia* remind one strangely of the early development of *Salpa*, as described by Salensky (28). This is true not merely of the segmentation of the ovum, but also of the later relations of the embryo to its follicle. Salensky states, for instance, that the blastomeres of *Salpa* may at first be entirely disconnected from one another (*l. c.* pl. x, fig. 10; pl. xxii, figs. 3, 4).

In the next stages, of which I have numerous preparations, but which I have not figured, the number of blastomeres gradually increases. I have been unable to make out any regu-

larity in the succession of the blastomeres, which are, in fact, inextricably entangled among the follicle-cells. They are not necessarily in contact with one another, but may be separated from one another by ingrowths of the follicle-cells, so that in most preparations it is almost impossible to count the number of the blastomeres, or to distinguish all of them from the follicle-cells. An excellent idea of the general relation of the blastomeres to the follicle-cells (or nuclei) may be obtained by referring to some of Salensky's figures of *Salpa*, as his pl. x, figs. 12, 13. The only difference that I can point out between *Crisia* and *Salpa*, as regards the relation of the blastomeres to the follicle-cells, is that in *Crisia* the follicle is somewhat larger relatively than in *Salpa*, and that the blastomeres occupy only the central region of the follicle instead of filling up most of that structure, as in *Salpa*. Remains of the follicle-cavity may still be detected in some of these stages.

In fig. 6 (which is connected with fig. 5 by numerous preparations, forming a perfectly continuous series, in my possession) the tentacle-sheath has increased in size so much as to fill up nearly the whole of the ovicell. The follicle has largely increased in size, and now forms a sub-spherical knob, projecting freely into the cavity of the tentacle-sheath. This stage is a perfectly constant and easily recognised one.

The scattered blastomeres have at last come together to form a small but compact embryo, in some of the nuclei of which karyokinetic figures are discernible. There is no trace of the differentiation of germ-layers in the embryo, which consists simply of a small rounded mass of undifferentiated embryonic cells, or rather of a continuous mass of protoplasm, containing nuclei scattered through it without any attempt to arrange themselves in definite layers.

At the distal end of the embryo is a clear part of the follicle which contains small nuclei. This is apparently a constant feature of the stages near this one; but I have not been able to make out its significance.

Fig. 7 is not cut quite medianly, so that it does not show that the attachment of the follicle to the tentacle-sheath is

much the same as in the former figure. The tentacle-sheath is, however, now becoming less definite. To the left of the figure it is hardly distinguishable from the follicle, with which it probably fuses.

The embryo is practically unaltered, except that it has come to the surface of the follicle; but the principal difference between this and the earlier stage concerns the follicle itself. This structure no longer forms a compact mass of granular, nucleated protoplasm, as in fig. 6; but it has become distinctly vacuolated. This vacuolation is the beginning of the process by which the follicle of earlier stages is transformed into the protoplasmic reticulum of later stages.

Fig. 9 (Pl. XXIII) well illustrates the manner in which this transformation is effected. The tentacle-sheath is not so clear as in the former stage, and can, indeed, hardly be distinguished except at its upper end. Whilst in earlier stages it filled up most of the ovicell, it has now collapsed to a large extent.

The proximal portion of the follicle is in this ovicell still solid, and is perfectly similar in structure to the solid follicle of fig. 6. Distally the follicle is almost unrecognisable, having become separated by enormous vacuoles into strands of anastomosing, nucleated protoplasm. These strands are, however, most unmistakably continuous with the proximal, solid portion of the follicle. The embryo is practically unaltered, still forming a small rounded mass of undifferentiated embryonic tissue lying in a part of the reticulum.

The great increase in the size of the follicle and in the number of its nuclei up to the stage shown in fig. 11 is probably connected with the development of a nutritive arrangement for the young larvæ. The minute egg-cell of fig. 1 gives rise, as I believe, to the embryogenic organ of fig. 11, and this to the numerous young larvæ with which the mature ovicell is crowded. These larvæ lie in the meshes of the protoplasmic reticulum, from which they are probably supplied with nutritive material.

In figs. 6 and 9 the base of the ovicell has a very characteristic structure, always noticed in young ovicells at certain stages.

Next to the ectocyst comes a very definite nucleated layer, which encloses a network of cells separated by smallish vacuoles.

In later stages the outer definite layer of nuclei disappears, and the network becomes continuous with the reticulum formed by the modification of the follicle (fig. 11). The basal network of cells is obviously part of the ordinary funicular tissue, which, as has already been pointed out, forms a continuous connection from zoëcium to zoëcium, or from zoëcium to ovicell, through the pores in the calcareous septa between neighbouring individuals. It can hardly be doubted that the rich protoplasmic reticulum in which the young larvæ lie is the means by which nutriment is conveyed to the developing larvæ.

Fig. 10 is a stage of which I obtained only one example, and I cannot be sure that what is there represented is really a normal process. This preparation indicates that a kind of invagination takes place in the embryo at this stage (which is certainly very near that shown in fig. 9). If this is really correct, the inner layer of the primary embryo may possibly be formed by a process of invagination, and the inner layer of the secondary embryos is then probably derived from this invaginated layer; but I make these suggestions with all reserve.

Fig. 8 is interesting partly because it supports the view advanced in my former paper (17) that the species there described as *C. ramosa* is not identical with *C. eburnea*. The figure is a longitudinal section of an ovicell of *C. eburnea*; and so far as the general development of the ovicell goes, the age corresponds with the stage shown, for *C. ramosa*, in fig. 6.

The tentacle-sheath is at its period of maximum development; but the relative sizes of follicle and embryo are widely different from their relative sizes in *C. ramosa*. This appears to be a constant difference between the two species. In *C. eburnea*, the follicle is reduced to a minimum, and the quantity of the protoplasmic reticulum of mature ovicells is,

consequently, appreciably smaller than that in *C. ramosa*, although in old ovicells of the latter species even, the quantity of the protoplasmic reticulum may be considerably reduced, by the development of the larvæ at its expense. The primary embryo, on the contrary, is relatively very large. It has differentiated a distinct external layer of nuclei, which will give rise to the external layer of the secondary embryos. Throughout the development, the budding secondary embryo of *C. eburnea* differs considerably from that of *C. ramosa*; although the fundamental facts are the same in both species.

I have, unfortunately, no satisfactory sections of the ovicells of other species, which I found more difficult to obtain than the two former species. It is necessary to have a large stock of material in order to study the development; as it usually happens that a very small proportion of the colonies found are provided with ovicells.

The stages intermediate between figs. 9 and 11 have not been figured; but it is easy to describe their general development. After the stage shown in fig. 9 (but not until then) the embryo increases in size, and rapidly transforms itself into the characteristic mass of embryonic cells from which the young larvæ are budded off.

The history of the aperture of the ovicell has, so far, not been considered in sufficient detail. Its commencement as an invagination of the endocyst has been seen in fig. 3. When the egg has begun to segment (fig. 5), the opening of the invagination has closed. The distal end of the tentacle-sheath is, however, now thickened; and the valve is commencing to develop.

In fig. 8 (*C. eburnea*), the valve is practically complete; the distal thickening of the tentacle-sheath has increased, but the invagination constituting the primary aperture has not materially altered. The ovicell is completely calcified except in the region of its aperture, which is beginning to grow out into its tubular form. This part is covered merely by uncalcified ectocyst.

Fig. 12 represents a slightly earlier stage in *C. ramosa*.



The primary aperture is still present; the distal thickening of the tentacle-sheath being already distinct, and showing a differentiation of an external epithelial layer, and a more internally placed mass of nucleated protoplasm.

It is very difficult to make out with certainty the later history of the aperture. In stages previous to that at which the solid follicle has its maximum size, the connection of the primary aperture with the distal wall of the ovicell seems to be completely lost in many cases. It is perhaps the case that the original invagination remains connected with the distal wall of the ovicell by a thin cord of cells which is not easily seen in sections—accounting for the apparent discontinuity between endocyst and apertural invagination which is frequently remarked; and that, later, this cord shortens, bringing the invagination once more nearer to the distal wall of the ovicell, where its aperture once more opens out widely.

In fig. 13, representing the aperture of an ovicell in which traces of vacuolation are beginning to appear in the follicle, the primary aperture still opens to the exterior; although, in accordance with what has just been said, its opening would probably not have been discernible at a somewhat earlier stage. The formation of the tubular definitive aperture has progressed, and the valve is complete. The differentiation of the thickened part of the tentacle-sheath into two kinds of cells, alluded to in the description of the last figure, has advanced a stage.

In fig. 9 the tubular aperture is practically complete. At its end is seen an invagination which I regard as the remains of the primary aperture, but which has now become disconnected from the thickened part of the tentacle-sheath.

The history of the aperture is thus, according to what I believe I have made out, as follows:—During the calcification of the distal end of the ovicell, the primary aperture, which at first opened in the middle of the mouth of the funnel, becomes shifted nearer the “back” wall of the ovicell, into the position where the tube of the ovicell is to be formed. The aperture is thus not closed by the calcification of the ovicell, but finally

disappears in the region of the permanently uncalcified part of the ovicell; i. e. of the definitive aperture.

Fig. 14 illustrates a condition of the tube of the ovicell which I have observed in one or two cases. The ectocyst is drawn out into a long narrow tube, which was probably uncalcified and which opens to the exterior. This recalls the condition described in the zoëcia of certain Cyclostomata, in which the zoëcium is closed by a (calcareous) lid, perforated by a small central aperture.<sup>1</sup> I am not prepared to state whether or not this is a normal character of ovicells at any particular stage, nor can I suggest any satisfactory explanation of the meaning of the phenomenon.

The central mass of cells differentiated from the thickened part of the tentacle-sheath in fig. 12 is destined to undergo certain very important modifications. In fig. 16 (more highly magnified than the previous figures, and belonging to the same ovicell from which fig. 6 was drawn) some of the nuclei of the central mass are growing larger. This is especially the case in the neighbourhood of the lumen of the tentacle-sheath, where there is a tendency for the nuclei to group themselves in small numbers. In fig. 9 some of these multinucleated masses of protoplasm are breaking off into the lumen of the tentacle-sheath.

From this stage onwards the characteristic multinucleated cells, which have been formed from the thickened distal part of the tentacle-sheath, are a normal feature of the ovicell, being found in the vacuoles of the protoplasmic reticulum in which the young larvæ lie. One of them is seen in fig. 11, and others are shown, more highly magnified, in fig. 18 (Pl. XXIV). In the latter figure the multinucleated cells contain nuclear and other structures which are obviously degenerating; and they are clearly not unlike the "giant-cells" which are known to occur in certain tissues in Vertebrates.

The giant-cells make their appearance at just that stage

<sup>1</sup> Cf. *Mesentipora meandrina* (Busk, No. 8, pl. xvii, fig. 2); *Reticulipora dorsalis* (Waters, No. 36, pl. xvii, fig. 4); and other cases referred to by Waters.

when the vacuolation of the follicle is commencing; and they appear to be closely connected with the carrying out of this process of vacuolation, although it is clear that the first small vacuoles (cf. fig. 7) make their appearance independently of the giant-cells.

At later stages each giant-cell is usually seen to lie in a large, sharply-marked vacuole of the protoplasmic reticulum. The cell may be apposed to one wall of the vacuole; or may, apparently, lie quite freely within it. There is good reason to believe that the vacuoles which are at first occupied by giant-cells are later occupied by the young larva. Each embryo, soon after its formation, comes to lie in a sharply-marked vacuole in the protoplasmic reticulum. Taking into consideration the facts (1) that the giant-cells are formed simultaneously with the appearance of large vacuoles in the follicle, and (2) that they contain fragments of degenerating cells or nuclei, it may be concluded that one of the functions of the giant-cells is to excavate spaces in the follicle in which the larvæ can develop. These spaces are probably filled with some albuminoid fluid, at the expense of which the embryos develop—probably by diffusion through their tissues, as they have no recognisable means of absorbing nutriment.

The function of the giant-cells would thus be closely similar to that of the osteoclasts or myeloplaxes of bone “which excavate small shallow pits . . . in the part which is undergoing absorption” (27, p. 104). Their structure, too, is in accordance with the descriptions of various observers of the multinucleated giant-cells in Vertebrates.

In the mature ovicell the remains of the distal thickening of the tentacle-sheath are always found as a dense mass of nucleated protoplasm which is attached to the ectocyst, not in the tubular aperture of the ovicell, but invariably at its base, on the side which is further from the back of the ovicell (figs. 9 and 16). The valve constantly projects from the back of the ovicell into the proximal part of this mass of cells in the manner shown in figs. 9 and 16. It appears to me probable that the function of the valve is to offer an obstacle to the

escape of the immature larvæ. When mature, the larvæ force their way one by one through the solid mass of protoplasm into the tubular aperture, and so escape to the exterior.

The tentacle-sheath is no longer easily distinguishable in the mature ovicell. With the commencement of the vacuolation of the follicle its distinctness vanishes, and it becomes confounded with the vacuolated follicle. The relations shown in figs. 9 and 17 probably indicate that the follicle ultimately fills up the whole of the original tentacle-sheath, and that that part of the ovicell which is not occupied by the protoplasmic reticulum and its contents is the original body-cavity of the ovicell.

The ovicells which are at their period of greatest activity can readily be recognised in the living condition by the pronounced yellow colour of their contents. This is sufficiently distinct to show clearly through the calcified wall of the ovicell. Although the embryos and larvæ are pale yellow, the colour of the ovicell depends mainly on the pigment in the reticulum which supports the embryos. In *C. cornuta* this is bright red-orange in colour, while in *C. ramosa* the orange colour is not quite so bright.

The oldest larvæ, which are almost ready to escape, lie each enclosed in a distinct vacuole of the reticulum, in close contact with the thick mass of protoplasm which fills up the aperture of the valve.

The production of embryos continues up to a very late stage, but embryos are always developed only from the budding mass of embryonic cells (primary embryo). The budding organ has, however, a somewhat different appearance in old ovicells from that which it first had, both the secondary embryos and their nuclei being markedly smaller than in the younger ovicells.

So far as my observations go, the whole of the budding organ is ultimately used up in the production of embryos. In ovicells which are nearly exhausted the embryos are few in number, and the budding organ has been reduced to small dimensions. Finally, the ovicell is found to consist merely of

a protoplasmic reticulum, which may be richly developed, and which no longer contains any embryos or larvæ.

It must not, however, be assumed that all ovicells in this condition have passed through an embryo-producing stage. I have repeatedly obtained evidence to show that degeneration of the ovicell may start at almost any stage in its development. The external form of the ovicell may develop completely, even if the embryo and its follicle are degenerating. It is common to find an ovicell which, from its proximity to the growing-point, should be a young one, but which appears completely empty in sections. I can only assume in these cases that the protoplasmic structures which the ovicell at first possessed have been absorbed through the pores into the neighbouring zoœcia. In other cases the ovicell may contain remains of a degenerating follicle, the degeneration having clearly commenced before the follicle became vacuolated. One may, therefore, distinguish between a "primary" degeneration of the ovicell occurring before any larvæ have been produced, and a "secondary" degeneration, which has taken place after the escape of the last larva. It is sometimes possible to distinguish between these two conditions by reason of the fact that the base of the young ovicell is limited by a marked epithelial arrangement of its endocyst (cf. figs. 6 and 9).

I have so far avoided the use of the term "endoderm" as an equivalent for the inner layer of cells of the secondary embryos. This layer is excessively distinct in the embryos soon after their liberation from the embryogenic mass of cells. It then forms an epithelium, lying more or less close to the inner surface of the ectoderm-cells, and completely surrounding the whole internal cavity of the embryo (fig. 22).

In later stages the distinctness of the cavity becomes lost, and its lining cells send off processes which grow across the cavity and convert it into an irregular set of spaces. At the sides of the sucker these spaces disappear altogether, while between the sucker and the middle of the aboral pole the cavity remains distinct for a time longer. Its cells become, however, almost indistinguishable from the epithelium of the

sucker on the one hand, and from the epithelium lining the mantle-cavity on the other.

I formerly assumed (15, p. 455), on the authority of Ostroumoff's statements (25, pl. vi, fig. 1), that the cavity lined by the inner cells represented the alimentary canal of the larva. But, taking into account the manner in which the larvæ are developed, it appears to me doubtful whether any representative of the endoderm occurs in them. It appears to me to be satisfactorily established that a young polypide-bud in any Polyzoon is developed at the expense of two layers, viz. the ectoderm and a layer of funicular tissue which may be regarded as mesoderm.<sup>1</sup> The metamorphosis of the larva of Cyclostomata has been described by Barrois (3) and by Ostroumoff (25). The observations of Barrois show that the processes of fixation and of metamorphosis take place essentially as in other Gymnolæmata. The larva fixes by the eversion of its sucker, its mantle being rolled downwards so as to come into contact with the flattened plate formed by the eversion of the sucker, and the greater part of the larval tissues undergo a process of histolysis. The larva thus enters into the condition of a zoëcium containing a "brown body," and the young polypide is produced by an invagination of the body-wall from the centre of the surface opposite to the basal surface. While the inner layer of the bud is formed by an invagination of the ectoderm, Barrois was unfortunately unable to trace the history of its outer layer.

Ostroumoff is but little more definite on this point. The inner layer of the bud is formed, according to this observer, not as an invagination, but as a plate of cells split off from the aboral ectoderm. The edges of this plate curve round, so as to transform the plate into a sac, to the outer side of which "mesenchym-cells" apply themselves, and form the outer layer of the bud. The origin of these "mesenchym-cells" is not traced. It is recognised that the "alimentary canal" of the earlier stage disappears, but there is nothing to show how its cells are related to the "mesenchym-cells" shown in

<sup>1</sup> Cf. especially Seeliger, Nos. 32 and 33.

Ostroumoff's pl. vi, fig. 2, which, by the way, are unlike any cells which I have ever seen in a Cyclostome larva.

Whatever be the origin of the outer layer of the bud which forms the primary polypide, it is quite clear that that polypide is formed in fundamentally the same way as any other polypide in the future colony. There can be no question of the "alimentary canal" of the embryo passing over directly into that of the primary zoëcium.

In default of sufficient evidence on this point I am inclined to regard the inner layer of the Cyclostome embryo as mesodermic rather than endodermic, and this principally on the following grounds :

1. The alimentary canal is an excessively rudimentary structure in the great majority of known Ectoproct larvæ.

2. The peculiar character of the early development of *Crisia* suggests that a representative of this rudimentary structure is likely to be found in the primary embryo only, and that the secondary embryos, formed by budding from the primary one, are no more likely to possess an alimentary canal than is a young zoëcium formed at the growing-point of an old colony.

3. The analogy of other Ectoprocta is in favour of this hypothesis.<sup>1</sup>

Prouho (26), for instance, has given an account (which I can confirm in the main from my own observations) of the metamorphosis of *Flustrella*. Even before the end of larval life, a distinct aboral mesodermic layer is present, from which the outer layer of the bud is directly developed.

In the course of the budding of an ordinary Ectoproct colony the polypide buds are formed from two distinct layers. The inner layer of the bud is developed at the expense of the ectoderm; the outer layer, either from an already definite layer of mesoderm (*Phylactolæmata*), or from mesoderm-cells of the funicular tissue which arrange themselves as an epithelium round the outside of the ectodermic portion of the bud

<sup>1</sup> Cf. particularly the larva of the *Phylactolæmata*, as described by Braem (5) and by Davenport (8A).

(most Gymnolæmata; cf. especially Seeliger, No. 33). There is no sufficient reason for supposing that a young zoëcium consists of anything but ectoderm and mesoderm. The Ectoproct larva may be considered morphologically as a young zoëcium containing a potential "brown body" (the remains of the purely larval organs), and it is not unreasonable to suppose that the structures found in the larva of the Cyclostomata, developed as it is by a process of budding, are comparable with those which are found in a zoëcium.

We arrive, therefore, at the provisional conclusion that the inner layer of the Cyclostome embryo is more likely to represent the mesoderm than the endoderm of the larva.

There can be no doubt that, on the assumption that my account of this process is in the main correct, the development of *Crisia* takes place in a manner to which there are few known parallels.

The most frequently quoted case of embryonic fission is that of *Lumbricus trapezoides*, in which, according to the statements of Kleinenberg (20), the embryo normally divides into two complete embryos at the gastrula-stage. In some abnormal cases, however (l. c., p. 217), a single embryo is first formed; and this gives rise to one or more embryos produced as buds on the margin of its mouth. The segmentation of the egg is described as being much less regular than in other species of *Lumbricus*, in which no embryonic fission takes place.

An equally striking case of the same kind had previously been described by Busch (7), in *Chrysaora*. In only a few cases does an egg develop into a single embryo. In the other cases, the embryo gives rise to one or two buds, apparently at the gastrula-stage; the buds becoming free larvæ, and developing fresh buds. Not only does Busch claim to have followed the whole process in an isolated individual, but he states that each time that the water in which the young larvæ were kept was changed, two thirds or so of the embryos were thrown away, and that this loss in number was compensated for, by the next day, by the gemmiparous habit of the larvæ



(l. c., p. 28). This account is confirmed by Haeckel (14), who observed the production, in three weeks, of 60—80 buds, from ten isolated gastrulæ of *Chrysaora*.

The process of larval fission or gemmation is known to be even more remarkable in *Aurelia* (Haeckel, l. c.). Not only do the gastrulæ multiply, in some cases, by budding or by fission, but the same processes are known to occur in the *Scyphostoma* stage; while numerous variations are recorded in the character of the strobilation, in the multiplication of the tentacles by incomplete fission or budding, and even in the number of the highly characteristic tæniolæ and in that of the *Ephyra*-lobes.

The property of giving rise to fresh individuals, whether by budding or by fission, has, in this case, become a normal feature of the species; and the process takes place even at very early periods of the development, just as is the case in *Crisia*. The striking variability in the number of the radii of the immature stages in *Aurelia* may possibly be connected with something in the constitution of the egg which predisposes it to develop in an unusual way.

For since the cells which are destined to give rise to a single individual are not normally separated off until a late stage, which varies in different individuals, the existence of a tendency to vary in the number of individuals produced from an egg might also, in all probability, make itself felt in variations in a different direction. If the gastrula contains in itself the power to develop into several individuals, it is hardly surprising that it should in some cases develop an abnormal number of radii.

Similar cases of larval budding have been recorded in other *Scyphomedusæ*. Thus Goette (12), confirming an older observation of Sars (1841), shows that the formation of a stolon may take place (presumably in *Cotylorhiza tuberculata*) in the larva which has just fixed, but which is still without tentacles. Ciliated buds are also given off from the *Scyphostoma* of *Cotylorhiza*, the buds fixing and developing a mouth after fixation.

A method of reproduction similar to the last is recorded by Bigelow (4) in *Cassiopea xamachana*.

In *Oceania armata*, Metschnikoff (24) characterises the process of segmentation as a regular "Blastomerenanarchie" (p. 38). The first two blastomeres almost separate from one another; while, in some cases, when the very slight connection which normally exists between them becomes ruptured, the separated blastomeres atrophy. *Oceania* further distinguishes itself, at the eight-cell stage also, from other *Medusæ* investigated by Metschnikoff; the blastomeres, instead of being arranged in an orderly manner, lying together "ganz unregelmässig." This extraordinary irregularity (see Metschnikoff's pl. i, figs. 33—35) is equally remarkable at later stages, and ultimately gives rise to irregularly shaped masses of cells; the embryos often assuming a quite "abenteuerliche Gestalt," due to the fact that they multiply by division. Those embryos which do not divide form much larger larvæ than the others.

As a converse to this may be mentioned some most interesting results arrived at by Driesch (9) and by Fiedler (10). Driesch showed that by violent shaking of the water containing *Echinus*-eggs which had divided into two blastomeres, or in other ways, the two cells could be isolated from one another. Each segmented in the same way that it would have followed if it had remained connected with its fellow, i. e. it developed into a half-embryo, right or left as the case might be. The segmentation cavity, at first widely open, closed up in course of time so as to form a blastosphere, consisting (as appeared from measuring the cells) of half the normal number of cells, and being half the normal size. Three of these embryos developed into complete *Plutei*, which differed from normal ones only in size. In cases where the two original blastomeres had been only partially separated, seventeen cases were recorded in which the embryo distinctly consisted, at the end of the first day, of two halves. In several cases each of these embryos divided into two complete embryos, some of which were shown to develop into small normal *Plutei*. In

another instance an injured two-cell embryo developed apparently normally up to the end of the blastosphere stage, but finally divided into two; and in another case the injury to the two-cell stage resulted in the formation of a double monster.

In *Crystallodes* (Siphonophora) the remarkable amœboid character of the superficial blastomeres suggested to Haeckel (13) that the embryo, at the end of the second day, could be compared to a colony of *Amœbæ*, in consequence of the great individuality of the separate blastomeres; and that, if this comparison were correct, an isolated portion of the embryo might be expected to have the power of further development. The experiments made to test this hypothesis were completely satisfactory. Embryos artificially divided at this stage developed into normal individuals of a smaller size than usual. The cut surface became concave, the edges ultimately joining, so that the embryo again became spherical, and then proceeded to develop in its normal manner.

It is hardly possible to overlook the fact that, in some at least of the above quoted cases, embryonic fission is specially connected with deviation from the normal type of segmentation of the egg. This is most clearly seen in the case of *Oceania*, where a superficial glance at Metschnikoff's figures is sufficient to convince one of the extraordinarily abnormal character of the segmentation. The same fact is, however, to some extent true of *Lumbricus trapezoides* and of *Crystallodes*, where Kleinenberg and Haeckel respectively call attention to remarkable features in the segmentation.

The segmentation of the egg of *Crisia* obviously belongs to an unusual type, and, as has already been pointed out, it finds its closest parallel in *Salpa*, an animal which is remarkable for the great extent to which asexual reproduction is carried out.

*Doliolum*, whose life-history agrees with that of *Salpa* in including two remarkably different generations, offers a further analogy to *Crisia* in the character of its asexual reproduction. The stolon of the asexual generation segments off, according to

the description of Uljanin (35), a series of buds in which there is a very small amount of differentiation. These "Urknospen" consist of a layer of ectoderm surrounding a mass of embryonic cells which are but slightly differentiated (l. c., pl. x, fig. 3). These buds divide up into numerous similarly-constituted buds, so that the sexual individual of *Doliolum* takes its origin from a group of cells which is very similar to the young "secondary embryos" of *Crisia*.

The same method of reproduction characterises the remarkable *Dolchinia*, recently described by Korotneff (22). This animal is closely allied to *Doliolum*, if, indeed, it should not be placed in that genus. The only phase in its life-history which is so far known is a gelatinous axis, bearing very numerous *Doliolum*-like zooids, and which probably corresponds to the dorsal process of *Doliolum*. The axis bears numerous buds, wandering about on its surface by means of pseudopodia. The buds have probably been derived from the segmentation of the ventral stolon of an asexual form. They increase in number by division. Should one of the daughter-buds fix itself on the base of a young zooid, it becomes a bean-shaped body, which gives rise to a large number (as many as forty) of new buds. The young buds, at the stage at which they become free, consist of a solid mass of cells in which a very small amount of differentiation has taken place.

The formation of the secondary buds, as shown in Korotneff's pl. xiii, figs. 14, 15, has thus a striking resemblance to the mode of development of the secondary embryos in *Crisia*; neglecting the not unimportant difference that in the former case the budding organ is itself a bud, and in the latter case an embryo.

A similar process probably takes place in *Anchinia* (21); and Uljanin (l. c., pp. 106—117) brings forward evidence to show that the same is true of some of the compound Ascidiarians. The larva of *Distaplia magnilarva*, for instance, gives rise to structures comparable with the "Urknospen" of *Doliolum*. Uljanin comes to the conclusion that the budding of adult Tunicates is derivable from a division of "very

young developmental stages." A similar suggestion with regard to the origin of alternation of generations among the Hydromedusæ has also been elaborated by Brooks (6), who supposes that the hydroid stage has been evolved by the acquirement of the power of budding by the fixed larval stage.

A slight modification of the "primary embryo" of *Crisia* would suffice to make it necessary to consider the life-history of that animal as a case of alternation of generations. But since, as I believe, the budding structure consists of a mass of embryonic cells, which ultimately becomes completely converted into "secondary embryos," leaving nothing behind, I have preferred not to describe it as a separate generation.

Enough has been said to show that in the Tunicata at least, and to a less extent in the Cœlenterata,<sup>1</sup> there are remarkable cases of the formation of buds from slightly differentiated masses of cells. These two groups, with the Polyzoa, are certainly the groups of animals in which budding in the adult condition is a more normal event than in other groups of animals.

It may thus be asserted that in the Polyzoa, the Tunicata, and the Cœlenterata the asexual reproduction of certain forms takes place at a stage before the individual which is reproducing asexually has had time to undergo more than the earliest steps in its development. A similar precocious formation of fresh individuals is well known in the reproduction of Trematoda.<sup>2</sup>

The investigations of Driesch (9) and of Haeckel (13) have shown that blastomeres which have been artificially separated from the embryo are able, in some cases, to give rise to complete larvæ. The question suggests itself: Has the gemmi-

<sup>1</sup> The case of *Cunina*, as described by Uljanin, Schulze, Metschnikoff, and Brooks, and more recently by O. Maas ('Zoolog. Jahrbücher,' "Abth. f. Anat. u. Ontog.," Bd. v, Heft 2, 1892), is another remarkable instance of the same kind.

<sup>2</sup> Compare particularly the remarkable account given by Heckert (18) of the life-history of *Distoma macrostomum*, and particularly the statements referring to its remarkable branched sporocyst, known as *Leucochloridium paradoxum*.

parous method of reproduction in the adults of the above-mentioned groups been preceded by larval fission, possibly induced by the separation from the embryo of individualised blastomeres or groups of blastomeres, or is the embryonic fission the result of the precocious acquirement of the budding habit which characterises the adult? Now in the Polyzoa, embryonic fission is by no means a common phenomenon, although the adults of all known Polyzoa possess the power of budding; and although it is probable that the method of reproduction above described in *Crisia* will be found to be characteristic of all Cyclostomes. I have no sufficient evidence on this point at present, but it may be pointed out that the ovicells of Cyclostomatous Polyzoa invariably (so far as I know) contain a large number of embryos. My own observations enable me to state further that the general structure of the ovicell in *Idmonea serpens* and in *Diastopora patina* agrees with that in *Crisia*; and I have little doubt that I shall be able to show that embryonic fission is characteristic of Cyclostomes in general. The development of the Phylactolæmata possibly offers some analogies to this process. The structure of the larva is somewhat similar to that of Cyclostomes, and the early development, according to the account given by Jullien (19), is not unlike that of *Crisia*. Braem (5) has also given an incomplete account of the development of *Plumatella*, which suggests further resemblances to the Cyclostomata. The two layers which form the wall of the embryo, and which are considered by Braem to represent ectoderm and body-cavity epithelium respectively,<sup>1</sup> are obviously comparable with the two layers shown in Pl. XXIV, figs. 22 and 23, of *Crisia*. The manner in which (in *Plumatella*) a rudimentary bud encloses the egg, forming the "oœcium," is again strikingly suggestive of *Crisia*.<sup>2</sup> The first stage in which the

<sup>1</sup> The same conclusion is arrived at by Davenport (8A), whose valuable paper should be consulted for a comparison of the larva of Phylactolæmata with that of Gymnolæmata.

<sup>2</sup> Compare in particular the woodcut given by Braem in his explanation to fig. 171.

egg is completely enclosed is shown in Braem's pl. xv, fig. 171, while in fig. 172 the "oœcium" has differentiated off a distal portion which may be the exact equivalent of the "tentacle-sheath" shown in my own fig. 3 for *Crisia*. The tendency to precocious fission shows itself in *Phylactolæmata*, however, in the precocious formation of a considerable number of polypides, particularly in *Cristatella*;—a process which is of course very different from the embryonic fission of *Crisia*.

The ovicells of the *Cheilostomata* are probably not homologous with those of *Cyclostomata*. They are probably not to be regarded as modified zoœcia, since the ovicell is an appendage of a fertile zoœcium, and ordinarily contains a single embryo.

Similarly in the other groups which have been mentioned precocious fission is not characteristic of the whole group, but occurs sporadically;—in *Cœlenterata*, in *Oceania*, *Cunina*, &c.; in *Trematoda*, in the *Distomeæ*; and in *Tunicata* in the *Thaliacea*, and in some *Synascidians*.

Although I must regard the question as a very open one, the conclusion which appears to me to be suggested by the above facts is that one is not justified in assuming that the budding of the *Polyzoa*, for instance, commenced with the acquirement of a habit of embryonic fission like that found in *Crisia*, but that the embryonic fission may be the consequence of the previously acquired power of adult budding. It may be pointed out that the embryonic fission of *Crisia* gives rise to numerous larvæ, each of which may form the starting-point of a new colony. In the case of adult *Polyzoa*, the result of budding is merely to increase the number of individuals in a colony, with the exception of *Loxosoma* (in which the bud normally becomes free) and of certain dendritic forms of colony, in which the decay of the proximal part of the colony leads to the separation as distinct colonies of what were at first merely branches, or of cases like that of *Crisia* itself, where new colonies are formed by the upgrowth of new stems from a creeping rootlet, which acts as a stolon for the production of

new colonies.<sup>1</sup> It should be further noted that the production of new polypides in old zoëcia is one of the most characteristic ways in which the property of budding manifests itself in Ectoprocta, and that this process is most easily interpreted as a process of regeneration of lost parts.

The provisional conclusion may therefore be stated as follows:—That the process of embryonic fission, which may appear abnormally in certain individuals in so many groups of animals which do not multiply by fission, has in *Crisia* become a normal phenomenon of the development; and that this process is correlated with the tendency which is so strongly marked in the Polyzoa to produce buds in the adult condition.

Giard (11) has recently published a note on what he terms "pœcilogonie," i. e. the phenomenon exhibited by certain animals of developing in a more or less "condensed" manner, in correlation with the amount of nutritive reserves in the egg, or with the conditions under which the parent is living. As examples of this process are mentioned, inter alia, the following cases:—In *Leptoclinum lacazii*, Gd., the same colony may produce two sorts of eggs; of these, one is poor in yolk, and gives rise to small larvæ, whose tail is absorbed early, and which do not begin to bud even on the third day. The other kind is rich in yolk, and produces larvæ which are still free-swimming on the fourth day, and which then already contain a colony of three individuals. *Ophiothrix fragilis*, Müll., lays eggs which develop, according to the conditions, either into perfect or into imperfect Plutei, or into embryos incapable of swimming, and which develop directly. The remarkable variations in the development of *Aurelia aurita* and of *Palæmonetes varians* are also included in this category; in the latter form the size and number of the eggs, as well as the rapidity of the metamorphoses, varying according as the animal lives in the brackish waters of the North or in the fresh-water lakes of the South.

Giard's observations suggest that the acquirement of em-

The statoblasts of the Phylactolamata are indeed a further exception since each of these bodies is able to give rise to a new colony.



bryonic fission in Cyclostomes may have been connected with the presence of the nutritive conditions which are suited to induce the precocious formation of buds. Nothing can be more striking than the obvious continuity of protoplasm between the several units of the colony in a decalcified branch of *Crisia*. In the individuals which are modified as ovicells the protoplasmic network is particularly well developed. The embryo is thus surrounded by a rich nutritive material; and just as the presence of a nutritive placenta in a Placental Mammal has resulted in the diminution of the size of the ovum, and in various abnormalities in its early segmentation, so in *Crisia* the size of the egg is reduced to a minimum, the whole of the nutritive substance being retained in the parental tissues and handed on to the egg or embryos as required, while the segmentation is entirely abnormal. Further, while the Mammalian embryo becomes easily comparable with that of any other Vertebrate embryo after a certain number of the early stages have been passed through, so the *Crisia* larva becomes, to some extent at least, comparable with the free larva of any other Polyzoan, although with this difference from other Polyzoa, viz. that the primary embryo has given rise to numerous larvæ, a process comparable with the artificial production of a complete embryo from a single blastomere of the two-cell stage in the experiments of Driesch (9) and of Fiedler (10).

Attention has already been called to the similarity between the early stages of the development in *Crisia* and those in *Salpa*. The latter is another example of the modification of the first processes in the development, associated with the presence of special maternal nutritive arrangements. The embryo of *Salpa* develops, as is well known, in close connection with a kind of placenta; and its early stages are, compared with those of most other animals, highly abnormal. The formation of buds from the individual developed from the egg does not take place at once, as in *Crisia*, but is deferred until the animal is mature, when buds are produced in very large numbers from the stolon.

Similarly the egg of *Pyrosoma*, like that of *Salpa*, makes its appearance in the same precocious manner as that of *Crisia*, being formed very early from the so-called "genital string" (Salensky, 29). The early development, which is modified by the presence of yolk, takes place in the interior of the old colony, and is very abnormal, the blastomeres being for a time completely separated from one another (Salensky, p. 443). The result of the development is the formation of the well-known "Cyathozoid," with its colony of four "Ascidiozooids," the formation of which is compared by Salensky (30, p. 92) with the embryonic fusion of *Lumbricus trapezoides*. The formation of a stolon (represented by the chain of four Ascidiozooids) in the *Pyrosoma*-embryo is further regarded as the precocious acquirement by the embryo of the power of budding already possessed by the Synascidians.

*Peripatus*<sup>1</sup> is well known to be viviparous, and the extraordinary character of the segmentation of its ovum may have some relation to the presence of external sources of nutriment.

The cases already quoted may be taken as showing that some of the abnormalities in the development of *Crisia* may be due to the nutritive conditions in which the development takes place. Just as the presence of food-yolk within the egg modifies the character of the segmentation and of the formation of the layers, so the presence of copious stores of nutrient material in the maternal tissues outside the egg may also affect the early developmental processes. Thus the large number of relatively large larvæ which develop from the minute egg of a *Crisia* could not be produced if the egg were not supplied with nutriment from outside itself. While some of the irregularity in the segmentation of the egg may be due to this cause, the extreme independence of the blastomeres at an early stage may be connected with the acquirement by the embryo of a habit of forming buds in the embryonic condition.

<sup>1</sup> See Sedgwick, No. 31.

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It hardly falls within the province of this paper to discuss the details of the normal budding in Polyzoa. Both Braem (5) and Davenport (8A) have shown that polypide-buds in general are derived from a mass of "embryonic" tissue, handed down from the beginning of the formation of the colony, some part of this tissue being left over for the production of fresh buds on each occasion when a polypide-bud is formed. Braem's account of the formation of the statoblasts in *Phylactolæmata* more nearly resembles the development of the "secondary embryos" in *Crisia* than any other process as yet described in Polyzoa. The funiculus is, indeed, not an embryo; but the young statoblasts are formed from it in much the same way as that in which the larvæ are developed from the "primary embryo" in *Crisia*. The funiculus consists of a core of ectoderm surrounded by a sheath of mesoderm (both kinds of cells having an "embryonic" character). The statoblasts are formed by a process which is to all intents and purposes a transverse segmentation of the funiculus.

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#### EXPLANATION OF PLATES XXII, XXIII, & XXIV,

Illustrating Mr. Sidney F. Harmer's paper "On the Occurrence of Embryonic Fission in Cyclostomatous Polyzoa."

#### PLATE XXII.

FIG. 1.—*C. eburnea*. Median longitudinal section through a young ovicell, showing the egg, which is already partially surrounded by the polypide-bud (Zeiss, DD).

FIG. 2.—*C. ramosa*. Part of a similar section at a more advanced age, showing the complete inclusion of the ovum (Zeiss, DD).

FIG. 3.—*C. ramosa*. Similar section at an older stage. The polypide-bud has become the "follicle." The tentacle-sheath and the aperture are well developed. Ovicell at the "funnel-stage" (Zeiss, DD).

FIG. 4.—*C. eburnea*. Spermatozoa. To the right, three mature spermatozoa, drawn in the living condition (Zeiss, F); to the left, three stages in the development of the spermatozoa, treated with osmic acid and picro-carmin (Zeiss, F); in the middle, four immature groups consisting of four spermatozoa each, killed with osmic vapour (Zeiss,  $\frac{1}{12}$  immersion, 4 oc.).

FIGS. 5—7.—*C. ramosa* (Zeiss, DD).

Fig. 5. (Combined from several sections of the same ovicell.) The egg has divided into three blastomeres; the valve is developing, and the distal end of the tentacle-sheath has become thickened.

Fig. 6. Proximal end of a longitudinal section (more advanced). The embryo consists of a compact rounded mass lying in a large follicle, which projects freely into the tentacle-sheath.

Fig. 7. A similar preparation at a stage when the vacuolation of the follicle is commencing.

#### PLATE XXIII.

FIG. 8.—*C. eburnea*. Ovicell at a stage corresponding to Fig. 6 in *C. ramosa*. The embryo is larger and the follicle is much smaller than in that species (Zeiss, DD).

FIGS. 9—14.—*C. ramosa* (Zeiss, D D).

Fig. 9. The vacuolation of the follicle is nearly complete. The tubular aperture is formed, and the structures connected with its base are well developed.

Fig. 10. Invagination (?) in a "primary embryo," at about the same stage as Fig. 9.

Fig. 11. Considerably later stage. The follicle has become a dense protoplasmic reticulum, containing the massive "primary embryo," now transformed into a budding organ, which is giving rise to numerous secondary embryos, three of which are seen lying freely in the reticulum. At the upper end a giant-cell, derived from the thickened distal end of the tentacle-sheath (cf. Figs. 5, 13 and 9).

FIGS. 12—14. Illustrating the development of the aperture of the ovicell. In Fig. 12, the primary aperture still remains open, the distal end of the tentacle-sheath being thickened. In Fig. 13, the tubular aperture of the adult ovicell is developing; it contains the remains of the primary aperture. The thickening of the distal end of the tentacle-sheath has increased in size, and the valve is well developed. In Fig. 14, the tubular aperture is almost complete. The thickening of the tentacle-sheath still extends into its base. At its distal end a depression occurs, which is possibly the remains of the primary aperture. The tube ends in a cap prolonged into a narrow tube, of unknown significance.

PLATE XXIV.

FIG. 15.—*C. eburnea*. A young internode decalcified, with a developing ovicell. For explanation of the letters (A, B and c) see p. 005 (Zeiss, A).

FIGS. 16—23.—*C. ramosa*.

FIG. 16. The aperture of the same ovicell from which Fig. 6 was taken. The origin of the giant-cells from the thickened distal end of the tentacle-sheath is shown (Zeiss, F).

FIG. 17. Longitudinal section of an ovicell which is filled with secondary embryos. To the left, the primary embryo (Zeiss, A).

FIG. 18. Protoplasmic reticulum with giant-cells, from an ovicell at about the stage of Fig. 11 (Zeiss, F).

FIGS. 19—21. Development of ovicell (Zeiss, A). The ovicell has in each case been numbered 4, in order to admit of ready comparison between the three stages.

FIG. 22. Young secondary embryo, in longitudinal section (Zeiss, F).

FIG. 23. Older embryo, in longitudinal section (Zeiss, F).





## Two New Genera and some New Species of Earthworms.

By

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With Plates XXV & XXVI

IN this paper I describe a number of new species of earthworms which I have received during the last year or two from friends resident abroad, or from the Royal Gardens at Kew. Some of these were received alive; I was therefore able to preserve them carefully for histological examination.

### 1. *Polytoreutus magilensis*, n. sp.

Through the kindness of the Rev. H. W. Woodward, priest in charge of the Universities Mission at Magila, East Central Africa, I obtained a quantity of earthworms from that district. My thanks are also due and tendered to Colonel Sir Euan Smith, who was so good as to mention my wishes to Mr. Woodward.

The earthworm fauna of eastern tropical Africa has been principally studied by Dr. W. Michaelsen, who has published several interesting memoirs upon the subject;<sup>1</sup> the bulk of the

<sup>1</sup> "Beschreibung der von Herrn Dr. Franz Stuhlmann im Mündungsgebiet des Sambesi gesammelten Terricolen," 'Jahrb. Hamb. wiss. Anst.,' vii.

"Beschreibung der von Herrn Dr. Fr. Stuhlmann auf Sansibar und dem gegenüberliegenden Festlande gesammelten Terricolen," 'Jahrb. Hamb. wiss. Anst.,' ix.

<sup>2</sup> "Die Terricolen der Berliner Zoologischen Sammlung," 'Arch. f. Naturg.,' 1891.

species belong to the family Eudrilidæ, and to that section of the family characterised by unpaired male genital orifices, which are grouped together under the name of "Teleudrilinen" by Dr. Michaelsen.

The worms which I received from Mr. Woodward belonged to two species; the majority of the specimens were small slender worms, apparently referable to Michaelsen's *Stuhlmannia variabilis*. There were also about a dozen large worms which I refer to the genus *Polytoreutus*, but distinguish as a new species.

#### § External Characters.

*Polytoreutus magilensis* is a larger species than *P. cœruleus*. An individual which I selected for measurement was  $14\frac{1}{2}$  inches in length, with a diameter of 8 mm.; this specimen consisted of 270 segments.

The colour of the preserved worms is of a dark violet dorsally, and yellowish below. The pigment is seen on a microscopic examination to be disposed in a network on each segment. The clitellum is yellowish.

The prostomium is broad, and is not continued on to the buccal segment. The setæ are disposed as in the only other species of the genus; the dorsal setæ are strictly paired, the distance between the two setæ being about half that which separates the two setæ of the ventral pair. On the anterior segments there is a tendency for the setæ to become obsolete; this is a rare occurrence among the terricolous *Oligochæta*, though not uncommon among the lower aquatic *Oligochæta*. There was nothing remarkable about the form of the setæ, and there were no modified setæ anywhere. On a good many segments of the body—particularly upon those behind the clitellum—there were a series of points conspicuous from the absence of pigment, and lying between the setæ; they have much the appearance of setæ when examined without the aid of a lens; and as they lie between the real setæ, they give the worm the look of a *Perichæta*—a resemblance which is increased by the fact that the segments are for

the most part marked by a median ridge. On mounting in glycerine a portion of the body-wall, embracing several of these clear spots, they are seen to be distinguished from the surrounding integument, not only by an absence of pigment, but also by an absence of glandular cells; they are, indeed, the representatives of the peculiar and characteristic sense-organs of the Eudrilidæ; as in *Hyperiodrilus*, and, in fact, in all other genera where these organs occur, they lie with the long axis horizontal; the central core as well as the numerous coats surrounding it were quite plainly visible in glycerine preparations.

The nephridiopores are very conspicuous; they lie in front of the dorsal setæ, but are not definitely related to either of the two setæ of the pair. They are especially obvious upon the clitellar segments, owing, of course, to the distended integument of those segments. The first pair of nephridiopores lie on the intersegmental furrow 2—3.

There are no dorsal pores.

The clitellum occupies Segments 13—17. It is developed all round the body, except on the 17th segment, where it is invaded by a portion of the large genital protuberance. The grooves between the clitellar segments are always more or less distinct.

The genital protuberance (see fig. 10) is an oval raised area about 8 mm. in length, which occupies the middle part of Segments 17, 18, and 19. The area which forms this protuberance roughly corresponds in extent to the space between the outer setæ of the ventral couples. Its colour is precisely that of the clitellum. It bears two apertures, one behind the other. The anterior of the two is the male genital aperture; it is a wide slit-like orifice between Segments 17—18; it has a crescentic form, the convexity being directed forwards, as illustrated in fig. 10. The posterior orifice is that of the spermatheca; it is small and also slit-like, so narrow as to be often invisible; it lies on the border line between Segments 18—19. The genital protuberance is marked by two ridges running at right angles to each other: one runs transversely

and bears the spermathecal orifice; the other runs along the middle line of the body, at right angles to the former. Four sucker-like depressions are thus formed, which are most marked in a specimen in which the muscular sac at the male pore is partially everted. They probably serve as accessory organs of copulation. The oviducal pores are paired, and lie upon Segment 14; they are placed at about the middle of the segment, and are more ventral in position than are the nephridiopores.

#### § Internal Anatomy.

The pharynx terminates at the end of the 4th segment, and is immediately followed by the gizzard, which lies in Segment 5. The œsophagus is furnished with three median, ventral, glandular diverticula—the “Chylustaschen” of Michaelsen. These are nearly spherical bodies of a reddish colour, and lie in Segments 9, 10, and 11. In Segment 13 are a pair of trilobed calciferous glands. The intestine commences in Segment 14. The alimentary tract is, therefore, in all respects like that of *Polytoreutus cœruleus*.

The dorsal blood-vessel is single, and communicates in some of the anterior segments with the ventral vessel by a series of hearts; those of Segments 10 and 11 are especially enlarged.

Some of the anterior intersegmental septa are thickened, those between Segments 5—11 particularly so. There is one septum in front of the first of these; the septum between Segments 11—12, though more delicate than those which come before, is stouter than those which follow. The thickened septa are cup-shaped, the concavity being forwards.

The nephridia are paired organs.

The reproductive organs are very remarkable. They are on the whole similar to those of the other species, but differ in detail; these differences are quite sufficient to distinguish the two East African species.

The testes I could not discover; they probably lie within the sperm-sacs, which have, as in *Polytoreutus cœruleus*, a very remarkable configuration. Attached to the septum dividing Segments 11—12 there is on each side of the intes-

tine a solid-looking white body, which is simply a dilatation of the sperm-duct filled with sperm; the opaque white colour is of course due to the contained sperm. The funnel which is connected with one end of this dilated region was evident in one specimen; it lies within the sperm-sacs. These latter commence at the septum dividing Segments 10 and 11 as a narrow tube placed below the intestine, and enclosing the ventral blood-vessel. The two hearts of this segment join the ventral blood-vessel within the sac, as is shown in the figure (fig. 8). A very short way back the sperm-sac divides into two narrow tubes, each of which runs close to the dilated extremity of the sperm-duct, and appears to be connected with it. Behind the septum the two sperm-sacs, which have still the character of very narrow tubes, gradually approximate and pass back in close continuity to each other, and to the dorsal wall of the intestine. In another example the sperm-sacs commenced at the septum, just behind the oval dilatation of the sperm-duct already referred to. In this worm the funnel of the vas deferens was quite visible; it lies just within the beginning of the sperm-sac, but in the 11th segment; the orifice of the funnels is directed backwards, as is so often the case with the Eudrilidæ. The sperm-sacs in this individual were of unusually great length; they passed back to as far as the 60th segment. The sperm-sacs are divided into two regions: the anterior part, as far as about the 30th segment, consists of a narrow tube which lies perfectly free in the body-cavity; it is not attached to the intersegmental septa, which are largely defective dorsally; when the body is opened the sperm-sacs require no dissection to set them free. The posterior section of these tubes has a different structure; the walls become thicker and sacculate, being constricted at the septa; in one specimen the two sacs were united at the distal extremity; in another the sacs remained independent, though closely approximated. The length of the sperm-sacs was 65 mm. in one worm; they were longer in another. They appear to be more extensively developed than in *P. cœruleus*; and Dr. Michaelsen says

nothing in describing that species of the specialisation of the sacs into two regions. The immense length of the sperm-sacs is only paralleled among the Geoscolicidæ; these organs are not, as a rule, very long in the family Eudrilidæ:

The sperm-ducts are single, one on each side of the body: they leave the dilatation which lies immediately behind the funnel, and pass straight back to the atria; they communicate with the atria a little before their opening into the terminal bursa.

The atria are large; they measure about 36 mm. in length. The greater part of the atrium is a tube of considerable calibre, with thick glandular wall. Internally it is longitudinally ridged; the proximal part of the atrium is much narrower: the two atria join before opening into the median bursa.

The sperm-duct of each side opens into its atrium some way in front of the external orifice. The atria extend through about sixteen segments. The glandular part is of a tube-like form, but of an irregular contour; it is partially constricted at intervals; there is, however, nothing like the regular diverticula figured by Michaelsen in *P. cœruleus* (1). Figs. 8, 9 show the arrangement of the atria in this species.

The female reproductive system is illustrated in figs. 7, 9; it differs in some respects from that of *P. cœruleus*. The external orifice of the spermatheca lies, as already mentioned, behind the male pore, on the boundary line between Segments 18—19. This aperture communicates with a sac, which immediately divides into two; these pass round on each side of the nerve-cord, and reunite at some distance from the point at which the sac divides: the sac does not embrace the alimentary canal. A wide unpaired sac is thus formed, which is not quite so long as the atria. It is of about the same calibre. The interior of the sac is marked by numerous folds, arranged to form a network. The sac is half an inch in length.

In dissections of the worm a pair of elongated pouches were always to be seen rising up on either side of the intestine, in

the neighbourhood of the termination of the median sac already described. These sacs really form part of the spermathecæ, with which they are connected as shown in the figure (fig. 9). At a distance of half an inch or so from the cæcal extremity each sac comes into close relations with the posterior part of the large spermathecal sac; at these points, which are quite close to the external orifice of the sac, there is a communication between the two. Each sac then passes forwards in close contact with the body-wall, and is slightly constricted at the septa. The two sacs (right and left) appear to be perfectly separate from each other, and indeed the muscular terminal sac of the atria intervenes; but on removing the nerve-cord, which fills up the space between them, the two sacs are seen to be joined by about seven narrow bridges, which form a ladder-like arrangement shown in the figure. Two of these transverse connections lie behind the atrial aperture, while the remainder lie in front; anteriorly each sac diverges to one side, and becomes connected with the oviduct and egg-sac. Although the above description of the complicated spermathecal apparatus of *Polytoreutus magilensis* appears to show a considerable difference from Dr. Michaelsen's species, a comparison of my figures (figs. 7, 9) with his (loc. cit., Taf. i, fig. 10) of the corresponding organs in *Polytoreutus cœruleus* will readily permit of a detailed homology. In both worms the spermathecal pouches are only incompletely fused; but the fusion between the originally separate sacs (?) has taken place in a different manner. In *Polytoreutus cœruleus* the spermatheca has two pairs of diverticula near to the external orifice; these correspond respectively to the parts lettered *b* and *c* in the figure illustrating *Polytoreutus magilensis*: *b* still retains considerable traces of the double condition. The unpaired median pouch in *Polytoreutus cœruleus*, which is continuous anteriorly with the egg-sacs, is nearly completely double in *Polytoreutus magilensis*.

It seems probable that the structures spoken of here as

“spermatothecæ” are, as in *Libyodrilus*,<sup>1</sup> for example, cœlomic pouches, which have acquired a connection with the exterior; such pouches occur apparently in all Eudrilids, and indeed are the most characteristic feature of that group of Oligochæta. They may, as in *Hyperiodrilus*,<sup>2</sup> contain a true spermatotheca. I have failed after careful search to find anything of the kind in the present species. The anterior end of the spermatothecal sac becomes connected with the efferent apparatus of the female organs in a way that hardly differs from *Polytoreutus cœruleus*. Fig. 7 illustrates the several organs as seen in a glycerine preparation; the results obtained by these means were checked by a comparison with a series of sections. The end of the spermatothecal sac is connected with a somewhat contorted tube which opens freely into its interior; this tube has thick muscular walls and a lining of ciliated epithelium; it passes into a wide chamber (*E. s.*) which lies close to the receptaculum (*R. o.*); with this is connected the oviducal funnel opening into the interior of the receptaculum and the oviduct, which passes in a straight line to the oviducal pore upon the 14th segment; the wide chamber also seems to give rise to a few cœcal tubes in which are lodged bundles of spermatozoa such as Michaelsen has figured<sup>3</sup> in *Polytoreutus cœruleus*. The region of the spermatotheca into which the oviducts open presumably lodges the ovaries, but I have not been able to see these organs; they are possibly, as in *Libyodrilus*,<sup>4</sup> only present in younger stages, and afterwards disappear. This region of the spermatothecal sac, however, contains an immense mass of spermatophores, which have the form illustrated in fig. 11. The spermatophores are of

<sup>1</sup> “On the Structure of an Earthworm allied to *Nemertodrilus*, Mich., with Observations upon the Post-embryonic Development of Certain Organs,” ‘Quart. Journ. Micr. Sci.’ vol. xxxii.

<sup>2</sup> “On the Structure of the Two New Genera of Earthworms belonging to the Eudrilidæ, and some Remarks on *Nemertodrilus*,” ‘Quart. Journ. Micr. Sci.’ vol. xxxii.

<sup>3</sup> Loc. cit., Bd. ix, Taf. iv, fig. 30, *sk.*

<sup>4</sup> Loc. cit., vol. xxxii, p. 568.



considerable length, and are coiled into an inextricable tangle. Each spermatophore is wider at one end; the spermatozoa are attached by their heads to a central core of a clear appearance, which is but faintly stained by borax-carminé. In transverse sections (fig. 12) the whole of the anterior end of the sac is seen to be filled with these spermatophores, which are cut in different directions. It is very interesting to notice the peculiar form of these spermatophores; peculiar, that is to say, as compared with other earthworms. They bear, on the other hand, a very close resemblance to the spermatophores of *Tubifex*<sup>1</sup> in course of formation. The immense number of spermatophores may perhaps be the cause of the enormous development of the sperm-holding apparatus; I found the spermatophores throughout the entire series of sacs which communicate with the female generative pore. In those Eudrilids (e. g. *Eudrilus* itself) where there are not spermatophores of this kind, the sacs are very much less developed. Michaelsen thinks that in *Stuhlmannia variabilis* the large size of these pouches is connected with viviparity. This would be a highly interesting fact were it proved. Michaelsen found in the interior of the spermatothecal sacs of this species granular masses which seemed to be surrounded with a peripheral layer of cells; naturally Dr. Michaelsen could not speak positively of the nature of these bodies, but he suggests that they may be embryos in course of development. I have examined the same species, and find that the large unpaired sac of *Stuhlmannia* contains only a mass of spermatozoa not agglutinated to form spermatophores. The circular canal surrounding the intestine, and also in communication with the median sac, is filled with what appears to be disintegrating spermatozoa, around which are numerous cells; but it is easy to see in my preparations that these cells are not ova, and that they have no relation to any embryonic structures; they are simply "lymph-corpuscles," the function of which, as it appears to me, is merely that of getting rid of dead or per-

<sup>1</sup> 'System und Morphologie der Oligochaeten,' Taf. x, figs. 12 and 15.

haps superfluous sperm. These cells were for the most part loaded with granules, and some of them stained very deeply.

It is curious that while, as already stated, the entire spermathecal apparatus of *Polytoreutus magilensis* is filled with the spermatophores, whose structure has been described, the extreme end of the sac close to the egg-sac itself should invariably contain only a few bundles of spermatozoa, not compacted into spermatophores. The facts suggest that it is in this region that impregnation of the ovum takes place; that here the spermatophores received from another individual are dissolved, and the spermatozoa set free to do their work.

## 2. *Trichochæta hesperidum*, nov. gen., n. sp.

I found this new genus and species upon a single example of an earthworm from Jamaica, which I received alive together with a number of specimens of a *Perichæta* from Kew Gardens.

As the worm was not fully mature I can only give an incomplete account of its characters.

### § External Characters.

The general form of the species is very like *Pontoscolex arenicola*; the colour also recalls that species, and the irregularly alternating setæ. As both worms come from the same island I imagined at first that I had before me a specimen of either *Pontoscolex arenicola* or of *Diachæta littoralis*. But the species which I describe here differs in so many points from either of these two that it should, in my opinion, form the type of a new genus. It belongs to the family *Geoscolicidæ*, mainly, though not exclusively, a New World family.

The specimen measures about  $2\frac{1}{2}$  inches in length, and is of a robust form. Schmarda's figure of *Pontoscolex arenicola* represents the general appearance of the present species. As in many of the *Geoscolicidæ*, there is a prostomium. Fig. 4 illustrates the first few segments of the body viewed laterally; a narrow process of cylindrical form, and

terminating in a blunt rounded extremity, projects apparently out of the mouth, and might easily be mistaken for a prostomium if the worm were in a poor state of preservation.

This structure, however, differs from the prostomium of nearly all other Oligochæta: in *Sutroa*, for example, which possesses a long prostomium, the buccal lobe is simply prolonged; this is also the case with the few Naids that have a long prostomium. In the earthworm described in the present paper the conical process which looks like a prostomium arises within the buccal cavity. The examination of a series of transverse sections (fig. 1) shows that it is a process of the tissues lying outside the epithelium of the buccal cavity, which is covered by a layer of epithelium continuous with that of the buccal cavity. In such a series of sections the process in question appears first of all as lying freely within the buccal cavity; it is covered with a layer of tall, closely packed epithelial cells. The interior of the process contains a few muscular fibres and a number of large nerve-twigs. Further back the process is seen to lie in a diverticulum of the buccal cavity, which it nearly fills. Further back still the epithelium lining this diverticulum becomes continuous with the epithelium covering the process. This occurs just above the cerebral ganglia. It is evident from the structure of this process that it can be everted and retracted; containing as it does nerve-filaments arising from the cerebral ganglia, it probably serves as a tactile organ. The only other earthworm which is provided with an organ that is at all comparable to this process is *Rhinodrillus*; Perrier, however, states that the anterior "tentacle" of *Rhinodrillus* has no relation to the digestive tract: it is simply a process of the body. But Vaillant<sup>1</sup> remarks of the same species, "D'après mes notes, ce ne serait pas une véritable trompe, mais une extroversion de la partie antérieure du tube digestive, elle paraissait entourée à la base par la bouche, ornée d'une sorte de lèvre frangée." My own description<sup>2</sup> of

<sup>1</sup> "Annelides," in 'Suites à Buffon,' t. iii, p. 190, foot-note.

<sup>2</sup> "On the Structure of a New Genus of Lumbricidæ (*Thamnodrilus*)," 'Proc. Zool. Soc.,' 1887.

"*Thamnodrillus*" Gulielmi (really a *Rhinodrillus*, as I pointed out later), and the figures published in illustration of that description, bear out, so far as they go, M. Vaillant's opinion, and are not confirmatory of the earlier view of M. Perrier. I figured (*loc. cit.*, p. 157, fig. 2) a conical body protruding from the mouth aperture, and surrounded by that orifice, which evidently corresponds to the structure described here in *Trichochæta*. As this process is not attached to the first segment of the body, I stated that there was no prostomium. The resemblance in this particular between *Rhinodrillus* and *Trichochæta* is, of course, of additional interest, inasmuch as they both belong to the same family of earthworms. A protrusible proboscis of this kind is not found in any other Oligochætous Annelid. It must be noticed that it is not a diverticulum of the pharynx, but of the buccal cavity, though arising close to the junction of the two sections of the gut. Both buccal cavity and pharynx belong, it must be remembered, to the stomodæum.

The epidermis presents the usual characters. The peculiar refractive bodies found in the epidermis of *Pontoscolex*, and so distinctive of that genus, are entirely absent. If a portion of the dermo-muscular tube be mounted in glycerine, and the different layers be successively brought into focus, the following is the appearance of the different structures:—The epidermis appears to consist of large nucleated polygonal cells only; these are, however, the gland-cells, between which lie the interstitial cells, forming a meshwork. Bringing the circular muscular layer into view, its fibres are seen to be limited to the anterior and posterior borders of each segment, leaving the middle free, or traversed by a few fibres only, which give the appearance of a loose meshwork. The longitudinal layer beneath this forms a nearly continuous sheet, broken only by the implantation of the setæ. In transverse sections the spaces in the circular muscular layer are seen to be filled with a granular substance containing interspersed nuclei. We have evidently to do with an exaggerated de-

velopment of the "lymph spaces" found in the muscular layers of all *Oligochæta*.

The setæ are, as in the Geoscolicine genera *Pontoscolex*, *Diachæta*, and *Onychochæta*, disposed irregularly, though there are but eight to each segment. As in *Diachæta*, there are fourteen rows; as in *Diachæta Thomasii*, the ventralmost seta on each side of the nerve-cord is repeated from segment to segment without any alteration in its position. There are thus two rows of setæ, which are perfectly regular and in line. The form of the setæ differs from that of any setæ that have been hitherto met with in the *Oligochæta*, unless, indeed, the setæ of *Hypogæon hirtum* are similar. Savigny<sup>1</sup> speaks of the setæ of that species, which has not been met with again, as being spiny; moreover, Savigny mentions that the clitellum is "entièrement recouverte de soies inégales, disposées confusement." It may be that *Hypogæon hirtum* is a near ally of, if not identical with, the present species. It comes from America, near to Philadelphia.

In *Trichochæta hesperidum* the free extremity of the setæ (see fig. 2) is furnished with six or eight short and delicate processes, which end in a point directed forwards; otherwise the shape of the setæ conforms to the usual pattern found in earthworms: the extremity is, however, as in the worm *Pontoscolex corethrurus*, slightly bifid at the extremity; there is a small semicircular notch. The setæ at the end of the body are exactly of the same form, and are no larger than elsewhere.

#### § Internal Anatomy.

The alimentary canal has a large gizzard in Segment 6. There are no calciferous glands.

Behind the gizzard are several thickened intersegmental septa. There are five of these—the same number as in *Diachæta Thomasii*.

The nephridia are, as in all other Geoscolicidæ, paired

<sup>1</sup> 'Système des Annélides, principalement de celles des Côtes de l'Égypte et de la Syrie, &c.,' p. 104.

structures. The external orifice does not appear to be provided with the cup-like sphincter found in *Pontoscolex* and *Onychochæta*. In the posterior segments of the body are the "pyriform vesicles" so characteristic of *Pontoscolex*; they seem to open, as in *Pontoscolex*,<sup>1</sup> into the duct of the nephridium, and not separately on to the exterior. As in many *Geoscolicidæ*, the anterior pair of nephridia are larger than those which follow: these enlarged organs correspond to the "glandes à mucosite" of *Pontoscolex*; but in that worm the glands do not open into the buccal cavity, although they may be sometimes temporarily retracted, so as to open into it by the introversion of the anterior segments. In *Trichochæta*, on the other hand, there is no doubt about the fact that these first nephridia do open into the buccal cavity. The only other species among the *Geoscolicidæ* in which these nephridia open in the same way into the alimentary canal is the recently described *Rhinodrillus ecuadoriensis*.<sup>2</sup>

One of the most noteworthy characters of this worm is the form of the sperm-sacs (see fig. 4); in many *Geoscolicidæ* the sperm-sacs are of great length, and present only to the number of a single pair. In *Geoscolex forguesi* the extreme is reached, the sperm-sacs occupying forty-six segments; but even those dimensions are exceeded by the Eudrilid *Polytoreutus magilensis* described in the present paper. In *Trichochæta* the sacs occupy about fifteen or twenty segments; they lie on each side of the gut, and appear on a dissection of the worm as two thin white threads which have not so great a diameter as the nerve-cord. Proximally—that is, near to their origin from the septa—the two sacs are narrow with even contours; further back they present the remarkable appearance shown in fig. 3. The sac is provided with a double series of diverticula, which vary in length from mere nipple-

<sup>1</sup> F. E. Beddard, "Observations on the Structural Characters of Certain New or Little-known Earthworms," 'Proc. Roy. Soc. Edin.,' vol. xiv, p. 160.

<sup>2</sup> "An Earthworm from Ecuador," 'Ann. Mag. Nat. Hist.,' ser. 6, vol. ix, p. 240.

like processes to long tubular cæca, many times as long as the diameter of the sac from which they arise. There appears to be no regularity in the arrangement of these cæca; they are not symmetrically disposed, nor are the longer outgrowths arranged in a definite fashion with reference to the shorter cæca. The walls of the sperm-sacs (fig. 6) appear to be almost entirely cellular; the muscular coat, though present, is extremely thin. They contained no developing spermatozoa, which may perhaps account for their fineness. There are three pairs of spermathecae, apparently lying in Segments 7, 8, and 9. Like the spermathecae of other Geoscolicidæ, they have no diverticula; they are exceedingly slender pouches of great length (see fig. 5), longer than those of any allied form: the muscular fibres in the walls of the spermathecae cross each other diagonally—forming, in fact, a double spiral.

The Geoscolicidæ of Rosa fall into two groups, which are also marked by their geographical distribution. The relation between the classification of the family and the distribution has not yet been pointed out; I may therefore call attention to the following facts.

I previously divided the group into three families—Urochætidæ, Geoscolicidæ, and Rhinodrilidæ, but I am now of opinion that my division is not the most satisfactory; nor do I think that Benham's two families are more satisfactory: these families are Geoscolicidæ and Rhinodrilidæ.

I am disposed to think that the scheme here advanced is more in accord with what we know of the structure of these worms; I would divide them into two families—Geoscolicidæ and Microchætidæ.

The first family—Geoscolicidæ—includes my two families Urochætidæ and Geoscolicidæ — Hormogaster and Glyphidrilus, and + Urobenus, Rhinodrilus, and Anteus; it equals Benham's Geoscolicidæ + Rhinodrilus and Urobenus.

It includes, therefore, the following genera:

Pontoscolex (=Urochæta).  
 Diachæta.  
 Onychochæta.  
 Trichochæta.  
 Rhinodrilus (=Thamnodrilus).  
 Anteus.  
 Geoscolex (=Titanus).  
 Urobenus.

These genera agree to differ from the next family in the following points :

1. Spermathecae one to four pairs, placed in neighbourhood of gizzard.

2. No copulatory papillæ.

Besides these characters, which are absolutely distinctive, there are others which are found in this family but not in the next—e. g. prostomium sometimes absent; setæ often ornamented, particularly upon the clitellum; peculiar glandular diverticula connected with the posterior nephridia; setæ often irregular in arrangement; sperm-sacs may be one pair, very long; egg-sacs absent (this is perhaps characteristic of the family).

These genera are, with the exception of *Pontoscolex*, confined to the New World; the genus *Pontoscolex* is so ubiquitous that it can hardly be safely assumed that its presence in the tropical parts of the Old World is due to man's agency.

The second family, *Microchætidae*, will include these genera :

*Microchæta*.  
*Brachydrilus*.  
*Bilimba*.  
*Kynotus*.  
*Glyphidrilus*.  
*Callidrilus*.

These six genera agree in the following assemblage of characters :

1. Spermathecae usually many small pouches in a segment, placed in the neighbourhood of the ovaries.

2. Copulatory papillæ present in nearly every case.



Perhaps Benham's genus *Eminodrilus* will prove to belong to this family. All these genera are natives of the tropical parts of the Old World, particularly of Africa and Madagascar.

### 3. *Pygmæodrilus lacuum*, n. sp.

I have had five or six specimens of this species, they were obtained alive from Kew; the habitat of the species is Lagos, West Africa.

#### § External Characters.

It is a small species, measuring about an inch in length, and is composed of about 120 segments. The anterior end of the worm (see fig. 14) is rather pointed, owing to the sudden increase in diameter of the segments after the 3rd. The prostomium is short, and rounded anteriorly; it is continued by grooves on to the buccal segment; these grooves (fig. 15) meet at an acute angle. The real demarcation between the prostomium and the peristomial segment is perhaps the transverse groove shown in the figure. There are dorsal pores which commence at any rate at the posterior boundary of the 6th segment, if not before.

The clitellum is extensive; it begins at the middle of Segment 13, and extends as far as the middle of Segment 26, occupying therefore thirteen segments; it is only developed on the dorsal side of the body: the ventral region between the ventral setæ is covered with epidermis which has the structure of that on the non-clitellar segments.

The setæ are paired; they show no modification upon any segment or segments; they commence as usual upon the 2nd segment of the body. The ventral setæ of Segment 17 are absent.

The first four segments of the body are not secondarily divided into annuli; Segment 5 is biannulate; the next four are triannulate; the next few are divided by furrows into about five annuli.

The only apertures visible upon the exterior of the body are those of the spermathecæ and the atrial pores.

The spermathecal pores lie on the boundary line between Segments 8 and 9, in line with the ventral couples of setæ.

The atrial pores are upon Segment 17, corresponding in position to the absent ventral setæ of this segment. Each is situated upon an elevation of oval contour, not fused across the middle line with its fellow.

There are no genital papillæ.

### § Internal Anatomy.

My investigations into the internal anatomy of this worm are less complete than they might otherwise have been, owing to the fact that the alimentary canal was full of sand, which greatly damaged the sections and prevented me from satisfactorily determining certain points.

As in many other earthworms, a few of the foremost intersegmental septa are greatly thickened, and are attached ventrally along lines which do not correspond with the intersegmental grooves. There are five of these thickened septa, which lie between Segments 5—10.

The body-cavity is largely occupied by numerous corpuscles; they are particularly abundant in the segments after the 12th, but I found them as far forwards as the cavity of the prostomium. These cells have a circular contour or are slightly oval; the outline appears crenate, an appearance which seems to be due to the presence of a peripheral layer of excreted particles, a few of which are also scattered through the cell. The nucleus is comparatively large, and always very much more darkly stained than the surrounding protoplasm, which is but faintly tinged by borax carmine. Among the cells were, here and there, aggregations of darkly stained spherules. The existence of numerous cœlomic corpuscles seems to characterise the tropical species of earthworms; but generally these cells are loaded with granules.

The nephridia commence in the 6th segment; in Segment 5 I found the funnel of this nephridium, but there was no

nephridium belonging to that segment to be discovered. The nephridia are paired, and are not absent from the genital segments.

The buccal cavity occupies the first three segments of the body; as usual, the cerebral ganglia lie at the junction of this with the pharynx. The epithelium of the first section of the buccal cavity is like that which covers the prostomium; that is to say, the cells are narrow and deep, with a few oval glandular cells scattered among them; there are, indeed, more glandular cells than in the prostomial epidermis, but not so many as in the epidermis of the general body surface. Behind this region, which is about half the length of the buccal cavity, the tube becomes contorted so as to be able to be stored away in the limited space available; this region is lined with columnar cells considerably wider than those of the first section of the buccal cavity. This part of the buccal cavity has an extraordinarily rich nervous supply; these nerves are not merely delicate filaments concerning whose existence there might be some doubt, but stout nerves which form an almost continuous layer (probably really a plexus) beneath the epithelium—immediately beneath it, and divided from it by no structures. These nerves are exceedingly conspicuous from the fact that the nerve-cords are unstained, and therefore contrast with the deeply stained epithelium beneath which they lie; frequent nuclei are interspersed among the fibres. These nerves are connected with a large visceral ganglion. A rich nervous supply, limited to the anterior part of the alimentary tract (or at least most highly developed there) of an animal which, as it swallows all before it, can hardly be accused of possessing a very delicate or discriminating palate, is remarkable. Earthworms, however, in addition to swallowing the earth as they tunnel their way through it, draw down leaves into their burrows; for the selection of these leaves the nervous mechanism referred to may be useful. It is also possible that the buccal cavity is everted as in *Perichæta*; but although I received the worms alive I did not notice anything of the kind. In that event it might be used as a tactile organ, which

one would imagine to be of more use to an earthworm than an organ of taste.

The pharynx begins in Segment 4. Septal glands are well developed. In Segments 6 and 7 are gizzards—one to each segment, with tolerably thick muscular walls. The œsophagus extends as far back as the end of the 11th segment; in the next segment the intestine commences. The calibre of the œsophagus is less than half that of the intestine; it is furnished in Segment 9 with a pair of diverticula which appear to be very like those of *Pygmæodrilus quilimanensis*: the basal part where they arise from the œsophagus is wide, but the pouches narrow towards the free extremity, which is obtusely pointed. The structure is that of the calciferous glands of other earthworms.

Generative Organs.—These are somewhat intermediate between those of a new genus, *Gordiodrilus*, recently described by myself, and other *Cryptodrilidæ*. There are only a single pair of testes, which are, as is the case generally among earthworms when there is only a single pair, in Segment 11; the sperm-sacs are in Segment 12, and are of a racemose form; in Segment 11 also there was a mass of developing sperm. The ovaries are in the 13th segment; the oviducts are perfectly normal, and there are no egg-sacs. The sperm-ducts in correspondence with the testes are a single pair, the funnels lying of course in Segment 11. The sperm-duct of each side passes back close to the peritoneum of the ventral body-wall; arrived at the 17th segment the sperm-duct perforates the body-wall; just before entering the body-wall it becomes slightly wider, and is invested by a moderately thick muscular tunic; but the lining epithelium is still ciliated. The sperm-duct at this part of its course lies behind the atrium; when it enters the body-wall it passes obliquely in a slightly forward direction, and opens into the duct of the atrium just before the external orifice of the latter, and on to its posterior side. The atria are a single pair of tubular bodies, which consist, as in most earthworms, of a distal muscular portion and of a proximal glandular portion. The

glandular portion is, as in *Gordiodrilus* and *Ocnodrilus*, lined by a single layer of large columnar glandular cells.

The calibre of the tube is, however, rather greater than in either of those two genera; but still there is no indication of the double layer of cells such as is found in *Acanthodrilus*, &c. As already mentioned, no penial setæ exist. There are a single pair of spermathecae in Segment 9. One of these is shown in fig. 16, partly in optical longitudinal section; the pouch itself is large and somewhat oval in form; the duct is long, but not so narrow in proportion to its length as in *Gordiodrilus tenuis*. The pouch is lined by a single layer of columnar cells (fig. 16, *a*) which are irregularly defined at the free extremities; they are here prolonged into short processes, and contain clear vesicles: this is no doubt associated with the production of a slightly granular substance occupying the interior of the pouch. There were no spermatozoa to be found. The duct of the spermatheca is lined by an epithelium of a non-glandular appearance, and has a muscular investment which is present as an excessively thin layer upon the pouch itself; there are no diverticula.

I refer this worm to the genus *Pygmæodrilus* chiefly on account of the form and position of the œsophageal appendages. In certain other points it differs from *P. quilimanensis*, *P. bukobensis*, and *P. affinis*, the remaining species of the genus, and from *Gordiodrilus*, with which *Pygmæodrilus* has affinities.

The investment of the end of the vas deferens by muscular fibres does not form a very important point of resemblance between *P. lacuum* and *P. quilimanensis*, since the same differentiation occurs in *Microdrilus* (nov. gen.). Michaelsen says nothing about the structure of the atria in the other species of the genus. The form of the spermathecae is very different in *P. lacuum* from what is found in the three remaining species. It is rarely the case that diverticula are present and absent in the same genus, or even in the same family. The only instances that I can at present recall are *Acantho-*

drilus *Spegazzinii*, in which Rosa asserts the absence of diverticula; as a rule this genus of course has diverticula. In the absence of diverticula, and in the length of the spermatothecæ, *P. lacuum* resembles *Gordiodrilus*. If Michaelsen had not described the genus *Pygmæodrilus* I should certainly have referred the present species to that genus.

#### 4. *Siphonogaster Millsoni*, F. E. B.

*Siphonogaster Millsoni*, F. E. Beddard, P.Z.S.,  
1890, p. 48.

Two or three years ago Levinsen<sup>1</sup> described a remarkable worm from the banks of the Nile, characterised by having a pair of long processes arising from the ventral side of the body a little behind the head. A year ago I contributed to the 'Proceedings of the Zoological Society' a short notice of another worm, evidently referable to the same genus, from Lagos, West Africa. I have lately, through the kindness of Mr. Alvan Millson acquired a large number of examples of the latter species, many of them in an excellent state of preservation for section cutting; I am able, therefore, to add something to the very fragmentary account I gave formerly of the structure of *Siphonogaster Millsoni*.

I shall give some of the most interesting facts in its anatomy, and refer to the specific characters at the end of the description.

#### § External Characters.

The most striking external peculiarity of the Oligochaete, which is of about the same bulk as the average-sized British *Lumbrici*, is of course the pair of appendages already referred to; they arise from the 18th segment. The appendages vary in size in individuals, a variation which I take to be indicative of

<sup>1</sup> "Om to nye Regnormslægter fra Ægypten," 'Vidensk. Medd. Kjøbn., 1889.

the stages of sexual maturity. In some specimens they were fully as long as they are figured by Levensen;<sup>1</sup> in others they were no longer than I have already figured them<sup>2</sup> in the present species. These outgrowths are undoubtedly penes, as Levensen thought. I have found that the vas deferens traverses them, opening on to the exterior at about the middle. But I imagine that they must perform some other function in addition to that of serving as intromittent organs for the sperm; they are so altogether out of proportion to the fine canal which perforates them; and besides, there are no correspondingly large organs to receive them during copulation. The structure of the penis is displayed in fig. 19. In cross section they are roughly semicircular; the ventral surface is, however, not flat; as shown in fig. 19, it has a broken surface. Here and there are deepish depressions, caused apparently by the unequal contraction of the muscular fibres. There was no regular infolding of the two edges of the penis, such as Levensen figures in *Siphonogaster ægyptiacus*.

The under surface of the penis is also broken by deep depressions, which serve probably as suckers. I generally found two of these near to the attachment of the organs to the body-wall; but there are others all along the penis, which are not as a rule so marked; from the bottom of these depressions arise the setæ. In sections through the penis they have the appearance represented in fig. 19. The epithelium which lines these semicircular pits is very glandular; the cells are deeply stained, and are laden with spherical granules. The setæ spring from the bottom of these pits; the shape of the setæ is illustrated in fig. 21. So far as I could ascertain all the setæ arose from pits, but these pits are of very various sizes; as a rule they are inconspicuous, not visible at all, in fact, by the unarmed eye; but there are usually two large ones near to the base of the penis, as figured in fig. 18, *Sv.*; these, however, are not always present, or are, at any rate, not always obvious. The epithe-

<sup>1</sup> Loc. cit., tab. vii, figs. 1 and 2.

<sup>2</sup> "On an Earthworm of the Genus *Siphonogaster* from West Africa," 'Proc. Zool. Soc.,' 1891, p. 48.

lium of the penis is like that of the general body surface, but underneath the epithelium is a layer of glandular cells, which are prolonged into fine processes that penetrate between the cells of the epithelium. Occasionally this was very apparent; owing to the fact that the cells in question were laden with darkly staining granules. The structure of the lower surface of the penis is, indeed, closely like that of the clitellum of other earthworms. In the present species I have been quite unable to discover a clitellum; it is rather risky to assert the absence of this characteristically Oligochætous organ; for a long time it was thought to be absent in *Moniligaster* until its presence was proved by Professor Bourne; in *Siphonogaster*, however, the structure of the penis, as well as its large size, is quite in accord with the view that it may possibly perform the function of a clitellum. This organ is, as Levinsen pointed out, very vascular; one particularly large trunk (fig. 18) runs along the whole length; besides this there are two smaller longitudinal vessels. All these send off branches which ramify in the walls of the penis.

The great vascularity of the organ led Levinsen to regard it as in all probability performing a respiratory function in addition to a reproductive. This may be so, but the large development of unicellular glands would surely need a correspondingly rich development of the blood-capillaries.

I should mention that the penial processes are quite solid; there is no prolongation into them of the body-cavity: they do contain irregular spaces due to the lax arrangement of the muscular and vascular tissues which fill up the interior; but these spaces appear to be perfectly independent of the cœlom. In relation to this question of cœlom an important fact in the structure of the penes is the presence of apparently excretory tubules; these are quite conspicuous, and (fig. 19, *n.*) show every resemblance to the nephridia; they are contorted tubes with an intra-cellular lumen. I traced them some distance into the thick lower wall of the penis, and was successful in discovering the actual orifice on to the exterior; traced in the other direction



they ceased to exist very soon. I could find no connection with the paired nephridia of the segment, and the apertures of these paired nephridia were visible quite close to the point of origin of the penis.

The nephridia lie at a lower level than the sperm-duct ; they cannot, therefore, be confused with it ; besides, their calibre is considerably less, as can be seen by an inspection of fig. 19. I could not discover any cilia in the nephridia ; cilia were extremely conspicuous in the sperm-duct. The nephridia appear to form a network ; it was common to see the tube showing indications of branching, such as are exhibited in fig. 19 ; here and there the tubes communicated with the exterior. I looked very carefully for any connection between the nephridia and the sperm-ducts ; no such communication could be found, and as a matter of fact the position occupied by the nephridia is different from that occupied by the sperm-ducts. I did not make any attempt to count the number of pores in the penis, but there are undoubtedly a considerable number. The occurrence of excretory tubules in this organ is a remarkable fact. I have already mentioned that the penial processes do not appear to contain any prolongation of the cœlom ; they are simply processes of the body-wall, solid processes without any continuation of the body-cavity. There is furthermore, as has also been mentioned, no connection between the nephridia of the penes and the nephridia of the segment whence they arise ; it is difficult, therefore, when we consider all these facts, to believe that the nephridia "are cœlom." Before taking leave of these organs I ought to mention that the funnels, if present, entirely escaped my notice. As there is no body-cavity in the penes the absence of internal apertures is not to be wondered at.

If the penes are ever broken off from the body, and can lead an independent existence for a short time, it would be quite excusable to put them down as aberrant and probably parasitic Annelids, connecting the Oligochæta with the Hirudinea ; the ciliated vas deferens passing along the middle line would be the alimentary canal, and the existence of independent excre-

tory tubes would almost decide the matter of their being independent organisms.

### § Internal Anatomy.

The reproductive organs are peculiar in a few respects; not, however, the testes and the sperm-sacs: the former occupy the usual segments in which those gonads lie, viz. 10th and 11th. The sperm-sacs are voluminous; they extend from the 9th to the 12th segment. The sperm-ducts open into Segments 10 and 11 by large folded funnels. The tubes connected with these plunge at once into the thickness of the body-wall, and the two tubes of each side fuse. The single sperm-duct thus formed passes back still embedded in the body-wall near to the junction of the circular with the longitudinal muscle layer, but distinctly in the latter; it runs into the penis, and opens, as already mentioned, at about the middle of this organ, on to the exterior.

The ovaries are paired, and lie in Segment 13; they are of rather a peculiar form, being narrow, transversely elongate bands; the ripe ova occupy the unattached margin of the gonads. The oviducts lie in the following segment; the funnel, however, does not open into Segment 13, as is nearly universally the case; indeed, the only exception hitherto described is *Plutellus*. M. Perrier stated<sup>1</sup> that in that genus the oviducts were limited to a single segment; this statement has not, however, met with entire acceptance.<sup>2</sup> There is no doubt about the matter in *Siphonogaster*; it is quite plain in longitudinal sections, which are adapted for proving such a point without leaving much room for doubt. There were, in one example at any rate, two pairs of egg-sacs in Segments 13 and 14 respectively; they are attached to the front wall of those segments.

I could not find any trace of spermathecae. But, as is well known, these organs are occasionally wanting in *Oligochæta*.

<sup>1</sup> 'Arch. de Zool. Exp.,' t. ii.

<sup>2</sup> W. B. Benham, "Description of Three New Species of Earthworms," 'Proc. Zool. Soc.,' 1892, p. 137.

The alimentary canal is entirely without a gizzard; after the pharynx the narrow œsophagus extends for a considerable distance, terminating in the intestine in Segment 17. The first part of the œsophagus as far back as Segment 9 is not greatly vascular; the rest of the œsophagus is particularly richly supplied with blood-capillaries; it has, however, no calciferous glands or diverticula of any kind; the terminal section of the œsophagus, occupying Segments 13—15, is wider than the portion in front; the intestine is at first (for one segment) hardly wider; it suddenly increases to double the previous width. There seems to be no typhlosole. I have not attempted to work out the anatomy of the circulatory system, but the few following points may be noted. In Segments 8—12 are a series of hearts connecting the dorsal with the ventral blood-vessel; there seems to be no supra-œsophageal vessel.

#### § Affinities of *Siphonogaster*.

In the incomplete description of the worm, which was based upon examples kindly forwarded to me from Kew by Mr. Thiselton Dyer,<sup>1</sup> I pointed out certain apparent differences from *Siphonogaster ægyptiacus* of Levinsen. The examination of the large series of well-preserved specimens recently received from Lagos through the kind instrumentality of Mr. Alvan Millson leads me to the belief that there is only one species of *Siphonogaster*; the only possible difference that I can see is that in *Siphonogaster ægyptiacus* the setæ upon the penial appendage are irregularly disposed; in all the worms from Lagos these setæ are largely paired, though not perfectly regular; in any case there were very rarely more than two setæ in a transverse row. Levinsen's account is necessarily so imperfect that the question of the species cannot yet be decided. Hence I retain provisionally the specific name applied by me to these worms.

Dr. Michaelsen has lately described two other species of

<sup>1</sup> "On an Earthworm of the Genus *Siphonogaster* from West Africa," 'Proc. Zool. Soc.," 1891, p. 48.

this same genus<sup>1</sup> from the shores of Victoria Nyanza; these have been named *S. Emini* and *S. Stuhlmanni*; both these species are founded upon fragments which, however, included the penial process. The small size of these processes in *S. Emini* I should look upon as a sign of immaturity. So far as can be gathered from the necessarily incomplete account given by Michaelsen, these species agree with that described in the present paper in their essential structures. Michaelsen considers that their systematic position is a matter of doubt; the presence of penial processes, as he remarks, suggest the *Teleudrilini*, a view which is of course not supported by the absence of prostates and spermathecae. My own observations recorded here serve, I think, to fix with something like certainty the systematic position of the worm.

It will be obvious from the above account of the anatomy of *Siphonogaster* that it is a member of the family *Geoscolicidae* of Rosa. I myself and others thought that the genus would prove to be, as are the majority of tropical African earthworms, a *Eudrilid*; it is abundantly clear that this surmise was incorrect. On p. 257 of the present paper I have attempted to revise Benham's classification of these intra-clitellian worms; since writing that passage a paper by Rosa<sup>2</sup> has come into my hands, which is practically in accord with what was there said. I may point out that the structure of *Siphonogaster* further confirms the justice of separating the Old from the New World genera. I would particularly direct attention to the presence of egg-sacs in *Siphonogaster*; these sacs do not, so far as we know at present, occur in the American forms; they have been found in a good many Ethiopian and Indian genera.

<sup>1</sup> "Beschreibung der von Herrn Dr. Fr. Stuhlmann am Victoria Nyanza gesammelten Terricolen," 'Jahrb. Hamb. wiss. Anst.,' Bd. ix.

<sup>2</sup> "*Kynotus* Michaelsenii, n. sp.," 'Boll. Mus. Comp. Zool.,' vol. vii, No. 119.

Genus *Siphonogaster*, Lev.

*Siphonogaster*, Levinsen. 'Vidensk. Med. fra den naturh. Foren. i Kjøbenhavn,' 1889, p. 319.

Moderate-sized *Oligochæta* belonging to the family *Geoscolicidæ*; setæ eight in a segment, ornamented,<sup>1</sup> paired; on the 18th segment a pair of penial processes, upon the middle of which open the sperm-ducts, armed with modified setæ and furnished with suckers; sperm-ducts running within the thickness of the body-wall; spermathecae absent; œsophagus without gizzard or calciferous glands.

*Siphonogaster* *Millsoni*, F. E. B.

*Siphonogaster* *Millsoni*, F. E. Beddard. 'Proc. Zool. Soc.,' 1891, p. 48.

Body square in transverse section behind the penial processes, the paired setæ lying at the corners; the dorsal region of the body-wall much thinner than elsewhere; penial setæ arranged in pairs, though not with absolute regularity.

Hab.: Lagos, West Africa.

5. *Alvania* *Millsoni*, nov. gen., n. sp.

Among a number of earthworms recently sent to me from Lagos by Mr. Alvan Millson, Assistant Colonial Secretary, are three or four examples of a small worm belonging to the family *Eudrilidæ*. So many new genera have been lately described of this characteristically African family, and so many of them are imperfectly known, that I hesitate before placing the species to be described here in a new genus; and yet it appears, as will be seen in the sequel, to possess characters which, as the genera are now limited, entitle it to generic rank. In any case I include it for the present in a new genus allied to *Heliodrilus*, which it approaches more closely than

<sup>1</sup> This is of course another reason for referring the genus to the *Geoscolicidæ*.

any other genus. The worms, of which I had about half a dozen specimens, measured two inches or so in length. The colour was evidently entirely lost in the process of preservation; but it appears that little or no integumental pigment is present.

### § External Characters.

In the disposition of the setæ this worm resembles the genera *Heliodrillus* or *Hyperiodrilus* (which Michaelsen would unite in one genus), *Paradrillus*, and *Preussia*. The setæ are paired, but the two setæ of the ventral couples are much further apart than are the two setæ of each dorsal couple, which are strictly paired; the setæ are, in fact, arranged precisely as in the genera above mentioned. There was nothing peculiar about their form that I could find. They tend to disappear upon the clitellum.

The most striking external character was exhibited by the male reproductive apparatus (fig. 23); the opening of the atria, a single pore, was upon the border line between the 17th and the 18th segment; it was marked by a slight protuberance of a hemispherical form. From this a groove, bordered by a raised margin on each side so as to form a trough, ran forward up to the 14th segment in one case, to the 15th in another; at the boundary line between Segments 15 and 16 this groove became divided into two at an angle of nearly forty-five degrees; the two grooves end in a rounded prominence; these no doubt serve the purpose of penes. The existence of these penial processes ought, perhaps, to have led me to refer the genus to my genus *Hyperiodrilus* or to *Stuhlmannia*, but in the present species the spermathecal orifices are further forward than in either of the two genera mentioned; they lie, in fact, upon the 10th segment, whereas in both *Hyperiodrilus* and *Stuhlmannia* these pores are upon the 13th segment. The oviducal pores, as in all Eudrilids with the remarkable exception of *Libyodrillus* (not an exception if we go by internal segmentation), lie upon the 14th segment.

The variability in position of the penes, though remarkable,

is precisely what we find in the two other genera in which there is a penis or are penes. I have pointed out that in *Hyperiodrilus* these processes of the body-wall may arise from either the 16th or from the 17th segment; in *Stuhlmannia variabilis*, which has received its name on account of the variability in the position of this organ, Michaelsen has depicted it as arising from either the 15th or the 17th segment.<sup>1</sup>

The prostomium is conspicuous, and extends for a little way on to the 1st segment.

The clitellum is developed all round the body, and occupies Segments 15—17. In one specimen which I examined, mounted as a flat preparation, there were no setæ upon the 17th segment, and only one pair (the ventralmost of each side) upon 15 and 16 (see fig. 24).

#### § Internal Anatomy.

In dissecting the worm the most salient character appears to be the existence of five separate gizzards lying in Segments 18—22; this character, of course, allies the worm to the genera *Hyperiodrilus* and *Heliodrillus*; the latter are the only Eudrilids in which the gizzards have this unusual location; this fact, indeed, seems to have led Michaelsen to associate the two into one genus.

In other respects the alimentary canal of this worm does not show any differences from the alimentary canal of *Heliodrillus*; there are three ventral pouches in Segments 9, 10, 11; in Segment 13 are the calciferous glands. The first recognisable septum divides Segments 4—5; this and the seven following are thicker and stronger than the other septa. The nephridia commence in the 4th segment; their external apertures are in front of the dorsal couple of setæ.

This species differs from *Heliodrillus lagosensis* and from *Hyperiodrilus* in having no integumental sense-organs, which are found in so many Eudrilidæ. This is one of the

<sup>1</sup> "Beschreibung der von Herrn Dr. Fr. Stuhlmann auf Sansibar und dem gegenüberliegenden Festlande gesammelten Terricolen," 'Jahrb. Hamb. wiss. Anst.,' Bd. ix, Taf. ii, figs. 13 and 14.

principal facts which lead me to doubt the justice of including this worm in either of those genera; and, as will be seen presently, there are other points, in the structure of the reproductive organs, that are at variance with that view of the systematic position of the species.

There are two pairs of testes attached to the anterior wall of Segments 10 and 11. The testes of the 11th segment are enclosed within the sperm-sac of that segment; the testes of Segment 10 are also enclosed in a sac, which also includes the dilated end of the sperm-duct. The sperm-ducts, as in so many Eudrilidæ, widen out just before opening by its funnel into the interior of the sperm-sac; furthermore the funnel is placed a segment behind that which it ordinarily occupies; this is so in many Eudrilidæ. The sperm-duct thus perforates the septum twice before opening into the cœlom; the facts are now so well known that I need not enter into the matter at length. The two atria open by a common pore upon the border line between Segments 17—18; they have the usual tubular form, and the sperm-ducts open into them considerably in front of their external orifices.

The female reproductive organs (fig. 26) are somewhat intermediate between those of *Heliodrilus* and those of *Paradrilus*; the ovaries, as in both genera, are each enclosed in a sac attached to the front wall of Segment 13. The stalk of this sac lodges the tube of the nephridium as it passes towards the funnel; the sac of each side runs forward and widens out to form a dilated sac which partially involves the end of the oviduct. From this dilated sac a narrow tube communicates with a long spermathecal sac; the spermathecal sac is divided into two regions separated by a slight constriction. At the constriction the lining of cells is much increased in thickness, and seems to obliterate the lumen; the mass of cells project for some distance into the anterior part of the sac, which is narrower than the posterior part. There appeared to be no actual connection between the lumina of the two. The arrangement of this part of the spermathecal sac is on the principle of a lobster trap; there is no facility for



the exit of any contents of the posterior section of the sac, but spermatozoa could seemingly pass up from the external orifice. The spermathecal sac, however, contained no spermatozoa and no ova. From the dilated sac above referred to as communicating with the spermathecal sac (called by Michaelsen "Eitrichterblase") arises a somewhat narrow tube which passes over the œsophagus and unites with its fellow of the opposite side of the body. I followed the course of these tubes with great care in a complete series of longitudinal sections, for I thought at first that they might open into the intestine, as Rosa has shown for *Paradrilus Rosæ*,<sup>1</sup> there was, however, no such connection.

This periesophageal sac contained a few ova. The egg-sacs (receptacula ovarum) lie in the usual position; they communicate by a short duct with the ovarian chamber; into them also opens the oviduct by a narrow aperture. The ripe ova are enclosed in a stoutish membrane, in which I did not observe any striations. The oviduct of each side opens on to the exterior upon the 14th segment. A little way in front of the external pore the oviduct gives off a short cæcum, which is enclosed in the same muscular sheath with the oviduct. I believe that this cæcum is not to be compared with a diverticulum of the ampulla of the ovarian tube figured by both Rosa and Michaelsen; for the oviduct has of course nothing to do developmentally with the series of cœlomic pouches which constitute the egg passages. I am not, however, in a position to suggest with what it is homologous.

The female reproductive organs of this Eudrilid are not exactly like those of any other species at present known; it approaches most nearly to *Hyperiodrilus* and to *Paradrilus*. It differs from the former and agrees with the latter genus in having no true spermatheca, but only a cœlomic pouch discharging those functions which in other earthworms are performed by spermathecæ. In *Metadrilus*, *Stuhlmannia*, and *Hyperiodrilus* the gut is surrounded by a

<sup>1</sup> "Die exotischen Terricolen des k. k. nat. Museums," 'Ann. nat. Hofmus.,' vi, p. 389.

ring of tubing derived from the cœlomic species connected with the egg-conducting apparatus. In *Paradrilus* the homologous pouches open into the interior of the gut.

The following may serve as a definition of the genus.

ALVANIA, nov. gen.

Setæ paired, ventral setæ separated by a wider interval than dorsal. Clitellum 15—17; male pore upon 17—18, connected by a groove with two penes upon 14 or 15. Spermathecal orifice upon 10. No integumental sense-organs. Alimentary tract with five gizzards beginning in 18; calciferous glands in 13; calciferous pouches in 9, 10, 11. Ovaries enclosed in separate sacs; ampullæ of egg-conducting apparatus communicating above gut, and connected with a long spermathecal sac; true spermathecæ absent. Funnels of sperm-ducts depending from anterior walls of Segments 11 and 12; sperm-ducts therefore perforating these septa twice, dilated before termination in funnels. Atria paired, but opening by a common orifice. No penial setæ.

I do not propose to attempt a definition of the species.

## EXPLANATION OF PLATES XXV &amp; XXVI,

Illustrating Mr. Frank E. Beddard's paper on "Two New Genera and some New Species of Earthworms."

FIGS. 1—6.—*Trichochæta hesperidum*.

Fig. 1. Diagrammatic longitudinal section through proboscis and anterior segments. *Neph.* First nephridium. *Or.* Its orifice.

Fig. 2. Seta. *a.* The whole seta. *b.* Tip of seta, more highly magnified.

Fig. 3. Part of sperm-sac.

Fig. 4. Anterior segments, twice the natural size.

Fig. 5. Spermatheca.

Fig. 6. A portion of sperm-sac, highly magnified.

FIGS. 7—12.—*Polytoreutus magilensis*.

Fig. 7. Portion of female reproductive apparatus. *R. o.* Receptaculum ovarum. *O. d.* Oviduct. *E. s.* Egg-sac. *a.* Tube leading to *sp.*, spermathecal sac.

Fig. 8. Reproductive organs. *v. d.* Dilated extremity of vas deferens. *Sp. s.* Sperm-sacs. *e.* Extremity of same. *b, c.* Spermathecal apparatus. *a.* Atrium. *O. d.* Oviduct. *Ca.* Calciferous gland.

Fig. 9. Spermathecal apparatus, more highly magnified. *R. o.* Receptaculum ovarum. ♀. Female pore. *B.* Bursa copulatrix. Other letters as in Fig. 8.

Fig. 10. Genital segments from below. *Od.* Oviducal pores: ♂, male pore; ♀, spermathecal pore.

Fig. 11. A spermatophore.

Fig. 12. Section through a portion of the spermatheca. *m.* Muscular walls. *ep.* Lining epithelium. *s.* Spermatophores cut in every plane.

FIGS. 13—16.—*Pygmæodrilus lacuum*.

Fig. 13. The worm, natural size after preservation.

Fig. 14. Prostomium and anterior segments, lateral view.

Fig. 15. Prostomium and anterior segments from above.

Fig. 16.—Spermatheca. *a.* lining epithelium.

FIGS. 17—22.—*Siphonogaster Millsoni*.

Fig. 17. Head end of the worm, natural size from below. *p.* Penial appendages.

Fig. 18. One of the penes more highly magnified; the three principal blood-vessels are indicated. *s.* Seta. *Sv.* Sucker.

Fig. 19. Longitudinal section through a portion of penis. *v. d.* Vas deferens, with its external orifice. *Bl.* Principal longitudinal blood-vessel. *n.* Nephridia. *Sv.* Sucker, with penial seta protruding.

Fig. 20. Seta: *a*, less highly magnified; *b*, more highly magnified, to show sculpturing at the tip.

Fig. 21. Penial setæ. *a*. Seta from below; *b, c*, in profile. *d.* Extremity, more highly magnified in profile. *e.* The same from beneath.

Fig. 22. Epidermis (*e.*) and subjacent glandular cells (*gl.*) of penis; the ducts of the latter are seen to have pushed their way between the epidermic cells.

FIGS. 23—26.—*Alvania Millsoni*.

Fig. 23. Ventral view of genital segments. ♂. Male pore. *p.* Penial processes. The clitellar segments are indicated by roman numerals.

Fig. 24. Another specimen, in which the penial processes are not developed.

Fig. 25. A portion of one of the ventral calciferous pouches. *e.* Lumen of gland-tubes. *G.* Cells of peritoneum (?) lying between them. *Bl.* Blood-capillaries.

Fig. 26. The female reproductive apparatus of one side. ♀. Oviducal pore. *O. d.* Oviduct. *c.* Cæcum of oviduct. *R. o.* Receptaculum ovarum. *b.* Sac crossing over intestine and fusing with that of opposite side. *Sf.* Spermathecal sac. *Sp. or.* Its orifice. *o. s.* Sac surrounding ovary, partially cut away to show ovary lying within it.

## Observations on the Gregarines of Holothurians.

By

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With Plates XXVII & XXVIII.

OUR first knowledge of the Gregarines of Holothurians dates back to KÖLLIKER (1), who in 1858 described "vesicles for the most part stalked, with a distinct envelope, and granular, dark, fat-like contents, which invariably contained two germinal vesicle-like bodies, each with a large, finely granulated, germinal spot-like structure. Some of these structures were sessile on the (blood-) vessels (of the intestine and respiratory trees), and were covered by ciliated peritoneal epithelium, while the stalked ones were apparently always naked." The author was at a loss to understand the significance of these structures, and "simply recommends them to later observers."

In the following year ANTON SCHNEIDER (2) identified these bodies as Gregarines, and termed them *Gregarina holothuriæ*. He found them in the intestine, blood-vessels, and free in the body-cavity, and figures a specimen from the blood-vessels, where by continually increased bulging out of the wall they form the stalked vesicles of Kölliker. In all those from the blood-vessels he observed two nuclei, as also in many from the body-cavity. In the latter by slight pressure of the cover-glass he observed a furrow dividing the contents into two halves, each with a nucleus; in the former he could not observe this furrow. In contradiction to Kölliker he found

even the stalked vesicles ciliated, but since they finally fall off into the body-cavity he thinks that at a certain period they would cease to be ciliated.

The author further figures the mature psorosperm, and identifies as a stage in the evolution of the Gregarine certain amœbæ forming the chief mass of the brown bodies. They are homogeneous, without nucleus, and of fat-like contours. For the most part they move slowly or are motionless. A gradation of size could be found in these amœbæ up to bodies as large as the smallest or middling-sized Gregarines.

In 1861, Sars (3, pl. xvi, figs. 2—7) figured Gregarine-like bodies from the gut of *Chiridota pellucida* (= *C. lævis*). Since this date no further works dealing specially with these organisms have, to my knowledge, appeared until the year 1891, when CUÉNOT (4) and MINGAZZINI (5) published researches upon the Gregarines of Holothurians quite independently of one another. LUDWIG (10) also gave an account of the parasites of Holothurians, together with a complete literature of the subject.

CUÉNOT (14) places the Gregarines of Holothurians in the genus *Syncystis*, Aimé Schneider, and describes three species, *Syncystis synaptæ*, E. R. L., sp., from the cœlom of *Synapta inhærens*, *S. holothuriæ*, Ant. Schneider, sp., from *Holothuria tubulosa*, and *S. Mülleri*, Giard, sp., from the cœlom of *Synapta digitata*. MINGAZZINI (5), on the other hand, places these Gregarines in the family *Syncystidæ*, but erects for them a special genus *Cystobia*, of which he describes two species, *Cystobia holothuriæ*, Ant. Sch., sp., and *C. Schneideri*, n. sp., from *Holothuria Poli* and *impatiens*. Further details in these authors' works we shall refer to below under the special descriptions of these Gregarines.<sup>1</sup>

<sup>1</sup> It should be mentioned that in 1852 Leydig described "dark planarian-like bodies, with egg-like structures embedded in them," and vesicles containing pseudo-navicellæ floating free in the body-cavity of *Synapta digitata* ('Archiv f. Anat. u. Physiol.,' 1852, in "Anatomische Notizen über *Synapta digitata*," pp. 517, 518, Taf. xiii, fig. 11).

My own acquaintance with these interesting parasites began in the year 1889, when as a student in the Oxford Laboratory I found a specimen of *Holothuria tubulosa*, from Naples, supplied for dissection, with its body-cavity filled with cysts, some containing sporoblasts, others ripe psorosperms or spores. Having investigated these cysts and their contents, and written a short description of them, I forwarded the description with some material to Professor Bütschli, of Heidelberg, whose pupil I had had the honour and pleasure to be for a short time during the previous summer. Professor Bütschli with characteristic kindness examined the material, and in a letter accompanied by a sketch pointed out to me that I had overlooked the most important points, viz. the formation of the sporozoites within the spore. I determined, therefore, before publishing anything, to examine fresh material, which I was fortunately able to do both at Plymouth in the summer of 1890, when as the occupant of a British Association table I studied the Gregarines of *Holothuria nigra*, and at Naples, during my occupation of the Oxford table there in 1891-2. The results of my investigations on the two closely allied gregarines found in these Holothurians are far from complete, but it seemed to me better to publish them in their present crude form than to wait, perhaps, some years before I can complete them. Like Kölliker, I would simply recommend these interesting forms to later observers, who will, I hope, fill up the gaps in the following description.

I shall begin with the description of the Gregarine of *Holothuria nigra*, in which my series of stages is most complete. This Holothurian occurs commonly at Plymouth, and can be obtained in numbers. The dissection of the animal is not without its difficulties, both on account of the large number of Cuvierian organs it emits, and by reason of the force with which its powerful body muscles contract on the least stimulation, thereby much impeding the examination of the fresh contents of the body-cavity. In the majority of the specimens of *Holothuria nigra* observed by me the blood-vessels could be seen to bear little stalked vesicles, which on exami-

nation were found to contain spores, sporoblasts, or (in one instance) sporoblasts together with nucleated protoplasmic masses of various sizes. Only in a single instance did I succeed in finding the adult Gregarine. In this instance the blood-vessels, which are of a rich brown colour, bore no vesicles, but a few opaque white spots could be plainly observed in the interior of the vessels, shining through the dark walls. The walls of the vessels were not evaginated in any way, and by gently pressing the wall of the vessels these white spots, which were the adult Gregarines, could be made to shift their position. By snipping the blood-vessel with scissors close to the white spot and pressing it, the Gregarine was made to emerge quite uninjured from the cut end. Examination with the microscope showed an opaque white mass, appearing black of course in transmitted light, quite motionless, of irregular shape (fig. 1), and of such strange appearance that at first I doubted if it was a Gregarine at all, the more so as even after fixing and staining, and clearing the object in oil of cloves, I could observe nothing of a nucleus or other structure, so great was the opacity of the protoplasm. By careful searching I found four more Gregarines, making five in all. Of these five, two were stained and mounted whole in Canada balsam, a third was teased up in order to try and find the nucleus (this preparation proved, however, useless), while the remaining two were carefully removed without disturbing them in the blood-vessel, fixed with Kleinenberg's picric, and cut into a series of sections.

Fig. 1 shows one of these Gregarines drawn living when freshly removed from the Holothurian. I have the same specimen now mounted in Canada balsam, but it is so opaque and granular that I can make out no more of the structure than is shown in the figure; the nuclei, which were probably faintly stained, escape observation even with the most careful focussing. Fig. 2 represents another animal, drawn from a Canada balsam preparation, in which eight faintly stained nuclei can be plainly made out, and have been drawn with the camera in their natural positions. In addition a faint but dis-



inct septum could be discerned, dividing the animal in two. This is probably an early stage in the encystation which we shall discuss later.

The best results were given by the two Gregarines which were cut into sections, and which I shall denote as A and B respectively. A was cut into sections of about  $10\mu$  in thickness, B into sections of about  $5-7\mu$ . In A the relations of the parts to one another were best shown, while B showed better minute structure, the relations of the parts to one another being often distorted. To begin with A: the entire Gregarine ran through exactly forty sections. In the 14th section from one end a nucleus makes its appearance, which runs through five sections, disappearing after the 19th section. Fig. 3 represents the 15th section, showing the blood-vessel with the Gregarine in the interior  $\times 128$ . Fig. 4 is the interior part of the same section  $\times 315$ . The 20th to the 30th sections contain nothing special. At the 31st section another nucleus makes its appearance, disappearing after the 35th section. Figs. 5, 6, and 7 represent the 34th, 33rd, and 31st sections respectively. The last five sections contain nothing special. It is thus evident that this Gregarine contains two large nuclei, each running through five sections  $10\mu$  in thickness. Similar results are given by B, which runs through ninety-six sections. The first nucleus appears at the 10th section, runs through eight sections, and disappears after the 17th. The second nucleus appears at the 78th section and vanishes after the 85th. Fig. 8 represents the inner part of the 80th section  $\times 315$ , while 8a represents the nucleus only, from the same section,  $\times 730$ .

To proceed now to study the finer structure of these animals.

The body is limited by a distinct cuticle, appearing as a sharp single contoured line, best seen in fig. 8, where the Gregarine is not in contact on one side with the blood-vessel. The protoplasm of the body is very opaque, and filled with coarse granules of various sizes. No distinction could be found between an ectosarc and endosarc.

The nuclei are very large, each surrounded by a clear space. In sections this space appears filled by a finely granular or streaky coagulum (fig. 7). It sometimes appears as if the nucleus were suspended in this place by threads (fig. 6), but I think this appearance is only due to coagulation of the fluid, probably albuminous, which filled these spaces during life. The nucleus itself is about  $50\ \mu$  in diameter, and surrounded by a strong nuclear membrane, which usually appears wavy in section, owing, doubtless, to shrinkage. It has a single large nucleolus about  $25\ \mu$  in diameter, the remaining space of the nucleus being filled with cloudy or very finely granular contents, with a number of darker spots. At first it seemed as if these dark spots might represent the nodes of a fine reticulum supporting the nucleus, but I was unable to detect any such reticulum with the Homogen. Immers.  $2\cdot0$  mm. of Zeiss (fig. 8 *a*), and the nucleus appeared to be filled with a fine coagulum, but of a different nature from that filling the clear space surrounding it. It is possible, or even probable, that the nucleolus is kept in place by fine strands of chromatin or other substance fastening it to the nuclear membrane, without, however, any definite reticulum.

The nucleolus itself deserves particular description on account of its peculiar structure. In the sections through A it appeared as a round spot, very darkly stained (with hæmatoxylin), containing a lighter vacuole-like spot somewhat excentrically placed. Examination of the thin sections through B made clear the real structure of the nucleolus (figs. 8, 8 *a*). It consists of a darkly stained ground substance containing an immense number of clear vacuoles of all sizes. One of the vacuoles is much larger than the others, and being excentrically placed, constitutes the clear spot seen in the thick sections. Some are excessively minute, and almost escape detection. In fig. 8 *a* the minute vacuoles can be seen in the obliquely cut wall of the large vacuole, producing an appearance which under lower magnification looks like a network.

The darkly staining ground substance of the nucleolus should, after the analogy with the cell nuclei of higher animals,

be chromatin, and the clear unstained vacuoles achromatin; but it would be unsafe to identify the two constituent parts of the nucleolus as such simply from their reaction to stains. With all due caution, however, a comparison may be made with, for instance, the results obtained by PICTET (8) in studying the spermatogenesis of Echinoids, where the achromatic portion of the nucleus of the spermatocyte separates out to form a number of vacuoles or "cytomicrosomes," which fuse together to form the single "Nebenkern." I am not aware that a nucleus of similar structure has as yet been described, though it is an old observation that the nucleoli of Gregarines often contain vacuoles (see BÜTSCHLI, 6, p. 525). WOLTERS (9), in his valuable studies on the conjugation and spore formation of Gregarines, describes the nucleolus of *Clepsidrina blattarum* as containing "more strongly stained spherules of varying size and shape" (p. 118): the nucleolus of *Monocystis agilis* is similarly described (p. 106). Schneider ('Tablettes zoologiques,' i, pl. vi, fig. 9) figures the nucleus of *Pileocephalus chinensis*, containing numerous spherical nucleoli, some dark, others light. The vacuolar structure of the nucleolus in the Gregarine seems to me to support strongly Professor Bütschli's theory of the frothy structure of protoplasm.

The greater number of Holothurians examined had, as has been said above, stalked vesicles attached to the blood-vessels which contained cysts. Some of these cysts I teased up and examined the isolated spores, while others I cut into sections. As it turned out I was not particularly lucky in my selection, for the only cysts which were found to contain perfectly mature spores were the very ones I had selected for sections; while among those teased up one was found to contain, besides sporoblasts, large nucleated masses of protoplasm, the relation of which to the sporoblasts it was of course impossible to ascertain by this method.

Fig. 10 represents one of these cysts attached to the blood-vessels, and fig. 9 shows another, which had an exceptionally long stalk; 9 *a* represents a portion of the edge of the same cyst in optical section.

The cysts are covered by a layer of flattened epithelium which also forms the hollow stalk, and is continuous with the peritoneal epithelium covering the blood-vessels. This is best seen in section (fig. 15 *a*). The wall of the cyst proper is formed by an external very thin jelly-like layer, which cannot be plainly seen in sections, and internally to this a strong structureless membrane, appearing in section as a double contoured line (fig. 15). The cysts themselves are exceedingly opaque, and nothing can be learnt as to their contents without further preparation. They are quite spherical, and have no ornamentation of any kind.

In the sporulation I have observed three stages:

1. The sporoblasts (fig. 11, *a, b, c*). Many cysts occur filled with little spherical nucleated masses of protoplasm. In the living condition (11, *a*) they are filled with strongly refringent granules, the central nucleus appearing as a faint clear space. They are surrounded by a double contoured membrane. After fixing and staining (fig. 11, *b, c*) the nucleus is distinct in many of them, but they do not stain easily, perhaps on account of the thick cell-wall. When visible the nucleus can be seen to have irregular aggregations of darker stained substance round the edge, and to be lighter towards the centre. These bodies are the final results of the segmentation of the protoplasm within the cyst, or the sporoblasts. They also occur singly in cysts containing spores, which is probably due to arrested development. In one cyst I found, besides great numbers of sporoblasts, a few nucleated masses of protoplasm of various sizes containing one to three nuclei (fig. 11, *d, f*) which were much larger than the nuclei of the sporoblasts. Their structure was difficult to make out on account of the opacity of the protoplasm, but in one instance a nucleus could be seen to contain vacuoles (fig. 11, *f*), and two other nuclei were found isolated and had a vacuolar structure (fig. 11, *c*), recalling the nuclei of the adult Gregarine. The exact relations of these masses of protoplasm could not be made out with the method employed, and it was only certain that they were

placed more in the interior of the cyst, and the sporoblasts more peripherally.

2. The stage found most commonly<sup>1</sup> was that of spores each containing four nuclei (figs. 12, 13). In this stage the cyst is completely filled with spores, and with the exception of a few sporoblasts occurring sparsely there is no unused protoplasm. The spores are egg-shaped, one end broader than the other. At the narrow end the membrane of the spore is continued into a well-marked funnel, the lumen of which is, however, shut off from the contents of the spore by a delicate diaphragm. The cuticle is composed of two distinct layers, an inner thicker one and an outer thinner one. Both layers appear to unite to compose the funnel, which is formed of a single contoured thin cuticle, but the diaphragm closing the mouth of the spore is probably derived from the inner layer only. These structures are best seen after treatment with a 10 per cent. solution of sodium carbonate, which clears the contents of the spore (fig. 14). In some spores the diaphragm lies close upon the spore contents (fig. 14, *b*), in others it is raised up from them and bulges into the funnel (fig. 14, *a*).

The spores contain four spherical nuclei (which, however, like the nuclei of the sporoblasts, are often not stained in preparations). The nuclei have a distinct membrane, and if carefully examined with a high power in a favorable preparation can be seen to have the chromatin substance aggregated round the periphery, being clear centrally. They are usually arranged more or less regularly in the angles of a rectangle, two being near the broad end and two near the narrow; but variations from this arrangement are common. In one instance a spore was found to have three nuclei (fig. 13, *c*); two of the ordinary size and appearance near the narrow end, and one larger nucleus placed close to the broad end, and distinctly elongated transversely to the long axis of the spore, as if about to divide. From this it may be reasonably inferred that the two pairs of nuclei placed at the narrow and the broad end respectively are each the product of the division of a single nucleus, so that

<sup>1</sup> These observations were made in the month of July.

in an earlier stage there was one nucleus at each end of the spore. Further, since these two nuclei must be derived from the single nucleus of the sporoblast, we may piece together the following history. Either before or after the assumption by the sporoblast of the elongated shape of the spore, its nucleus divides in two, the two halves going to opposite ends of the spore. The two nuclei thus produced then each divide again into two in a plane at right angles to their former plane of division, so that we get the stage here described with four nuclei, the protoplasm of the spore having in the meanwhile secreted the cuticle and its appendages. It may be pointed out in passing how much larger the nucleus of the sporoblast is than that of the spore.

3. Ripe spores were found in four cysts which were removed attached to a blood-vessel and cut into sections (figs. 15, 16, 17, and 18). The external form of the spore and the structure and arrangement of its cuticle are the same as in the last stage; but each spore now contains instead of four nuclei eight sporozoites<sup>1</sup> (falciform bodies). It is a little difficult in studying the sections to be certain of the exact number, since a spore might often be halved or partially removed, leaving only a few of the sporozoites. Nevertheless, wherever an uninjured spore could be satisfactorily observed, eight sporozoites could be plainly made out, and in very many cases where a spore was cut transversely eight sporozoites could be seen (fig. 16, *b*); and it may, I think, be taken as certain that this is the full and normal number in each spore.

The sporozoites are exceedingly minute, and by no means easy to make out. Nevertheless careful focussing with a Zeiss's oil immersion 2.0 mm. showed them to consist of an elongated darkly staining nucleus forming the head, to which is attached at one end a delicate flame-like tail, doubtless vibratile, and at the other end, which we may term anterior, a minute conical point; but the latter structure was exceedingly

<sup>1</sup> Wolters uses the term "sporocysts" for what are here termed spores, and "spores" for what I have used the name sporozoites. I have kept to the nomenclature of Bütschli and Schneider.

difficult to be certain of. Their typical arrangement appears to be in two rows of four, with the nucleus towards the narrow or infundibular end of the spore, and the tail pointing away from it. Nevertheless variations occur constantly from this position, one or more of the sporozoites being turned round with the tail towards the spore-funnel. The thin diaphragm at the base of the funnel is probably the spot at which the spore-wall breaks to liberate the sporozoites, and the more or less constant position of the latter, with their heads turned towards the funnel, doubtless is in connection with this fact. It is probable that the sporozoites are motile within the spore, which would account for their not unfrequent reversal of position.

They very often appear closely applied to the wall of the spore. Since the tails of the front row overlap the heads of the hinder row, we can understand how it is that all the eight are to be seen in section. They lie embedded in the granular mass or "nucleus de réliquat" (sporophore—WOLTERS) filling the spore, which doubtless serves as nourishment for the growing sporozoites. If we compare fig. 15, *b*, or 16, *a*, with fig. 13, *c—g*, which are drawn to the same scale, it is evident that the bulk of the nucleus of a sporozoite is about half that of a nucleus of a spore in the last stage, and it is scarcely to be doubted that each nucleus in the stage with four nuclei has divided in two to furnish two sporozoite nuclei, which elongate to form the "head" of the sporozoite, while protoplasm becomes aggregated round them to form the tail. In the four cysts which I cut into sections I was able to find two stages of the sporozoite. The first is shown in fig. 16: *a* represents a spore in which six sporozoites could be seen; *b* and *c* show two other spores, one showing five sporozoites, the other in transverse section showing eight, both magnified about 1000; *d*, *e*, and *f* show three sporozoites much more magnified. In this stage the nucleus is not more than twice as long as broad, and the tail is short and stumpy. The second stage, and probably the final one, is shown in figs. 15 and 17, and in fig. 18, which is a combined semi-diagrammatic figure. The nucleus

is now four or five times as long as broad, and the tail longer still. Both nucleus and tail are often slightly flexed, especially when the sporozoite lies close along the side of the spore. Both in this stage and the last the nucleus does not stain evenly, but more darkly in some parts than others.

There remains now only to be considered the Gregarine represented in fig. 2. This is seen to be separated into two halves by a septum, in each of which are four nuclei. I was at first inclined to consider the septum as produced by the fusion of two animals, but am now more inclined to consider, for reasons which will be set forth below, the ordinary binucleated adult form as itself produced by the fusion in early life of two separate individuals. In this case it is more probable that the form shown in fig. 2 is the commencement of segmentation in an animal that is about to encyst and form sporoblasts, and that the septum separates what we may term the first two sporoblastomeres. No enveloping cyst-membrane was to be seen in this specimen, but that might have been torn off in removing it from the blood-vessel.

It would be extremely interesting to follow the first stages of segmentation in the encystment of this form. By the analogy of what WOLTERS (9) has observed in *Monocystis magna* and *agilis* it is to be supposed each nucleus would give off a polar body. Only by the observation of this process could the meaning of the vacuolar structure of the nucleolus be properly understood. After formation of the cyst the enclosed animal segments into sporoblasts, which are formed, in a method yet to be described, first at the periphery. While this process is going on the wall of the blood-vessel becomes evaginated to form the stalked vesicle containing the cyst. What causes this evagination it is difficult to understand. It must be due to active growth on the part of the tissues of the host, brought on, however, in some way by the parasite. In *Holothuria tubulosa* we shall see that the evagination takes place at an earlier stage in the life of the Gregarine than in *H. nigra*.

To recapitulate, the following are the characters, as far as



I have been able to make them out, of this Gregarine, for which, on account of the irregular form of the adult, I propose the name—

*Gregarina irregularis*, n. sp.

Gregarines of relatively large size (about .5 mm. in length) and of extremely irregular form. The body consists of opaque coarsely granular protoplasm, limited by a distinct cuticle, and containing two large nuclei, each floating separately in a clear space free from granules. The nucleus has a distinct membrane and a single large nucleolus of peculiar vacuolated structure floating in a nuclear fluid. After encystment the protoplasm segments and is entirely used up to form spherical sporoblasts, each of which develops into an egg-shaped spore with a funnel-like expansion of the cuticle at the narrow end. The nucleus of the sporoblasts divides into eight nuclei, which elongate and acquire at one end a flame-like tail, at the other end (?) a minute conical point. Thus are formed the eight sporozoites, which are embedded in a coarsely granular "noyau de reliquat," and are typically arranged in two rows of four, the tail of each sporozoite being parallel to the long axis of the spore and pointing away from the infundibular end of the spore.

Habitat.—Blood-vessels of *Holothuria* at Plymouth. The adult form lies free in the lumens of the blood-vessels, but the cysts evaginate the wall of the vessel to form a stalked vesicle.

We shall now consider the Gregarine of *Holothuria tubulosa*, the *Gregarinæ holothuriæ* of Anton Schneider. In the specimens of *H. tubulosa* examined by me at Naples I found the adult binucleated form occurring as little stalked vesicles attached to the blood-vessels, often in great abundance. In one specimen in particular there must have been thousands, mostly attached to the dorsal blood-vessel of the intestine, and easily seen with the naked eye. In fig. 19 I have represented some of the vesicles as they appeared in the

fresh condition under low magnification, and in fig. 20 I have shown a single vesicle stained and mounted in Canada balsam, with the contained Gregarine. The animal is egg-shaped or nearly spherical, with two distinct nuclei, and no trace of any septum visible, either in preparations in toto or in section (fig. 21).

The form under which I have found this animal agrees, therefore, with the description given by KÖLLIKER (1). SCHNEIDER (2) found it not only in the blood-vessels, but also in the intestine and cœlom. MINGAZZINI (5), however, seems to consider the water-vascular system ("vasi acquiferi") as the home of this Gregarine. He states that it was first found by Kölliker in the water-vessels and intestine, which, however, is not the case. Kölliker's words, "An den Darm- und Lungengefässen der Holothuria," leave no doubt as to his meaning. At first I thought that MINGAZZINI must mean blood-vessels by the words "vasi acquiferi," till I found that he terms blood-vessels of Holothurians "vasi sanguigni" or "lacune connettivali," in which he incidentally mentions the occurrence of this form in the following words:—"A peculiar property of this species is the production of special cysts, which are formed in the water-vessels ('vasi acquiferi') when it is present. Nothing of like kind occurs when it is found in the connective lacunes of the intestine" (p. 314). If by cysts ("cisti") the author means the stalked vesicles in which this form is found, he is certainly in error in saying they do not occur on the blood-vessels, which are, in fact, their chief seat, as described by KÖLLIKER and SCHNEIDER. For my part, I am inclined to doubt the occurrence of this form in the water-vascular system at all. Mingazzini further states that he has found them free in the body-cavity. Those in the connective lacunes of the intestine have more or less irregular contours. With Schneider he describes the vesicles as detaching themselves and falling into the cœlom when they are ripe for sporification. Up to the commencement of sporification he finds the animal divided in two by a septum. SCHNEIDER (2), on the other hand, only found a septum in some of the speci-

mens floating free in the body-cavity, and could observe none in those still attached to the blood-vessels. My observations agree completely with SCHNEIDER, as I never could observe any septum in the specimens still attached to the blood-vessel. On the other hand, since sporulation certainly takes place in the body-cavity, it is probable that the septum seen by SCHNEIDER was that dividing the first two sporoblastomeres, as I have termed them above.

If we sum up the above somewhat conflicting evidence, the following seems to me the most probable history of this parasite. The adult form inhabits the blood-vessels of *Holothuria tubulosa*, probably coming there from the intestine. As it grows in size it evaginates the walls of the vessels, and hangs into the cœlom. When it is ripe and ready for sporulation the vesicle breaks off and drops into the cœlom, and sporulation then takes place.

To return now to our specimens. Like *Gregarina irregularis*, this form has a distinct cuticle singly contoured. In sections it seemed to me that I could distinguish an outer zone of protoplasm marked off from that more internal, which I have represented in fig. 23, *a*. The granules in the outer zone are more regularly and evenly arranged than in the inner part, and appear also more of a size. If this differentiation, however, can be compared with what is known as ectosarc and endosarc in other forms is very doubtful. The nuclei are placed in a clear space, relatively larger than in *G. irregularis*. In its general characters the nucleus resembles that of *G. irregularis*. It has a distinct membrane, generally somewhat shrunk in preparations made with Kleinenberg's picric, but retaining its even round contour after Flemming's fluid. The nucleus contains a large space, which often appears very granular; but I have never been able, with the highest power, to see the "delicate reticulum" described by MINGAZZINI (5, p. 315). The nucleolus has the same vacuolar structure as that described above, but not quite so well marked, and there is not always a vacuole specially marked out by its size.<sup>1</sup>

<sup>1</sup> This seems to me the proper place to notice the recent work of FRENZEL  
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In none of the Holothurians studied by me at Naples was I so fortunate as to find any cysts. Other work prevented me from giving as much time to these interesting organisms as I could have wished. I have, therefore, only the material to go upon which I found in the specimen of *Holothuria tubulosa* from Naples, supplied for dissection at Oxford. In this specimen the body-cavity contained numerous spherical cysts floating free in the body-cavity, each containing an opaque central spherical mass, usually placed slightly excentrically. The diameter of the cysts varied from about  $640\ \mu$  to  $820\ \mu$ , and the diameter of the internal opaque sphere from about  $550\ \mu$  to  $590\ \mu$ . The difference between these two measurements gives the thickness of the jelly envelope. I found in all cases the cysts perfectly smooth, and am astonished that MINGAZZINI (5, 314) gives a characteristic of the genus that the wall of the cyst is covered with little spines. I have observed

JOH., "Ueber einige Argentinische Gregarinen, &c." ('Jena. Zeitschr. f. Naturwiss.,' xxvii, pp. 233—336, Taf. viii), which only came into my hands after my paper was finished. The memoir in question, which describes five new Polycystids from Argentine hosts, being mostly filled with details of the microchemical analysis of these animals, contains little which I need notice here with the exception of the peculiar structure of the nuclei in some of the forms. In *Gregarina statiræ*, *G. bergi*, *G. panchloræ*, and the young form of *Pyxinia crystalligera*, the nucleus is described as possessing a peculiar nucleolus, which the author terms a "morulite." This body is described in *G. statiræ* as "having a peculiar dull shine [eigentlich trübe glänzend] with a feebly yellowish light, and being in addition rough, with warty wrinkles on the surface just as in many other Protozoa, and especially *Rhizopoda* (amœbæ), on which account it is usually termed mulberry-like." It reacts like nuclein, but is specialised to resist digestion, and hence its substance may be termed "morulin" (p. 270).

It seemed to me at first that this might be a vacuolar nucleolus, like those in my *Gregarines*; but as this could only be made out by very thin sections, a method which Frenzel does not seem to have practised, this point cannot be determined.

By treatment with concentrated acetic acid a delicate wide-meshed network arises in the nucleus, which before appeared homogeneous. In strong nitric acid the morulite slowly vanishes, and only the network is left. It seems to me not impossible that this network is an artificial coagulation of the "Kernsaft."

nothing of the sort either in *Gregarina irregularis* or *Holothuria*, and am inclined to think that what MINGAZZINI took for spines were little bits of dirt (bacteria?) sticking to the cyst, as commonly occurs. Nor have I observed anything like the sporoduct described by MINGAZZINI, though it is quite possible that a structure of this kind is formed later. The internal cavity of the cyst is limited by a strong and distinct membrane.

All the cysts which I observed contained either spores or sporoblasts. It was noteworthy that in the latter case the cysts could be recognised by their contents being more or less shrunk by the action of the alcohol, while in cysts containing spores the inner mass was perfectly spherical.

In the case of the sporoblasts, what I have described above for *G. irregularis* is perfectly applicable here; they are spherical bodies with a distinct membrane filled with strongly refringent granules, and containing an internal nucleus appearing as a clear space, as MINGAZZINI has already described (p. 316).

Fig. 24 represents a spore in outline  $\times 730$ , and fig. 25, *a* and *b*, two others with the contents drawn in, from a preparation of Professor Bütschli. It can be seen that the spores agree closely in the majority of details with those of *G. irregularis*. Like them they are egg-shaped, and have a funnel-like expansion of the cuticle at the narrow end. The cuticle has a delicate external layer and a thick internal one, which stains more readily, as Professor Bütschli first pointed out to me. Both layers take part in the formation of the funnel, at the base of which a thin diaphragm is formed by the internal layer. But at first sight these spores appear to differ strongly from those of *G. irregularis* in the fact that the external layer of the cuticle is prolonged into a delicate caudal process—as we may call it—at the broad end, which is nearly as long as the spore itself. The caudal process is simply a flattened sheet-like extension of the cuticle ending in a point. At its edges it appears to be continuous with two ridges, which run forwards along one surface of the spore to the funnel, curving inwards

slightly towards one another about the middle of their course. Whether these ridges are natural, or are the result of shrinkage from the action of the spirit, I cannot say. The caudal process appears to be broader in its distal half than at its origin, but this is obviously an optical effect due to the caudal process being curled up at the sides and concave on one face.

SCHNEIDER (2), who first saw these spores, described them as having two caudal processes instead of one. MINGAZZINI (5) in his description follows Schneider, but it would appear that he has simply copied Schneider in his description of the spores, and does not describe what he has seen himself. I have examined a very large number of spores from different cysts, and have never observed anything but a single caudal process. Moreover, since the process is extremely delicate, and is slightly curved at the edges, which would hence appear thicker in optical section, it would be easy in a bad light to have the appearance of two processes instead of one. I am more inclined to adopt this explanation of the difference between my observations and those of SCHNEIDER and MINGAZZINI than to suppose that so great a difference could occur in the spores of the same species.

In none of the spores which I examined could I see anything but a confused granular mass in the interior. But in the material which I sent to Professor Bütschli he was able, after staining with hæmatoxylin, to see and draw eight sporozoites. After this I carefully re-examined my material and stained spores in different ways, both with Delafield's and Kleinenberg's hæmatoxylin, but still was unable to get anything stained in the interior of the spores. I wrote, therefore, to Professor Bütschli to ask his leave to reproduce the sketch he sent me, whereupon he most kindly sent me his beautiful preparation of the spores, in which I was able to make out easily all the details described by him in his letter. I am inclined to think that the cyst examined by Professor Bütschli was one exceptionally well preserved; perhaps from greater proximity to the anus, or some other cause, the alcohol in which the Holothurian was preserved reached it quicker and fixed it in

good condition. However that may be, it can be seen from fig. 25, *a* and *b* (drawn from Professor Bütschli's preparation), that the spore contains eight sporozoites, each with a nucleus and flame-like tail embedded in a granular "nucleus de reliquat." Like those described above, they are typically arranged in two rows of four each, with the tail pointing away from the spore funnel, some of the sporozoites, however, being often displaced in position. They differ slightly in details from the sporozoites of *G. irregularis*, but are perhaps not quite so mature; the nucleus is spherical, and the shape of the whole organism is slightly different.

The only author who has mentioned these sporozoites is MINGAZZINI (5), who finds that each spore contains three falciform bodies and a granular nucleus de reliquat. I am at a loss to know how this author has arrived at this result, which I can neither confirm nor express my belief in. I am inclined to think he has inferred the presence of three falciform bodies not from his own observation, but from SCHNEIDER's fig. 7 (2, pl. xii). SCHNEIDER has drawn in the interior of the spore three oval figures and a patch of granules, which he says nothing about. It seems to me, however, that Schneider did not mean to express hereby the presence of three falciform bodies and a nucleus de reliquat, but rather the presence of a granular undefined mass in the interior. In any case I think we are justified in setting aside MINGAZZINI's statement, and ascribing eight falciform bodies or sporozoites both to this species and to *G. irregularis*.

To sum up the above observations, we may give this species the following characters:

*Gregarina holothuriæ*, Anton Schneider.—Gregarines of somewhat large size, and at first of irregular form, contained in the lumen of the intestinal blood-lacunæ (MINGAZZINI), but later in life becoming regularly egg-shaped, and then enclosed in stalked epithelial vesicles formed by evagination of the walls of the blood-vessels. Body formed of opaque, coarsely granular protoplasm, limited by a distinct cuticle, with two large spherical nuclei, each floating in a clear space free from

granules. The nucleus has a distinct membrane, and contains a granular (?) fluid in which floats a single nucleolus of peculiar vacuolated structure. The cysts are formed free in the body-cavity. The protoplasm segments to form sporoblasts, which develop each into egg-shaped spores, with a funnel-like expansion at the narrow end, and a caudal process formed from the outer layer of the cuticle at the broad end. The spore contains eight nucleated falciform bodies embedded in a granular "nucleus de réliquat," and each provided with a flame-shaped tail.

Habitat.—Intestine, blood-vessels, and cœlom of *Holothuria tubulosa* at Naples and Nizza.

We shall now proceed to discuss the systematic position of these Gregarines. But first it is necessary to consider one question: are these binucleated adult forms to be looked upon as one individual or two? The only author, as far as I know, who has touched upon this point is MINGAZZINI (5), who considers each specimen to represent a pair of conjugated adults; without, however, excluding the possibility of their double nature being due to fusion of a single individual. He further describes the animals as divided by a septum, on each side of which is one of the nuclei. I have not been able to see a trace of this septum, and much doubt its existence; nevertheless I am inclined to consider MINGAZZINI'S view as the correct one for the following reasons: (1) there are no cases known in which it is the normal condition for a Gregarine to have more than one nucleus; see on this point BÜTSCHLI (6, p. 523); (2) though it cannot yet be said by any means to be the rule, yet, whenever the life history of a Gregarine has been carefully observed, it is found in the majority of cases that two individuals fuse to form a cyst, whereas here a cyst is formed from a single binucleated adult; and (3) I would call attention to the peculiar Gregarines figured by Sars (3, pl. xvi, figs. 2, 3, 5, 6, and 7, *a*, and fig. 8), observed by him in the intestine and blood-vessels of *Chiridota lævis*, Fabr. sp. (= *Ch. pellucida*, Vahl sp.). Here one sees little Gregarines attached to the tissues, always in pairs, but quite distinct



from one another. It seems to me not improbable that this represents young specimens of a Gregarine allied to those described in this paper. Nevertheless I do not consider it as by any means proved that these Gregarines are really each a pair of individuals, and have therefore not included this character in the diagnosis of the species.

To discuss the affinities of these forms it will be convenient to begin by tabulating the characters in which the two species agree with, and differ from, one another respectively.

A. They agree with one another—

(1) In the general structure of their cuticle, protoplasm, and nucleus.

(2) In the possession of two nuclei.

(3) In using up all the body protoplasm to form sporoblasts, from each of which a spore develops.

(4) In the shape of the spore, the arrangement of its cuticle, and the possession of a funnel at the narrow end.

(5) In forming eight sporozoites.

(6) In the general structure of the sporozoites, which have a nucleus at the anterior end, to which is attached a flame-like tail posteriorly.

(7) In the fact that both pass the chief period of their existence in the blood-vessels of Holothurians.

B. Leaving out mere details, they differ in the following points :

(1) In form ; *G. irregularis* appears to keep its irregular shape up to the time of encystment, while in *G. holothuriæ* it is only present in the young stage.

(2) In the presence of a caudal process to the spore in *G. holothuriæ*, which is entirely wanting in *G. irregularis*.

(3) Perhaps in the form of the sporozoites, especially in its nucleus.

(4) *G. holothuriæ* is contained in stalked vesicles formed by evagination of the blood-vessel long before encystment, and breaks loose into the body-cavity to sporulate, while *G. irregularis* appears not to evaginate the wall of the blood-vessel until ready to encyst, and to sporulate in the vesicle.

Since these differences in two such closely allied forms must be the result of different adaptation to circumstances, we ought to be able to find in the life conditions of these forms some explanation of it, and I believe that such an explanation can be given. As I have shown elsewhere,<sup>1</sup> *Holothuria nigra* possesses immense numbers of Cuvierian organs which are thrown out on stimulation, and in the ejection the wall of the rectum is ruptured, so that the contents of the body-cavity can escape. If now *G. irregularis* lived in stalked vesicles while still simply in the adult form, it would often run the risk of having the stalk of the vesicle ruptured, and being thrown out before its time. When once it is encysted, however, it may be of advantage to be thrown out, and thus escape to the exterior. On the other hand, *Holothuria tubulosa* is entirely without Cuvierian organs, hence *G. holothuriæ* does not run the same risk of being cast out. In fact, it must be rather hard for the spores in this form to escape, and I am rather inclined to attribute to the caudal process some action in the escape of the spores from the body-cavity, perhaps being used to bore through the tissues in some way. On the other hand, SEMPER (11) has suggested that the autotomy of Holothurians may be of biological importance to the parasitic *Entoconcha mirabilis* in their body-cavity, the young of which could become free by producing autotomy through internal stimulation, and the same might apply to the Gregarines. The irregular form is perhaps due to life in the complicated anastomosis of the blood-plexus, and is only retained as long as the animal continues to live in the lumen of the blood-vessel, i. e. throughout life in *G. irregularis*, but only in the young stage of *G. holothuriæ*. Thus the difference in form would also be indirectly caused by the presence or absence of Cuvierian organs.

It is obvious that if a genus is to be constructed for these forms, it must not be defined by characters that are not constant in all the species. Armed with this axiom, let us consider previous attempts to classify these organisms.

<sup>1</sup> 'Annals and Magazine of Natural History,' October, 1892.

CUÉNOT (4) places the three known to him in the genus *Syncystis*, Aimé Schneider, namely, *S. synaptæ* from the intestinal vessel and cœlom of *Synapta inhærens*; *S. holothuriæ*, Ant. Schn. sp., from *Holothuria tubulosa*; and *S. Mülleri* from cœlom of *Synapta digitata*. He does not appear to be personally acquainted with "*Syncystis holothuriæ*," or with the fact that it had been described as binucleated by Kölliker and Schneider, or he would certainly not say it was similar to the form he describes, more especially "*Syncystis synaptæ*" (= *Monocystis synaptæ*, E. R. L.), in which we may note from his description the following points:—a doubly contoured cuticle; a single nucleus; cyst limited by a cuticle like that of the Gregarine, with in the centre a spherical nucleus de réliquat (a quite unusual use of the term, which is always applied to unused matter in the spore); spores oval or navicular, with three or even four nuclei. In a foot-note we are informed that Professor Aimé Schneider had considered this form as belonging to the genus *Urospora*. Professor Bütschli also wrote to me "Ein Schwanzanhang der Sporen ist von der Gattung *Urospora*, Aimé Schneider bekannt, es scheint daher wahrscheinlich, dass die Gregarine der *Holothuria* zu dieser Gattung gehört." MINGAZZINI (5), on the other hand, places them in the family *Syncystidæ*, but establishes a new genus *Cystobia* for them, considering that they differ from the genus *Syncystis*, in which the spores have at each pole four diverging bristles (setole), while in the genus *Cystobia* the spore has only two bristles, and only at one pole. The genus *Cystobia* is characterised as follows:—"Lives conjugated in special cysts formed in the tissues, especially in the walls of the vasi acquiferi. Cysts proper with the wall covered with little spines. Sporulation complete. Spores very numerous, fusiform, bicaudate, with three falciform bodies." As we have seen, almost the only details in this diagnosis which are correct are "sporulation complete, spores very numerous." In this genus the author puts two forms, *Cystobia holothuriæ*, Ant. Schn., and a new species, *Cystobia*

Schneideri, from *Holothuria poli* and *impatiens*, which is characterised as follows:—"Has a general facies and a method of sporification similar to that of the preceding species, differs from it in being smaller and much less resistant to the direct action of sea water, while *C. holothuriæ* can stand it much longer." I should think it probable that no new species of animal which has been described within the last fifty years has been founded on such a meagre and insufficient diagnosis as this—without, moreover, any figures.

Since one of these Gregarines possesses a caudal process to the spore and the other not, it is obvious that this caudal process cannot be used for classification. This at once sweeps away the genus *Urospora* for these species, and also Mingazzini's arguments for placing them in the family *Syncystidæ*.

The genus *Syncystis* was founded by AIMÉ SCHNEIDER (7) in 1885 for a Gregarine found by him in the fat bodies of *Nepa cinerea*. The body is pear-shaped or spherical, and in the latter forms Schneider was unable to see "la moindre trace d'une division du noyau" (p. 92). Two such individuals fuse before encystment, as occurs in many, if not all Gregarines. The sporulation is not complete, since a central mass of protoplasm remains over. The spores are oval, and usually have four bristles at each end; they contain eight sporozoites, each with a nucleus and nucleolus, "arranged obliquely, giving lines which cross one another from one face of the spore to the other; at the centre a nucleus de reliquat" (p. 94). From figs. 21, 22, and 23, pl. xxiii, it can be seen that the nucleus of the sporozoite is placed in its centre.

If this summary of Schneider's description of *Syncystis* be compared with that given above of the Holothurian Gregarines there only appears to be one point common to the two—the formation of eight sporozoites in the spore, which occurs also in the *Monocystis* of the earthworm, and in *Clepsidrina ovata*, a *Polycystid* (Schneider, 'Tablettes zoologiques,' i, pp. 25—28, pl. xi), as well as in *Coleophora heros* (Schneider, op. cit., p. 98, pl. xxv, figs. 11—13, a), &c.

so that not much stress can be laid on this point for classification. The spores of *Syncystis* lack the characteristic funnel of the spores of our Gregarines, and the caudal process of the latter can be in no way homologised (even if it were a constant phenomenon, which is not the case) with the bristles of the spore of *Syncystis*. Hence I think we are justified in concluding that the Gregarines of Holothurians have no affinity whatever with the family *Syncystidæ*.

On the other hand, in regard to their double nature, these Gregarines have a considerable resemblance to the remarkable *Diplocystis Schneideri* described by KUNSTLER (12) from the body-cavity of *Periplaneta americana*. This form lives in a conjugated condition, and "presents normally the aspect of two monocystid Gregarines in syzygy, and preparing for encystment," p. 45 (= 21). Each half, however, has a *membrana propria*, but the whole is surrounded by a general membrane which passes from the one to the other without penetrating their plane of separation. But in the very young stage (pp. 26, 27, pl. ix, fig. 16) it occurs attached to the digestive tract of the *Periplaneta* in a serous sac, contains two nuclei which differ in structure from one another, and is not divided by a septum. The conjugation takes place very early in the life-history, almost immediately after the intra-cellular phase, p. 61 (= 37), figs. 18, 19. According to M. Kunstler, p. 62 (= 38), the conjugation does not appear to be the result of union of two individuals primitively separate, but a single intra-cellular form divides, to afterwards fuse completely and then to separate again. I am therefore rather inclined, on a priori grounds, to doubt if these observations are quite correct; it seems to me more probable that the little couples shown in Kunstler's fig. 18 are derived from two separate intra-cellular individuals which he has overlooked, as the best of observers might very easily do. In any case I would point out the striking parallel between Kunstler's fig. 16 and my fig. 20.

The spores of *Diplocystis* are oval or spherical without any appendages. The sporozoites, eight in number, cross one

another obliquely. Hence I do not think the Gregarines of Holothurians can be placed in the genus *Diplocystis*, though they show a great affinity with it.

Where, then, are these Gregarines to be placed? I suppose if a genus is to be made for them, the genus *Cystobia*, Mingazzini, has the priority; but the genus remains reduced to the mere shell, the name only, for the kernel, Mingazzini's diagnosis, must be changed, and the genus itself must be removed from the family *Syncystidæ*. As a matter of fact I do not consider our knowledge of these Gregarines sufficiently advanced as yet to discuss their zoological position within the group *Monocystidea*. Not until the Gregarines of many Holothurians have been thoroughly worked out and compared can it be known what characters are constant peculiarities and what are merely characters of adaptation. It seems to me highly probable that the different species of Holothurians will prove to have closely allied species of Gregarines, derived from a common ancestor which inhabited the ancestor of the genus *Holothuria*. In order to obtain characters of classificatory value sufficient to found genera and families, the Gregarines inhabiting allied species of animals should be carefully studied and compared in order to find out in what points they agree and differ. The custom at the present time seems to be, however, to open any animal that comes to hand, and at once describe the Gregarine that inevitably occurs in it as a new genus and species, usually without even giving a figure. Our knowledge of the group is not advanced in the least thereby, but confusion and many vexed questions of nomenclature are stored up for the unfortunate zoologists of the future.

I prefer, therefore, to leave these Gregarines for the present in the old genus *Monocystis*, and to wait for future researches to determine their true affinities.

As to the development of *G. holothuriæ* and *irregularis* from the sporozoite to the adult form, I have unfortunately no observations to offer. As Bütschli says, "we touch here upon the section which is as yet the darkest in the developmental

history of the Gregarinida." It seems most probable that the animals come originally from the intestine, penetrating from thence into the blood vascular system, and that they get into the intestine by the animal swallowing spores with its food.

One cannot but be struck, in considering these forms, by the great resemblance of the adult to an ovum, and of the sporozoite to a spermatozoon. Both these resemblances are doubtless due to the action of similar conditions. The adult Gregarine is a resting cell fed by the surrounding tissues and only biding its time to undergo developmental changes, which it commences, as WOLTERS (9) has shown, by throwing off half the nucleus as a polar body. On the other hand, the function of the sporozoite is to reach and burrow into a cell, for which purposes an elongate shape and locomotory organs are necessary. It is probable, as SCHNEIDER (7, p. 94) has said, that "the spores must be introduced into the digestive tract, and that the sporozoites, set at liberty by the digestive juice, have the energy necessary to perforate the mucosa."

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12. KUNSTLER, J.—“Diplocystis Schneideri (nov. gen., nov. sp.),” ‘Tablettes zoologiques,’ ii, pp. 25—66, pl. ix.

#### ADDENDUM.

While the above was in the press a new work appeared by L. Cuénot, entitled “Commensaux et Parasites des Échinodermes (Deuxième Note),” in the ‘Revue Biologique du Nord de la France,’ vol. v, part 1 (October, 1892). The author describes the Gregarines of *Synapta inhærens* and *digitata*, which he now places in the genus *Urospora*, namely, *Urospora synaptæ*, Ray Lankester, and *U. Mülleri*, Giard. The former of these is found under two forms in the adult condition. Cysts are found in the cœlom. The spores have as a maximum four sporozoites; they have at one pole “a tuft [aigrette] of four little bristles,” at the other a caudal filament two or three times the length of the spore.

The author does not make any definite statement as to the number of nuclei in the adult, so it may be presumed that there is only a single nucleus. The spores seem to show some resemblance to those of the forms described by me. The tuft of bristles is doubtless homologous with the funnel in the spore of my *Monocystis irregularis* and *holothuria*. The presence of a caudal process to the spore is made use of to place these forms in the genus *Urospora*. After what I have said above on this point further comment here seems to me needless.

On the whole these forms from *Synapta* have considerable



affinity with my Gregarines from Holothuria, in spite of certain differences, such as the single nucleus and the four sporozoites. It is probable that not much stress can be laid on these points of difference. The double nucleus in Gregarines from Holothuria is probably due, as has been pointed out above, to precocious conjugation, while the number of sporozoites is, of course, dependent on the number of times the nucleus of the sporoblast divides, and is a character which may be subject to variation.

The author also figures and describes the adult and the spores of *Lithocystis Schneideri*, Giard, from the cœlom of *Echinocardium cordatum*, which certainly has a striking resemblance to the Gregarines of Holothuria, both in the form of the spores and sporozoites (eight in number), and in the characters of the adult. In the latter M. Cuénot figures a nucleus with vacuolated nucleolus, resembling closely that of the forms described by me. At the narrow end of the spore the author figures a truncated process, which is evidently homologous with the funnel in my two species. Is it possible that this process represents a stage in the development of such a funnel?

It would appear from these facts that the Gregarines of different Holothurians, Synaptids, and Echinoids have a strong family likeness, and that a careful study and comparison of them would furnish valuable data towards a natural classification of this class of Protozoa.

M. Cuénot quotes frequently from a paper by Léger ("Recherches sur les Grégarines") in 'Tabl. Zool.,' vol. iii, 1892. I have unfortunately not been able to see this paper. I gather, however, from M. Cuénot that the author "attributes solely to the form of the spores a value" for classificatory purposes, and "adjourns the generic denomination of every species of which the complete cycle is not known." I think I have sufficiently expressed my opinion above on the value of the form of the spore for classification, and may refrain from further criticism here.

## EXPLANATION OF PLATES XXVII &amp; XXVIII,

Illustrating Mr. E. A. Minchin's "Observations on the Gregarines of Holothurians."

## PLATE XXVII.

All the figures on this Plate refer to *Gregarina irregularis*, n. sp., inhabiting *Holothuria nigra*.

FIG. 1.—A specimen from the blood-vessels, drawn living.

FIG. 2.—Another specimen from the blood-vessels. Flemming's fluid, borax carmine. Zeiss, compens. ocular 4, obj. B, camera lucida.  $\times 128$ .

FIG. 3.—Section (from a series of 40 sections, the 15th of the series) through a blood-vessel with the contained Gregarine. Kleinenberg's picric, hæmatoxylin. Zeiss, compens. ocular 4, obj. B, cam. luc.  $\times 128$ .

FIG. 4.—The inner part of Fig. 3,  $\times 315$ . Zeiss, compens. ocular 4, obj. D, cam. luc.

FIG. 5.—Another section (34th of the series) passing through the other nucleus of the same Gregarine. Zeiss, compens. ocular 4, obj. D, cam. luc.  $\times 315$ .

FIG. 6.—The section (33rd of the series) immediately before that drawn in Fig. 5. Ocular and objective as in the last figure; cam. luc.  $\times 315$ .

FIG. 7.—The section next but one before the last (31st of the series). Ocular and objective as in the last figure; cam. luc.  $\times 315$ .

FIG. 8.—Section through another blood-vessel and the contained Gregarine (from a series of 96 sections, 85th of the series). Zeiss, compens. ocular 4, obj. D, cam. luc.  $\times 315$ .

FIG. 8*a*.—The nucleus from the same section. Compens. ocular 4, obj. F, cam. luc.  $\times 730$ .

FIG. 9.—One of the stalked vesicles, containing a cyst, from the blood-vessels, as seen living. Drawn with Zeiss, oc. 2, obj. B.

FIG. 9*a*.—The edge of the same in optical section. Oc. 2, obj. D.

FIG. 10.—A portion of the blood-plexus, with a cyst attached.

FIG. 11.—The contents of a cyst teased up. *a*. Drawn living. *b, f*. Fixed with picric-osmic-acetic mixture, and stained with Kleinenberg's hæmatoxylin. Zeiss, compens. ocular 4, obj. F, cam. luc.  $\times 730$ . *a, b*, and *c*. Sporoblasts, each with a single central nucleus. *d, f*. Nucleated masses of proto-

plasm from the interior of the cyst. *e*. An isolated nucleus from the internal masses of protoplasm.

FIG. 12.—Spores with four nuclei from another cyst, drawn living, using Zeiss, oc. 2, obj. D.

FIG. 13.—Spores from another cyst. *a*. A spore with four nuclei, and *b*, an undeveloped sporoblast, drawn living, using Zeiss, oc. 2, obj. D. *c-h*. Picric-osmic-acetic, Kleinenberg's hæmatoxylin. Zeiss, compens. ocular 4, obj. F, cam. luc.  $\times 730$ . *c-g*. Spores with four nuclei. *h*. An abnormal sporoblast with five nuclei.

FIG. 14.—Two spores from another cyst after treatment with 10 per cent. sodium carbonate (glycerine preparation). Zeiss, compens. ocular 4, obj. F, cam. luc.  $\times 730$ .

FIG. 15.—From a series of sections through a cyst. *a*. The cyst-wall, covered by epithelium. *b*. A spore with eight sporozoites. Zeiss, compens. ocular 4, cam. luc., obj. F.  $\times 730$ . *c*. Another spore with eight sporozoites. Zeiss, compens. ocular 4, homogen. immers. 2 mm., cam. luc.  $\times 900$ . *d, e, f*. Sporozoites from other spores of the same cyst, much enlarged.

FIG. 16.—From a series of sections through another cyst. *a*. Spore in longitudinal section, showing six sporozoites. Zeiss, compens. ocular 4, obj. F, cam. luc.  $\times 730$ . *b*. Spore in transverse section, showing eight sporozoites. *c*. Another spore in longitudinal section, with five sporozoites. Zeiss, compens. ocular 4, homogen. immers. 2 mm., cam. luc. (with the tube of the microscope drawn out).  $\times 1000$ . *d, e, f*. Sporozoites from spores of the same section, much enlarged.

FIG. 17.—*a, b, c, d*. Four sporozoites, much enlarged, from the spores of another cyst which was cut into sections.

FIG. 18.—Combined semi-diagrammatic figure of a ripe spore, with eight sporozoites.  $\times$  about 1150.

## PLATE XXVIII.

All the figures on this Plate refer to *G. holothuriæ*, from *Holothuria tubulosa*, Naples.

FIG. 19.—Some blood-vessels from *Holothuria tubulosa*, with vesicles containing Gregarines. Drawn living.

FIG. 20.—One of the Gregarines shown in Fig. 19, after fixation with Flemming's fluid and staining with alum carmine.  $\times 210$ .

FIG. 21.—From a section through a Gregarine, showing the two nuclei (Kleinenberg's picric, borax carmine, hæmatoxylin). Zeiss, compens. ocular 4, obj. D, cam. luc.  $\times 315$ .

FIG. 22.—*a, b, c*. Nuclei from other Gregarines in the same series. Zeiss, compens. ocular 4, obj. D, cam. luc.  $\times 315$ .

FIG. 23.—From a Gregarine fixed with Flemming's fluid, and stained with safranin. Zeiss, compens. ocular 4, obj. D, cam. luc.  $\times 315$ . *a*. Part of the edge in optical section. *b*. A nucleus.

FIG. 24.—A spore in outline. Zeiss, compens. ocular 4, obj. F, cam. luc.  $\times 730$ .

FIG. 25.—*a* and *b*. Two spores containing eight sporozoites, from a preparation of Professor O. Bütschli, of Heidelberg. Zeiss, compens. ocular 4, homogen. immers. 2.0 mm., cam. luc. (the tube of the microscope drawn out).

## A New Sporozoon in Amphioxus.

By

**E. C. Pollard, B.Sc.**

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With Plate XXIX.

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My work has been carried on in the Laboratory of Comparative Anatomy at Oxford; and I wish at the commencement of this brief notice to offer my best thanks to Professor Ray Lankester, both for allowing me to work here and for his valuable suggestions and help.

Quite recently I had occasion to cut a series of transverse sections through *Amphioxus lanceolatus* for the purpose of demonstrating the working of the microtome, rather than with any idea of obtaining sections of any particular interest.

To my surprise, however, the series, although cut without any particular care and in a hot atmosphere, proved to be well worth examining, chiefly from the fact that the cochineal stain which was used had differentiated the tissues to a remarkable extent. This differentiation is chiefly noticeable in the intestine, which is stained a deep violet, in strong contrast to the cochineal red of the notochord and other tissues.

On examining the sections a peculiar structure in the intestine at once attracted notice.

In various parts of the posterior region of the gut the epithelium appeared to differ from that of the rest of the wall, the cells seeming to contain much larger nuclei, and being apparently curved round to form small cup-shaped organs (figs. 1—4).

As will be at once seen from the figures, these cups present

on cursory observation an appearance very similar to that of Vertebrate taste-bulbs.

Appearances, however, proved absolutely deceptive, for in thinner sections examined with a higher power the nuclear-like bodies (figs. 1—9, *p.*) were seen to be not nuclei, but each in itself a minute cell parasite, evidently a stage in the life history of a Sporozoon.

Each of these parasites is elongate, tapering at each end, and on an average only  $\cdot 01$  mm. in length.

The protoplasm presents a coarsely granular appearance (figs. 8 and 9), the granules staining more deeply than the rest of the cell protoplasm.

Centrally there is a clearer space, and within this again a deeply staining round body, which I at first took to be the nucleus.

After careful examination of my slides with Zeiss's homogeneous immersion lens I am, however, inclined to regard the deeply stained body (fig. 9, *n.*) as the nucleolus, and the clearer protoplasm (*N.*) in which it is situated as the nucleus.

It is extremely difficult to make certain of this point in such minute organisms, and I have not been able to absolutely satisfy myself as to the presence of a nuclear membrane.

Nevertheless the forms depicted in fig. 9 give one the impression that the part marked *N.* is a large nucleus whose chromatin is all collected into the globular nucleolus (*n.*), and this appearance gains confirmation when compared with the nucleus of other Sporozoa.

Close to the nucleus in many of the specimens a clear round structure may be observed (*v.* in fig. 9, *b* and *c*). This structure is refringent and well defined, but is not visible in every specimen. It has the appearance either of a centrosome or a vacuole. One would not, however, expect to find the former, since there is no sign of nuclear division; whilst if it be a vacuole it is of great interest from the fact that, so far as I am aware, such a structure has never been previously described in a Sporozoon.

The parasites, though occasionally seen at the distal ex-

termitities of the epithelial cells, are usually situated in cavities at the proximal ends of the cells. Sometimes a single parasite is found in an isolated position in the digestive epithelium; but most frequently they occur in groups, and seem to exert some irritating influence over the epithelial cells, causing these to curve round to form the curious cup-like structures drawn in figs. 1 and 4. Not unfrequently the distal extremities of the cells containing parasites are broken away (figs. 7 and 8); but this by no means invariably occurs, and may be due to the preparation of the sections.

The extremity of the parasite nearest the free edge of the cell is in close proximity to the cell nucleus (*M* in figs. 7, 8, and 9). The nucleus of the infected cell, moreover, differs considerably in form from that of the normal epithelial cell (figs. 7 and 8, *M'*). It seems probable that the parasite, by pushing against the nucleus, had altered its form until, as in figs. 7, 8, and 9, *a* and *b*, it has the appearance of a granular cap to the parasite.

I have not seen stages showing the alteration of the nucleus; but Schneider, in his 'Tablettes Zoologiques,' figures such a change brought about by the pressure of a growing Sporozoon (vol. i, pl. ix and xxix). In the form described by Schneider the nucleus is situated at the proximal end of the cell, the parasite being more distal in position, whilst in the form now described the nucleus is nearer the free end of the cell than the parasite.

As for the distribution of these parasites in *Amphioxus*, they occur all round the intestinal epithelium, but are limited to the posterior region of the gut from the atriopore to the anus. In this post-atrioporal region they may be extremely numerous, the epithelium, as in fig. 3, being crammed with them.

The epithelium of the hepatic cæcum is so similar to that of the intestine that I had every expectation of finding these cells also infected.

Although, however, I have sought with the utmost care, both in my own sections and in some excellent series, for the

use of which I am indebted to Mr. Willey, I have been unable to find any trace of the parasite in the cæcum; and, as a matter of fact, I have never seen it so far anteriorly in the digestive tract.

Further, I regret to be obliged to state that I have not yet succeeded in obtaining any other stage in the life history of this form.

#### Methods.

From its differentiating properties cochineal is an extremely useful stain for *Amphioxus*, and the parasites are easily seen in sections prepared with this; but the details of protoplasmic and nuclear structure I have made out best in specimens stained with a mixture of borax-carmin and picro-carmin as prepared by Bolles Lee.<sup>1</sup>

The use of the homogeneous immersion lens was essential, and figs. 6—9 were drawn under this with the aid of a Zeiss's camera.

In conclusion, my sincere thanks are due to Dr. G. H. Fowler, who first drew my attention to an unusual appearance in my sections of *Amphioxus*, which I investigated with the results now published; to Mr. Willey for the most kind loan of his sections, and to Dr. Benham and Mr. Minchin for ever ready advice and help.

OXFORD; October, 1892.

#### Addendum.

In fig. 10 I have figured specimens of a ciliate parasite which occurs in considerable numbers in the atrium of *Amphioxus*.

Professor Lankester noticed these years ago, and has recently drawn my attention to them, with the suggestion that the cell parasite described above might possibly be a stage in the life-history of this ciliate form.

<sup>1</sup> Bolles Lee, 'Vade Mecum,' p. 122.



Whether this be so or not, a brief description of this Protozoan may not be without interest, no parasite having been previously described in Amphioxus.

This member of the Ciliata is one of the Aspirotrichous Trichostomata, varying in length from .4 to .7 mm. There is a definite mouth and short pharynx in a lateral position (fig. 10, *a*, *O*). A large nucleus is situated more or less posteriorly, and is not unfrequently lobed in a curious fashion (fig. 10, *c*), an appearance which is, however, probably due to shrinkage, since it is not of invariable occurrence.

The cell protoplasm is very granular, the granules sometimes, as in fig. 10, *d*, being extremely large.

These parasites occur in considerable numbers, and are found in the atrium both anterior and posterior to the atrio-pore.

## EXPLANATION OF PLATE XXIX,

Illustrating Miss E. C. Pollard's notice of "A New Sporozoon in Amphioxus."

*Reference Letters.*

*M.* Nuclei of epithelial cells, altered in form by pressure of parasites.  
*M'*. Typical nuclei of normal epithelial cells. *N.* Nuclei of parasites. *n.* Nucleoli. *p.* The parasites. *v.* Vacuole-like appearance.

FIGS. 1—3.—Transverse sections through post-atrioporal region of the intestine of Amphioxus, showing the parasites in groups.

Fig. 1. Zeiss, oc. 2, obj. A.

Fig. 2. Zeiss, oc. 4, obj. B.

Fig. 3. Zeiss, oc. 2, obj. B.

FIG. 4.—Group of the parasites within cells, giving cup-like appearance. Zeiss, comp. oc. 4, obj. D.

FIG. 5.—Small portion of intestinal epithelium, with cells containing parasites. Zeiss, oc. 4, obj. D.

FIG. 6.—Some of the parasites from Fig. 5 under a higher power. Zeiss, comp. oc. 4, homog. imm. lens.

FIGS. 7 and 8.—Groups of parasites in intestinal epithelium.

Fig. 7. Zeiss, oc. 4, homog. imm. lens.

Fig. 8. Zeiss, comp. oc. 4, homog. imm. lens.

FIG. 9.—*d-f*, drawn from parasites found isolated from the cell, probably due to the breakage of the cell by the razor; *a-c*, drawn from groups of parasites seen in Fig. 7. Zeiss, oc. 8, homog. imm. lens.

FIG. 10.—*a-d*. Ciliate parasites occurring in the atrium of Amphioxus. *Nn.* Nucleus. *O.* Mouth. Zeiss, obj. D, oc. 2.

**Studies on the Protochordata.**

By

**Arthur Willey, B.Sc.Lond.,**  
Columbia College, New York.With Plates XXX & XXXI.**I.**

**On the Origin of the Branchial Stigmata, Præoral Lobe, Endostyle, Atrial Cavities, &c., in *Ciona intestinalis*, Linn., with Remarks on *Clavelina lepadiformis*.**

IN continuation of some work on the development of Amphioxus, which, thanks to Professor Lankester, I had been enabled to do, I undertook—at his recommendation, and with the assistance of a grant from the Royal Society—a course of study on Ascidian development, with a view to coming to some definite conclusion as to the relations between the Urochorda and the Cephalochorda, and to control by actual investigation the general conclusions expressed in my paper on the “Later Larval Development of Amphioxus,” which, in so far as they related to the Ascidiæ, were mainly based on the results arrived at by Éd. van Beneden and Charles Julin in their ‘Recherches sur la Morphologie des Tuniciers.’

I accordingly spent six weeks at the Marine Biological Laboratory at Plymouth, in the long vacation of 1891, followed by ten months at the Zoological Station of Naples, at both of which institutions I had the privilege of occupying the table of the British Association.

Having now made personal observations on the development

of the Ascidians, I shall have to make a nearly complete volte-face from my previous position (32, pp. 217—222) in regard to the homologies existing between the various organs of the Ascidians and Amphioxus. It was chiefly the position of the endostyle in the larva of Amphioxus, seeming as it did to correspond so closely to the requirements of van Beneden and Julin, which led me at first to place unbounded confidence in their results. Singular to say, it is, to a large extent, that very position of the endostyle which now leads me to conclusions diametrically opposed to theirs.

Before proceeding to the description of my observations, I must express my deep sense of the obligation I am under to my master, Professor E. Ray Lankester, to whose counsel and assistance I owe the possibility of pursuing these studies.

I also have the greatest pleasure in acknowledging the many kindnesses I received from Drs. Dohrn, Eisig, Paul Mayer, and Schiemenz, and Signor Lo Bianco.

#### Methods of Obtaining and Preserving Material.

The embryos of *Ciona intestinalis* can be obtained in unlimited quantity by artificial fertilisation. It is sufficient to open an adult from the right side, cut across the oviduct and vas deferens, having previously noticed that the former contained ova, and then collect the ova and spermatozoa as they pass out from the point of incision with a glass tube, and transfer them to a glass containing fresh sea water, and mix them well, but gently, together by stirring. Gradually the ova sink to the bottom of the glass, and in about an hour after the above operation they commence to segment.

After some twenty-four hours the water in the glass is seen to be crowded with myriads of tadpoles swimming about, the mass of them being nearer the surface of the water. Again, after a few hours the tadpoles are no more to be seen, but if the glass be held in the proper light, the surface of the water is found to be covered with greyish patches, which, on examination, turn out to be nothing else than scores of larvæ

which have fixed themselves to the surface of the water. They attach themselves in this way to the surface-film of the water in the glass, both isolated and in groups.

If one of these newly fixed individuals be examined under the microscope, a small globule of air is invariably seen to occur at the end of the adhering disc. It seems extremely probable that this is secreted by the cells of the disc.

The larvæ would also fix themselves to pieces of ulva at the bottom of the glasses, but I found it more convenient to leave out the ulva, and get them to fix at the surface. Once fixed, the young individuals can be kept for weeks in the same water covered up. They apparently, however, never attain their full dimensions under these conditions; in fact, it could hardly be expected that they should, so that for very late stages I was driven to the tanks, where a constant supply of *Ciona* was kept.

As for the embryos of *Clavelina*, they are to be taken, as is well known, from the peribranchial cavity of the parent, but, in contrast to those of *Ciona*, cannot be obtained all the year round, as the colonies of *Clavelina* die off about the month of May.

As for the preservation, the method which gave the best results consisted in fixing the larvæ of all stages was the solution employed by Davidoff in his work on the 'Development of *Distaplia magnilarva* (8), namely, 3 parts concentrated corrosive sublimate and 1 part glacial acetic, the shrinking tendency of the former being thus neutralised by the swelling power of the latter ingredient.

## 1. Metamorphosis of the Larva of *Ciona intestinalis*. Origin of Branchial Stigmata.

"In den letzten 20 Jahren," says Kowalevsky in a memoir which has recently appeared (22), "haben sich sehr viele Forscher mit der Anatomie und Entwicklung der Ascidien beschäftigt und man konnte hoffen, dass die meisten Fragen schon gelöst sind, und doch erweist es sich, dass bis jetzt die Hauptmomente der Metamorphose noch ganz unerklärt sind."

That this is a correct statement of the situation will become evident to the reader of the following pages; and the reason for it is to be found in the fact that most zoologists who have worked at this part of the development of Ascidians have not had a sufficient number of different stages before them.

Several observers, including P. J. van Beneden (4), Krohn (23), Kowalevsky (20), and Kupffer (24), have seen young Ascidians with two gill-slits on each side; but they have neither described the exact origin of these, nor have they, with the exception of Krohn, described the formation of new slits. Éd. van Beneden and Julin (6), in their account of the post-embryonic development of *Phallusia scabroïdes*, commenced with the stage at which four gill-slits were present on each side. The transition from the stage with two pairs of branchial apertures to that with four forms precisely what Kowalevsky would call a "Hauptmoment" in the development, and has been overlooked by all previous observers.

In their youngest specimen of *Phallusia scabroïdes* van Beneden and Julin found that the four slits were of unequal size, and thought it probable that the sizes of the slits indicated their order of formation as follows:—III, I, IV, II. In the next stage which they examined six stigmata were present on each side, and they constructed the following table to show the relation which they supposed to exist between the age (as determined by the size) and the order of position of the respective slits:

Age relatif.	Ordre de Position.
Premier stigmaté formé.	Quatrième de la série.
Second " "	Premier " "
Troisième " "	Cinquième " "
Quatrième " "	Second " "
Cinquième " "	Troisième " "
Sixième " "	Sixième " "

In their 'Recherches,' (7) the same authors recur to this assumed irregularity in the formation of the primary stigmata, and lay great stress upon it as showing that the gill-slits of Ascidians are not in any sense true metameric organs.

We shall see, however, that the difference in the dimensions of the primary stigmata was misinterpreted by van Beneden and Julin, and that the irregularity in their order of formation does not really exist.

Krohn (23), in a paper remarkable for the number and comparative accuracy of the observations contained in it, on the 'Development of *Phallusia mammillata*,' Cuv., describes and figures a young individual with two gill-slits on each side, and describes accurately for the first time the two atrial apertures, which afterwards fuse into one. The first two gill-slits appear simultaneously. He says, further (p. 326), "Auf diese zwei Paar Oeffnungen die sich mittlerweile verlängern und spaltenähnlicher werden, bleibt der Athemsack noch längere zeit hindurch beschränkt. Endlich entstehen jederseits in der Brücke zwischen ihnen zwei neue Oeffnungen und bald darauf tritt hinter der ursprünglichen hinteren Spalte noch eine Oeffnung hinzu so dass die zahl sämtlicher Oeffnungen jetzt schon fünfe beträgt."

In this description we shall see that Krohn came nearer the truth than any other investigator up to the present. His account of the mode of origin of the transverse rows of stigmata is wrong, as has been already shown, at least with reference to the first six rows, by van Beneden and Julin.

Commencing, then, with a stage at which two branchial apertures are present on each side (Pl. XXX, figs. 2—4), we find that they elongate considerably in the transverse direction, and meanwhile, as time goes on, become curved in opposite directions, so that their concave sides face each other (fig. 6).

The next and most important stage shows us that from the inner extremities—that is, from the ends nearest the endostyle of each of the two original slits—a small portion is in process of being constricted off (figs. 5 and 7—10). The various stages in this remarkable and hitherto undescribed mode of formation of the two intermediate slits are shown in Pl. XXX, figs. 7—10. These intermediate apertures, then, are what Krohn saw after, but not during their formation;

and we have before us the stage with four primary stigmata on each side, which have hitherto been regarded as arising by four independent perforations. The budding off, so to speak, of the two intermediate slits (II and III) from the two first-formed slits (I and IV) is subject to a good deal of variation. The constriction appears to take place first from IV in most cases, but occasionally it proceeds in the first case from I (fig. 8). The slits II and III are, however, not distinct productions of I and IV respectively, but are essentially a joint production of the two latter slits. This is shown clearly in the figures. The ends of the two first-formed slits come into intimate contact—in fact, fuse with each other prior to and during the formation of the intermediate slits.

A very interesting variation, demonstrating the common origin and single nature of the two intermediate slits, is shown in Pl. XXXI, fig. 20, where the two slits in question are represented by one elongated dumb-bell shaped aperture, which would later divide as indicated by the constriction in the middle.

The fact that the slits I and IV join together in giving rise to II and III is alone sufficient to render it extremely probable that I and IV, the two simultaneously first-formed slits, are themselves derived from one original slit. This view is further brought to the highest pitch of probability by the occurrence of such a variation as that represented in fig. 16, where the two slits in question have fused together to form one large incurved orifice. In the individual from which this drawing was made the two corresponding slits of the other (right) side were independent.

In the actual ontogeny, however, these two slits arise by independent perforations, but in such a way as to leave no doubt that they represent one slit divided into two halves by a tongue-bar, the latter forming at an early stage before the actual perforation of the slit, so that the two halves of the slit break through separately. In the case of the secondary slits of *Amphioxus*—that is, the slits of the primitive right side which are late in appearing (see author, 33)—shortly after their



perforation, and while their primary long axis is still at right angles to their future long axis (being longitudinal instead of vertical), the tongue-bars form by a downgrowth from the dorsal walls of the slits, while the primary slits have already existed for several weeks without any sign of a tongue-bar. The tongue-bars of the secondary slits of *Amphioxus* are, therefore, considerably hastened in their development. A little more and the two halves of the slit would break through separately. Such a precocious development of a tongue-bar has recently been described by Morgan (29) in *Balanoglossus*, and this is what occurs in connection with the first two gill-clefts of *Ciona*, as the following account will demonstrate.

We must first, however, consider Kowalevsky's account of the origin of these slits (21). He says, namely, that the two first gill-slits of each side arise by the fusion of two outgrowths from the wall of the branchial sac with the floor of the corresponding atrial invagination, and he figures the two slits in his fig. 37, which was reproduced by Balfour. But it is practically certain that what Kowalevsky figured as the gill-slits were not the slits at all. If reference be made to Balfour's 'Comparative Embryology,' vol. ii, p. 11, fig. 6, it will be seen that in this figure the connection of the œsophagus with the branchial sac is not even indicated. But the opening of the œsophagus into the branchial sac is very large indeed, the former arising as a direct continuation of the latter. Now that portion of the wall of the branchial sac in which the gill-slits occur, which may be called for convenience the branchial tract, lies at first precisely at the niveau of the junction between the branchial sac and the œsophagus, and Kowalevsky has apparently mistaken the small portions of the lumen of the branchial sac which are visible on each side of the branchial tract for the gill-slits themselves (compare my fig. 2 with the above-mentioned figure of Kowalevsky's). This mistake, it should be added, is, on account of the extremely small size of the larvæ and of the primary crowding of the organs very easy to make and very hard to rectify if later stages are not examined.

In fig. 2 an individual is represented at a stage shortly after fixation, when the tail has been entirely drawn inside the body of the Ascidian, but before any change of axis has set in. It is here seen that a line drawn through the two slits at right angles would be parallel to the direction of the endostyle. The two slits arise already in the older free-swimming larvæ, but are first clearly recognisable just after fixation on account of the fact that the spaces in the body, namely, the lumen of the intestine and the body-cavity, undergo a considerable expansion at that period of the development, as will be seen on comparing fig. 1 with fig. 2.

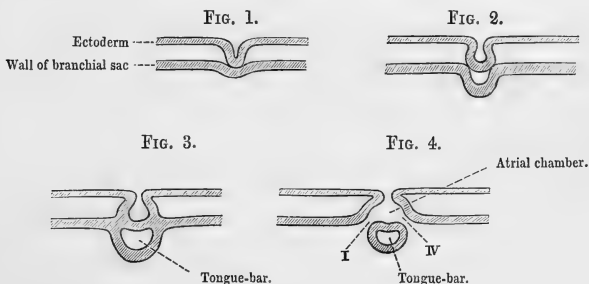
As to the actual mode of formation of the first two slits which arise simultaneously, it is necessary to have recourse to transverse or horizontal sections. It will suffice to describe the conditions observed in transverse sections, as the only essential difference to be noticed between a transverse and horizontal section of a larva at the time of fixation is that in the latter direction the endostyle is cut transversely (cf. Pl. XXX, fig. 13), while in the former it does not occur at all in sections through the region of the branchial sac which lies behind the mouth. The primary position and relations of the endostyle will be described below.

Figs. 11 and 12 represent transverse sections through the region of the branchial tract of an individual of about the stage shown in fig. 2. The sections have the advantage of being slightly oblique, so that on the left side of the section the wall of the branchial sac immediately in front of the branchial tract of that side is shown, and can be compared with the wall on the right side of the section in which the latter passes through the branchial tract. It will thus be seen at a glance in fig. 11, on comparing the two sides of the branchial sac together, that what we have to do with in the branchial tract is not two outgrowths from the wall of the branchial sac, but one ingrowth or involution of the wall projecting into the branchial cavity and involving with it a space which communicates freely with the body-cavity and contains blood-corpuscles. This ingrowth necessarily gives rise to two angles

in the wall of the branchial sac, and it is at the points of these angles that the first two gill-slits simultaneously break through into the atrial cavity (Pl. XXX, fig. 12).

It is this ingrowth of the wall of the branchial sac which I interpret as a tongue-bar dividing a primitively single slit into two.

The following diagrams will render the mode of origin of the first two slits as above described easy to understand. In fig. 1 an atrial invagination is shown, causing a slight depression in the subjacent wall of the branchial sac (cf. Pl. XXXI, fig. 27). In fig. 2 this depression has deepened, and the wall of the branchial sac has separated itself, except at the two angles from the floor of the atrial invagination, the space thus produced being continuous in front and behind with the body-cavity. In fig. 3 the wall of the branchial sac has fused at the two above-mentioned angles with the floor of the atrial cavity, and, finally, in fig. 4 the two gill-slits (I and IV) have broken through, and now open into the common atrial chamber.



I have thus endeavoured to show that the first four primary stigmata of *Ciona*, and probably of all the *Ascidia* proper (*A. mentula*, *mammillata*, &c.), represent and are derivatives of one primitive gill-slit.

After the first four stigmata have become fully established in the way just described, two more branchial apertures, v and vi, arise behind them one after the other by independent perfora-

tion (Pl. XXX, fig. 14, and Pl. XXXI, fig. 21), and in this way we arrive at the stage with six primary stigmata on each side, which was also described by van Beneden and Julin for *Phallusia scabroides*.

Assuming that the stigmata v and vi have the value of true gill-slits, and are each of them equivalent in morphological value to the first four stigmata taken together, we conclude that in the simple Ascidians under consideration three pairs of primary gill-slits are formed in due order of succession from before backwards, as follows :

$$\begin{array}{r}
 \text{Stigmata} \\
 \begin{array}{l}
 \text{I} \\
 \text{II} \\
 \text{III} \\
 \text{IV}
 \end{array}
 \left. \vphantom{\begin{array}{l} \text{I} \\ \text{II} \\ \text{III} \\ \text{IV} \end{array}} \right\} = \text{1st gill-slit.} \\
 \text{V} = \text{2nd } ,, \\
 \text{VI} = \text{3rd } ,,
 \end{array}$$

The irregularity in the order of appearance of these primary stigmata has not, therefore, in any sense the signification which van Beneden and Julin attached to it, and as soon as the stigmata are properly identified with gill-slits we have seen that there is no irregularity at all, so that this argument cannot be used against homologising the gill-slits of Ascidians with those of Amphioxus. If the above table be compared with that given by van Beneden and Julin, which I have repeated above, it will be seen how great is the difference between them.

For convenience of description it is necessary to make a mental distinction between the terms "primary stigmata" and "primary gill-slits." The former expression refers to the six simple, undivided apertures which are developed in the way above described, while the latter is a morphological term. Thus while there are six primary stigmata, they only represent three gill-slits.

As time goes on, the six primary stigmata elongate very considerably in the transverse direction, and eventually become divided into two by the formation of small tongue-like projections, which arise indifferently from the anterior or

posterior walls of the stigmata, and, growing across the aperture, fuse with the opposite wall. This process of subdivision, which was correctly described by van Beneden and Julin (6), is then continued, and we arrive at the stage with six transverse rows of secondary stigmata derived by repeated subdivision from the six primary stigmata (cf. fig. 17). In the next stage occurs the change in the direction of the axes of the stigmata, which was first observed by Krohn. Hitherto transverse, their long axes now become vertical or longitudinal. A single row of stigmata in process of changing their axes is shown in Pl. XXXI, fig. 18. From this figure it can be seen that the individual stigmata undergo a bow-like curvature, and then divide in the hollow of the bow, the result being that the new stigmata thus produced have approximately a vertical instead of a transverse long axis.

The next question relates to the way in which the numerous transverse rows of stigmata which compose the adult branchial system are produced. Van Beneden and Julin (6) appear to think that, after the formation of the first six rows of secondary stigmata, the stigmata which are formed later arise by fresh perforations. What they actually say is as follows:—  
“Ces premiers stigmates, au nombre de six, se subdivisent par une sorte d'étranglement en stigmates secondaires. Six rangées de stigmates secondaires naissent ainsi des six stigmates primaires. À une période plus avancée du développement le processus génétique primitif [this means the method of independent perforation], reparait pour donner naissance à de nouvelles fentes stigmatiques interposées entre les stigmates secondaires formés par étranglement.”

In *Ciona* this is certainly not the case, and, judging from the closely parallel development of the members of the *Phallusia* group, it is difficult to believe that the condition of things can be entirely different. In fact, the new transverse rows of stigmata arise by division of the pre-existing transverse rows.

This is easy to establish by an examination of any young specimen of *Ciona*, as well as the fact that the very small stig-

mata which lie interspersed between the normal sized stigmata have not arisen by fresh perforation, but by unequal division of other stigmata (Pl. XXXI, figs. 23 and 24). It is impossible to say absolutely that no fresh perforation occurs in these later stages, but at least no evidence of any such has been brought forward, while contrary evidence is now being adduced.

A portion of two adjacent transverse rows from the branchial sac of an individual with eleven rows is represented in Pl. XXXI, fig. 22. On the left are two stigmata occupying their normal places in their respective rows. In the middle is seen one long slit stretching from the anterior limit of one row to the posterior limit of the other. The blood-vessel which is seen to cross the slit has nothing to do with it, as it lies on a different level, and forms part of the well-known internal vascular scaffolding of the branchial sac. Finally, on the right is seen a similar slit, which, however, is in process of dividing into two in the usual way.

The complicated origin of the transverse rows of stigmata of *Ciona* having now been described, it remains to point out that in *Clavelina*, as shown by Seeliger (31) and Garstang (14), and as I have also satisfied myself, these transverse rows of stigmata are developed in the first instance; that is to say, that ontogenetically they are primary and not secondary in origin, and each aperture arises by independent perforation. Here, then, is a very good demonstration of abbreviation of development in the case of the branchial stigmata of *Clavelina*. I have already drawn attention to this remarkable evidence of the modified character of the development of *Clavelina* (34).

## 2. Præoral Lobe and Endostyle of *Ciona*.

By the name præoral lobe I refer to a structure which has long been known, but which has been assumed hitherto to have no special significance, to which, however, from a morphological point of view, I propose to attach a capital importance. I have already given a preliminary account of this structure under the name of proboscis cavity (34). The

cavity in the præoral lobe would, however, be better described as the anterior body-cavity.

In a young larva the endoderm is in contact anteriorly with the ectoderm; but in a rather older larva the anterior ectoderm bearing the adhering papillæ springs away from the endoderm, leaving a space which becomes filled with a compact mass of mesoderm-cells (Pl. XXX, fig. 1).

The mesoderm which comes to lie in this anterior body-cavity has a bilateral origin, in that it proceeds from the two lateral mesodermic plates. Fig. 15 shows a transverse section through the præoral region of a larva of the stage of fig. 1, cutting the endostyle vertically; and on either side of the latter is seen a group of mesoderm-cells, which form part of the lateral mesodermic bands. The latter pass directly into the mesoderm of the anterior body-cavity.

In *Distaplia magnilarva*, Davidoff (8) has found that a portion of this anterior mesoderm is derived directly from the anterior extremity of the endoderm, from which cells are given off into the body-cavity.

The mesoderm so produced is called by Davidoff the prægastral mesoderm. The occurrence of this prægastral mesoderm in *Distaplia* is in itself, apart from other considerations, a serious argument against van Beneden's and Julin's theory of the prechordal vesicle of the Ascidian embryo and its homology with that portion of the enteric cavity of *Amphioxus* from which the anterior intestinal diverticula arise, as will appear from the following definition which they give of their prechordal vesicle. They say (7, p. 385), "Le mésoblaste et la notochorde se forment aux dépens de l'endoderme primitif de la *Gastrula*, dans toute la longueur de la larve, à l'exception de son extrémité antérieure. L'on peut donc distinguer dans la longueur du corps de la larve une partie antérieure préchordale dans laquelle la chorde et le mésoblaste font défaut et une portion chordale, dans les limites de laquelle s'étendent la notochorde et les bandes mésoblastiques. Il en résulte aussi que, chez l'*Amphioxus* comme chez la *Claveline*, le tube digestif des jeunes larves se constitue de

deux portions bien distinctes, une portion préchordale et une portion subchordale."

When the larva of *Ciona* fixes itself the above-mentioned anterior body-cavity which, as has been indicated, is at first almost filled up by a compact mass of mesoderm proceeding from the two mesodermic plates, swells up enormously, and then presents the aspect of a large cavity bounded by ectoderm, and containing loose scattered mesoderm-cells. The position and relations of the præoral lobe with its contained anterior body-cavity are shown very plainly in the figures on Pl. XXX.

The adhering papillæ flatten out shortly after fixation, and give place to a thickened disc of ectoderm at the anterior extremity of the præoral lobe.

The præoral lobe has been figured by Kowalevsky (20) in the case of *Phallusia mammillata*, and by Kupffer (24) in the case of *Ascidia canina*, but was for them nothing more than a peculiar "Haftapparat."

Kupffer says (p. 158), "Die prononcirt dorsale Stellung der Mundöffnung darf nicht ausser Zusammenhang mit dem am vordern Ende entwickelten specifischen Haftapparate beurtheilt werden. Durch diesen wird die dorsale Lage der Mundöffnung bedingt." The dorsal position of the mouth in the *Ascidian* tadpole will be considered later.

As to the endostyle, it is a remarkable fact, the significance of which has not yet been properly recognised, that its primary position in the free-swimming larva, and also for some time after fixation, is at right angles to its definitive position. In fact, the endostyle lies at first præorally and dorso-ventrally, and eventually post-orally and antero-posteriorly.

Kowalevsky (21) and Kupffer (24) both stated that the endostyle extended from the neighbourhood of the mouth in front to the hinder extremity of the branchial sac, and Kowalevsky figures it accordingly along the whole ventral side of the branchial sac of the larva. Kowalevsky's account of the endostyle in the larva, which was repeated by Balfour (1, p. 18),



is quite wrong, as may be seen at a glance from Pl. XXX, figs. 1 and 2, especially the latter.

The most anterior portion of the wall of the enteric cavity of the larva of *Ciona*—namely, that which lies in front of the mouth and immediately behind the præoral lobe—becomes the endostyle, the primary position of which is, therefore, clearly anterior and dorso-ventral (fig. 1). At a later stage the long axis of the endostyle becomes changed in its direction owing to a rotation through an angle of  $90^\circ$ , which the whole body of the Ascidian undergoes with the præoral lobe for the fixed pivot about which the rotation takes place. In figs. 3 and 4 a stage is drawn in which this rotation of the body of the Ascidian has just commenced. While in fig. 2 the long axis of the endostyle was at right angles to the præoral lobe, in figs. 3 and 4 the former lies obliquely with reference to the latter. Fig. 5 shows a stage long after the completion of the rotation, and the præoral lobe is posterior and has relatively smaller proportions than at first; the mouth, at first dorsal, is now anterior and terminal; and the endostyle, at first præoral and dorso-ventral, is now post-oral and longitudinal. The long axis of the adult Ascidian is, therefore, at right angles to the long axis of the larva.

At a later stage the præoral lobe commences to branch and send out secondary processes, but the constancy of its primary position, relations, and form is absolute.

In *Clavelina* the peculiar behaviour of the adhering apparatus (Haftapparat) has its effect indirectly on the axial relations of the endostyle. In the free-swimming larva of *Clavelina* the endostyle, owing to another hastening in the development, is already in its definite antero-posterior position. It, however, lies at first dorso-ventrally in the unhatched larva as described by Seeliger (31); but the change in the axis is effected in a somewhat different way from that described above for *Ciona* before the hatching, and therefore long enough before the fixation of the larva. This is what Seeliger says (pp. 33, 34): "An der vorderen Wand tritt der Endostyl immer mehr als differenter Abschnitt des Kiemendarmes

hervor. . . . In fig. 40 fanden wir die Endostylwand auf dem vorderen Chordaende nahezu senkrecht stehen und mussten sie als vordere bezeichnen. Dieses Verhältniss finden wir noch auf dem in fig. 42 gezeichneten Stadium; von jetzt ab aber beginnt die Drehung. . . . Als die Ursache dieser Verschiebung kann ich nur die Umbildung des vor dem Endostyl liegenden Ektodermlappens durch eine Einschnürung zum Haftstolo erkennen, mittelst dessen die Larve sich später festheftet." Seeliger does not, however, perceive any contradiction between his description of the primary position of the endostyle in *Clavelina* with that of Kowalevsky for *Phalusia mammillata*.

### 3. The Præoral Lobe and Endostyle of Ascidians compared with the corresponding Structures in Amphioxus.

The cavity of the præoral lobe, or, as it is sometimes called, the snout of *Amphioxus*, is derived, as is well known from the description given by Hatschek (15), from the right of a pair of anterior intestinal diverticula.

These diverticula are at first perfectly symmetrical, but soon the right one begins to enlarge, and ultimately gives rise to the large cœlomic cavity which occupies the anterior extremity of the larva of *Amphioxus* (see Lankester and Willey, 28, pl. xxix, figs. 2 and 5, and pl. xxx, fig. 1).

The left diverticulum remains comparatively small, and then acquires a wide opening to the exterior and becomes the præoral pit (Wimperorgan, Hatschek).

It is necessary to emphasise the fact, which would appear to be sufficiently obvious, that these two anterior intestinal diverticula of *Amphioxus* are not the first pair of metameric cœlomic pouches. They first arise, as shown by Hatschek, at a stage when already some eight pairs of cœlomic pouches are present. Their origin, therefore, and subsequent fate show that they are structures *sui generis* in front of the mouth and in front of the first pair of trunk somites.

The anterior body-cavity of *Amphioxus* has, therefore,

at first a bilateral origin, but its left half becomes arrested at an early stage of development, and is then modified into the præoral pit. The essential part of this præoral body-cavity in *Amphioxus* is of course the epithelium lining it.

The first differentiated hypoblastic structure that comes behind the præoral or anterior body-cavity in *Amphioxus* is the endostyle, which, while being slightly oblique and asymmetrical on the right side (author, 33), has essentially a dorso-ventral position. As to the general homology of the endostyle in the two groups of the Cephalochorda and the Urochorda no one would think of entertaining a doubt. In both groups we have shown that its primary position is dorso-ventral and at right angles, or nearly so, to its definitive position, and it lies in both cases immediately posterior to the præoral lobe. There is, therefore, at once strong presumptive evidence that the præoral lobes or anterior body-cavities are themselves homologous in the two groups, and this, I am convinced, is the case.

In the development of the mesoderm in the Ascidiæ it does not come to a formation of cœlomic pouches, although the latter was affirmed by van Beneden and Julin for *Clavelina*, but contradicted by Davidoff for the same form; and I have also been unable to find any archenteric pouches in the embryos of *Cynthia papillosa*, which spawned in the tanks at Naples in the month of November. Shortly after its formation at the expense of the hypoblast, the mesoderm in the Ascidian embryo, except in the tail, breaks up into a system of loose mesenchyme consisting of round cells scattered in the general body-cavity.

It would, therefore, be unreasonable to expect to find a mesodermic epithelial lining to the anterior body-cavity or cavity of the præoral lobe, when there is neither splanchnopleur nor somatopleur in any other region of the body. We should expect to find and do find that the præoral lobe contains scattered mesodermic cells, the bilateral origin of which has been described above. The differences in the origin and character of the mesoderm of the anterior body-cavity in the

Ascidians and *Amphioxus* are far from being unintelligible. The epithelial lining of the præoral cavity of *Amphioxus* is represented by scattered cells in the Ascidians. The anterior body-cavity of *Balanoglossus*, as described by Bateson (2 and 3), seems to offer an intermediate condition in that an epithelium and a loose mesenchymatous tissue co-exist there. Bateson found that the rounded extremities of the cells lining the anterior body-cavity of the embryo of *Balanoglossus* are continually budding off cells into the cavity itself, and this proliferation of cells continues until the proboscis cavity is to a great extent occupied by loose masses of cells.

The similar position, relations, and behaviour of the endostyle in the larvæ of Ascidians and *Amphioxus* are the foundation on which the present system of homologies is being built. The actual way in which the endostyle arrives at its definitive antero-posterior position is somewhat different in the two cases, but the main features are essentially the same (author, 33).

From what has been said above, therefore, I draw the conclusion that the anterior body-cavity of the Ascidians, that is the cavity of the præoral lobe or adhering stolon, which appears in a comparatively unmodified form in *Ciona*, in contrast to the condition in *Clavelina* and the compound Ascidians generally, with its loose mesodermic cells, is homologous with the anterior cœlomic cavity and præoral pit of *Amphioxus* with their epithelial lining, the two latter structures being taken together as representing a primitively symmetrical and bilateral præoral body-cavity, the two halves of which have become secondarily differentiated from one another.

#### 4. Gill-slits of Ascidians and *Amphioxus*, with Remarks on *Ammocœtes*.

If we consider the succession of the various organs from before backwards, and allow for the secondary change of position of the mouth in *Amphioxus* (author, 33), we find that the following is the order in which they occur in both *Ciona* and *Amphioxus*:—1. Præoral lobe or anterior body-cavity. 2. Endostyle. 3. Mouth. 4. Neuroporus (vide infra).

5. First pair of gill-slits. 6 and 7. Second and third pairs of gill-slits. In *Ciona*, as shown above, the first gill-slit of each side is composed of the primary stigmata I, II, III, and IV. These stigmata serve the young *Ciona* for respiration for a considerable period, during which it is feeding itself up for further growth.

In *Amphioxus*, as I have previously shown (*loc. cit.*, p. 225), the first pair of gill-slits consists of the first primary gill-slit proper and the club-shaped gland. This pair of gill-slits, of which apparently only one member functions as a true gill-slit, alone serves the young larva of *Amphioxus* for respiration during a similar period, namely, the first period of independent feeding, when there is not much progressive development, but the larva is preparing itself for the future effort of growth. In *Amphioxus*, towards the end of the larval development, the club-shaped gland and the first gill-slit proper, which played such an important rôle in the early stages, simultaneously close, atrophy, and disappear (33). In both the *Ascidians* and *Amphioxus*, therefore, the first pair of gill-slits has peculiarities which distinguish it from all the succeeding gill-slits.

From these considerations, and on account of its topographical relations, I conclude that the first pair of gill-slits of *Ciona*, consisting of the first four primary stigmata on each side, is homologous with the first pair of gill-slits of *Amphioxus*.

The second and third pairs of gill-clefts, of course, follow suit.

The above conclusion is in direct opposition to that arrived at by van Beneden and Julin (5 and 7). In consequence of their theory of the prechordal vesicle they denied that any homology existed between the stigmata of the *Ascidians* and the gill-slits of *Amphioxus*. They say, for instance (5, p. 360), "Nous ne pouvons donc admettre l'homologie entre les stigmates des *Ascidiens* et les fentes branchiales de l'*Amphioxus*;" and further, "Les *Ascidiens* comme les *Appendiculaires* sont des *Chordés* pourvus d'une seule et unique paire de fentes branchiales."

We have already seen, especially with the reference to the mode of origin of the branchial stigmata in the two cases, that on the whole the development of *Ciona*, as well as that of the *Ascidia* proper, presents obviously much more primitive features than that of *Clavelina*, which was the object studied chiefly by van Beneden and Julin. It may, therefore, be stated generally that the stigmata in the branchial sac of the *Ascidians* are derived from and represent three pairs of primary gill-clefts.

The independence of the metamerism of the gill-slits from that of the trunk as a whole is shown in the plainest possible way in *Balanoglossus*.

In consequence of the view, based on embryological data, which was put forward in 1873 by Wilhelm Müller (30), as to the homology of the thyroid gland of *Ammocetes* with the endostyle of the *Ascidians* and *Amphioxus*, and which was confirmed and in fact definitely demonstrated by Dohrn in 1885 (10), who also first pointed out the homology of the pericoronal ciliated groove of *Ascidians* (sillon péricoronal—Julin) with the so-called "Pseudo-branchialrinne" of *Ammocetes*, it is necessary to say a few words about Dohrn's conception of the morphological value of the latter structure.

I may first, however, point out that I have on a former occasion (33, p. 209, and plates) figured and described a corresponding peripharyngeal ridge in *Amphioxus*.

Dohrn says (11, p. 310), "Die Pseudo-branchialrinne [of *Ammocetes*] geht factisch hervor aus der nicht mehr zum Durchbruch gelangenden beiderseitigen vordersten Entodermausstülpung des *Ammocetes*, welche [on account of the relations to it of the *Trigeminus*] der Spritzlochspalte der *Selachier* und *Ganoiden*, der Pseudo-branchie der *Teleostier* homologisirt werden muss." Although Dohrn may be said to have demonstrated the homology of the so-called "Pseudo-branchialrinne" of *Ammocetes* with the pericoronal groove of the *Ascidians*, yet he was far from proving the identity of the former with the rudimentary spiracle of *Ammocetes*, as appears at once from a careful perusal of the detailed and

magnificently illustrated description, intended to prove this point, which he gives in his thirteenth study (12).

From the latter memoir it appears that the spiracular evagination of the pharyngeal wall on each side gradually flattens itself completely out; and then, at the place where it formerly existed, a new groove (eine neue Vertiefung) arises, namely, the so-called "Pseudo-branchialrinne." The latter is, therefore, something new and distinct from the spiracular evagination. The fact that it occurs at the spot formerly occupied by the latter structure is rendered explicable by the small space into which the various parts have been crowded in the anterior region of *Ammocœtes*, so that the groove could not form more anteriorly than the site of the rudimentary spiracle, since the position of the latter is itself most anterior. Apart, however, from such considerations as these, it is not quite clear why the former existence of a pair of gill-slits should be necessary for the formation of the so-called "Pseudo-branchialrinne," and not for the formation of the other exactly similar longitudinal grooves which occur dorsally, and behind the duct of the thyroid ventrally, in the pharynx of *Ammocœtes*.

On the other hand, on account of its contiguity to the "Pseudo-branchialrinne," I should be emphatically inclined to regard the anterior pair of rudimentary gill-slits of *Ammocœtes*, which according to Dohrn correspond to the spiracles of Selachians, as homologous with the first pair of gill-slits of the Ascidiæ and *Amphioxus*, especially since in the latter there is the further point of resemblance to the condition in *Ammocœtes*, that the first pair of gill-slits becomes obliterated towards the end of the metamorphosis. In *Ammocœtes*, as shown by Dohrn, these slits never break through, only the endodermic pouches being temporarily formed.

The homology of the endostyle and pericoronal groove of Ascidiæ with the thyroid gland and "Pseudo-branchialrinne" of *Ammocœtes* was finally established by Dohrn, and I believe, by a comparison of my observations on the Ascidiæ and *Amphioxus* with those of Dohrn on *Ammocœtes*, that the

homology of the first pair of gill-slits in all three cases, whether permanently, temporarily, or never functional, is no less clearly demonstrated. Dohrn's argument, therefore, against the primitive character of the Ascidians, based on the supposition that the pericoronal groove was the remnant of a pair of gill-slits, falls entirely to the ground.

It will probably come to be recognised that the first pair of gill-slits of the Ascidians, Amphioxus, and Ammocœtes is in every sense of the word, morphologically and actually, the first pair of gill-clefts, there being absolutely no evidence of the mouth and endostyle of the Ascidians and Amphioxus having each proceeded from a pair of gill-clefts, but a great deal of evidence to the contrary, as we have seen and shall see.

It is hardly necessary to add that the prodigious degeneration postulated by Dohrn for the Ascidians and Amphioxus cannot be accepted in the light of the above considerations.

#### 5. The Atrial Cavities of Ascidians.

After what has been said above as to the primary positions of the several organs relative to the endostyle in the larval Ascidian and Amphioxus, the homology which van Beneden and Julin sought to establish between the primary atrial cavities of the Ascidians, and the two anterior præoral intestinal diverticula of Amphioxus, will appear almost inconceivable (see Pl. XXX, figs. 1—5, for position of atrial apertures).

The idea of a prechordal vesicle, which was the starting-point of the above-named authors in their comparison of the Ascidians with Amphioxus, and led them to a remarkable series of positive and negative homologies, and which in ignoring the presence of a very large and prominent præoral lobe, which we have shown to occur in the Ascidians, seemed plausible enough, is undoubtedly in its main features a misconception.

From observations made on *Ciona intestinalis* and *Clavelina lepadiformis* I can confirm Kowalevsky (21) and Seeliger (31) in saying that the atrial cavities of Ascidians



are derived essentially from ectodermic invaginations; and the idea that the visceral wall of the atrium is derived from the hypoblast, as put forward by van Beneden and Julin, is entirely without foundation. It may be added, further, that the expression "primary branchial canal," which van Beneden and Julin employ for the canal formed by the fusion of the floor of the atrial invagination on each side with the wall of the branchial sac to form the first pair of stigmata in *Clavelina*, has no morphological meaning.

On account of the crucial importance of a correct appreciation of the atrial cavities from the point of view of the relations between the Urochorda and Cephalochorda it is necessary to make a somewhat lengthy quotation from the work of van Beneden and Julin (7). They say (p. 402, et seq.), with reference to the formation of the atrial cavities in *Clavelina*, "Indépendamment des invaginations épiblastiques . . . . il se forme, chez la Claveline, des culs-de-sac hypoblastiques qui procèdent de la voûte du sac branchial, se soudent aux invaginations épiblastiques et se mettent en communication avec elles. . . . Les culs-de-sac épiblastiques et les diverticules hypoblastiques interviennent concurremment dans la formation des canaux branchiaux de la larve urodèle. Ces canaux sont évidemment homologues à ceux des Appendiculaires. . . , . Les deux ébauches qui coopèrent à la formation d'un canal primitif, interviennent l'une et l'autre dans la formation des cavités péribranchiales; il est difficile de dire dans quelles limites. . . . Nous pensons que le feuillet viscéral de la membrane péribranchiale . . . est en grande partie d'origine hypoblastique."

Further on they go on to say that it is doubtful whether these "primary branchial canals" persist and function with the rest of the stigmata, or whether they close up as they do in the buds, where the peribranchial cavities arise by constriction from the inner vesicle of the bud. They incline to the latter view.

In the first place, it follows clearly, from the description I have given above of the origin of the gill-slits in *Ciona*, that

the primary branchial canals in their capacity as distinct structures deserving a special name do not exist; and, in the second place, it is precisely the way in which the atrial cavities arise in the bud that shows conclusively that they are perfectly homogeneous structures, and do not originate from two "ébauches," hypoblastic and epiblastic respectively.

The question then arises as to what the "culs-de-sac hypoblastiques" which were seen by van Beneden and Julin might be, and it would appear to be not very difficult to answer.

A transverse section through the pharyngeal region of a larva of *Clavelina lepadiformis* is shown in fig. 29, from which it is seen that the branchial sac has a peculiar and characteristic structure at this stage, brought about by the occurrence of certain definite foldings in its wall. It consists of a median portion and two lateral portions. The median ventral wall forms a deep fold with high cylindrical cells; this is the endostyle. The lateral portions consist also of two large folds with a lower cubical epithelium. Between the lateral folds and the ectoderm are seen the two peribranchial cavities, which have begun to spread themselves out. Stigmata are present at this stage, but this particular section does not pass through any. A somewhat oblique section is represented in fig. 28, so that the atrial cavity is only seen on one side with two stigmata in connection with it, one of which, however, has apparently not yet broken through.

The section also involves the opening of the neuro-hypophysial canal into the branchial sac; but I will not enter into the question of the nervous system here, reserving it for the next "study."

The stigmata arise by simple fusions occurring at regular intervals between the wall of the branchial sac and the floor of the atrial cavity on each side. The "culs-de-sac hypoblastiques" of van Beneden and Julin can be nothing else than the two lateral divisions of the branchial sac which I have just described. But it was largely on the strength of the supposed part which these "culs-de-sac hypoblastiques" took in the formation of the atrial chambers that van Beneden and Julin

came to the conclusion that the "primary branchial canals" of the Ascidians were homologous with the anterior intestinal diverticula of *Amphioxus*, the two structures being to a greater or less extent formed from hypoblastic evaginations, while in *Amphioxus* the epiblastic element was entirely wanting. If now the conception of "primary branchial canals" be abolished this homology ipso facto falls to the ground. And it is otherwise, as I have said above, rendered very improbable, if not impossible, from the topographical relations of the respective structures.

Are, then, the atrial cavities of Ascidians, which subsequently fuse together dorsally to form the single peribranchial chamber of the adult, homologous with the atrial chamber of *Amphioxus*? Van Beneden and Julin, involved in their hypothesis of the prechordal vesicle, denied that the atrial cavities, together with the branchial stigmata of the Ascidians, were in any way homologous with the atrial cavity and gill-slits of *Amphioxus*. The question of the gill-slits has been already discussed above.

As for the atrial cavities, I could for a long time find no ground for homologising them with the atrium of *Amphioxus*, and in my short paper in the 'Proceedings of the Royal Society' (34), I spoke of them as being, at their first origin, nothing but the ectodermic portions of the first pair of gill-slits. By a subsequent renewed study, however, of their origin in *Clavelina* I have become convinced that the atrial cavities of Ascidians are structures sui generis, apart from the stigmata which open into them.

In fact, in *Clavelina* the atrial cavities appear at first as longitudinal grooves, shallow anteriorly, and gradually deepening posteriorly up to the point where the actual permanent involution occurs. In the series of transverse sections, for instance, from which figs. 26 and 27 are taken, these longitudinal grooves extend over at least eight sections cut at a thickness of 7  $\mu$ . Five sections intervene between those represented in figs. 26 and 27.

In *Amphioxus* (28 and 32) the atrial chamber has a dis-

tinctly bilateral origin, in that it is formed by the fusion of the two subatrial ridges. Before the actual fusion of these ridges the two angles formed between the body-wall and the metapleura are really the two halves of the future atrium, which fuse together before being closed in. If they closed off separately and fused together secondarily, we should have essentially the same conditions as in the Ascidians; always, however, with the difference that in *Amphioxus* the two halves of the atrium are in communication ventrally below the endostyle, while in Ascidians they fuse together dorsally—that is, on the side opposite to the endostyle. This distinction, however, need not be regarded as at all fundamental, when we consider the extreme modification which the Ascidians have undergone in comparison with *Amphioxus*, in correlation with their sessile habit of life, and especially the absence in the adult of the notochord and the reduction of the nervous system.

FIG. 5.



FIG. 6.



FIGS. 5 and 6.—Diagrammatic transverse sections to illustrate the formation of the atrium in an Ascidian (Fig. 5) and in *Amphioxus* (Fig. 6).

The object we have in view is to determine as far as possible which organs are homologous in two related groups, which, however, diverge widely from one another. As soon as the homology between any two organs is established, then is the time to notice the different directions in which they have been modified in the respective groups; but to expect to find individual organs modified in the same direction in two groups in which the whole organisation has become adapted to totally different conditions of life is unreasonable, and I therefore do

not regard the fact that the atrial cavities fuse together dorsally in the Ascidiæ, and ventrally in Amphioxus, as a valid objection to their complete homology in the two groups.

Van Beneden and Julin (6) lay great stress on the cloaca of the Ascidiæ being a special formation, produced not only by the conrescence of the two primary atrial apertures, but also by a new depression in the dorsal wall of the body, and, in contrast to the atrial chambers, being delimited on all sides by ectoderm. They say that before their fusion the two atrial apertures do not project from the body of the Ascidian in the form of siphons. I must, however, confirm Krohn (23) in saying that they do. The special dorsal depression, however, might very well occur, although I have not been able to see it; but the contrast to the atrial chambers in regard to the derivation of the epithelial lining of its walls does not, as we have seen above, exist.

#### 6. Intestine and Cæcum of Ascidiæ and Amphioxus.

Since, according to van Beneden and Julin the prechordal vesicle, including the first trunk somite of the Ascidiæ, had enlarged itself at the expense of the trunk generally, so as to contain in itself all the organs which usually belong to the trunk proper, it followed among other things that the intestine of Ascidiæ was a new formation, a special outgrowth from the posterior end of the prechordal portion of the enteric cavity, and was not homologous with the intestine of Amphioxus. The tail of the Ascidian tadpole represented for them the trunk of Amphioxus, and the solid cord of endoderm-cells arranged in a double series, each series being composed of single cells placed end to end and lying immediately below the notochord, which is a constant feature of the tail of the Ascidian tadpole, was for them the rudiment of a primitive intestine which formerly extended to the end of the tail, and there discharged by the anus. It might, at first sight, appear that this view of a rudimentary intestine in the tail of the Ascidian tadpole had certainly much to be said for it on mor-

phological grounds, but physiologically the atrophy of an old intestine and the formation of a new one in animals which are not pretended to have phylogenetically passed through an intermediate parenchymatous condition, is hard to conceive.

Van Beneden and Julin got over the difficulty by supposing the presence, in the ancestor of the Ascidians, of an anterior "collateral organ," which served some function or other concurrently with the existence of a terminal anus, and which, as the old intestine atrophied, took on the definite function of an intestine. In *Amphioxus* this collateral organ, which has become the present intestine of the Ascidians, is represented by its supposed homologue, the club-shaped gland.

I have previously (33) given reasons which seemed to me to prove conclusively that whatever else it might be, the club-shaped gland of *Amphioxus* is a modified gill-slit pairing with the first primary gill-slit proper. This being the case, it becomes at once practically impossible to homologise it with the intestine of the Ascidians. In the system of homologies which I am seeking to establish I have already disposed of the club-shaped gland as far as its morphological value is concerned, so that we are driven to consider whether there is really any sufficient ground for supposing that the tail of the Ascidian tadpole represents the trunk of *Amphioxus* and contains the rudiment of a primitive intestine. In fact, on consideration it becomes evident that, taken alone, there is no more to be said in favour of the view that the tail of Ascidians represents the trunk of *Amphioxus* than there is for the view that it is merely an organ of locomotion homologous with the tail of Vertebrates and the post-anal region of *Amphioxus*.

If the tail of the Ascidian tadpole was primitively segmented, as most authors seem to think, or represents only one segment, as Seeliger (31) thinks, there is in either case no more reason, on this or that account, for regarding the endodermic cord in the tail as representing a rudimentary intestine than for regarding it as the remains of a post-anal gut. The latter was the view which Balfour held (1, p. 634), and is most probably

correct, the post-anal gut being typically in many of the higher Vertebrates—e. g. Selachians—that portion of the enteric cavity into which the neurenteric canal opens, just as it is in the Ascidians.

In *Amphioxus* the neurenteric canal, according to Hatschek (15), persists much longer than in the Ascidians, but the post-anal tract of the body does not grow out until after its closure. In Ascidians the neurenteric canal, as shown by Kowalevsky, and as I have seen by sagittal sections through embryos of *Cynthia papillosa*, becomes obliterated at a very early stage, namely, as soon as the tail commences to grow out, this being also the time at which the curvature of the embryo begins.

The tail, therefore, of the Ascidian tadpole is a solid outgrowth from the trunk involving the nerve-cord, notochord, lateral mesodermic bands, and a solid one-layered cord of endoderm-cells. The latter, as Kowalevsky (21) discovered, become converted into blood-corpuses, and not, as Balfour says (p. 634, loc. cit.), probably by inadvertence, into blood-vessels.

If reference be made to Davidoff's (8) pl. xxi, fig. 54, the contrast between the tail and the trunk in the embryo of *Distaplia magnilarva* will be found to be particularly striking.

With reference to the tail of the larva of *Phallusia mammillata*, Kowalevsky says (21, p. 112), "Er wächst als eine einfache Verlängerung des Hinterendes, immer in der Längsrichtung zum Embryo; also ganz in derselben Weise und Richtung wie der auswachsende Schwanz der Wirbelthiere."

The extreme probability from physiological considerations that the intestine of Ascidians is homologous with that of *Amphioxus*, together with the fact which I believe to have proved above, contrary to the opinion of van Beneden and Julin, that the pharynx or branchial sac of the Ascidians is essentially homologous with that of *Amphioxus*, would appear to render any opposition to the view that the tail of the Ascidian tadpole is a new tail and not an old trunk, gratuitous. In making use of the expression "new tail," I refer to the

fact that it has undoubtedly been specially elaborated in the Ascidians to serve as a larval locomotor organ. In *Amphioxus*, although there is a post-anal portion of the body, there is no tail *sensu stricto*, locomotion being effected by serpentine movements of the whole body.

In view, therefore, of the above considerations I regard the tail of the Ascidian tadpole as homologous with the tail of Vertebrates generally, and the conclusions to which Oscar Hertwig has recently come (19) as to the nature of the Vertebrate tail must be taken as applying equally well to the tail of the Ascidian tadpole.

Hertwig says (p. 457), "Wir finden in seiner Zusammensetzung nur dorsal gelegene Organe betheiligt, Nervenrohr, Chorda, Ursegmente, während Leibeshöhle, Geschlechtsorgane, Nieren, sich nicht in ihn hinein fortsetzen. Ob wir von einem wirklichen Schwanzdarm reden dürfen, erscheint mir fraglich. Allerdings verlängert sich das innere Keimblatt als ein Strang in die Schwanzanlage hinein, als eine Ausstülpung der Beckendarmwand. Es scheint aber meist nicht zur Ausbildung einer Höhlung zu kommen und später schwindet der Strang und löst sich in andere Gewebe auf. Bei keinem Wirbelthier wird er wohl als Darm functionirt haben, so dass ich vorschlage, den Namen Schwanzdarm ganz fallen zu lassen und ihn durch die zu keinen falschen Vorstellungen führende Bezeichnung 'Entodermstrang des Schwanzes' zu ersetzen."

How then, considering the different topographical relations in the two cases, can the Ascidian intestine be homologous with that of *Amphioxus*? In answer to this question I can only apply the principle which Lang (25) applied in his discussion of the relations between *Cephalodiscus* and *Balanoglossus*, and say that the Ascidians are forms allied to *Amphioxus* which have adapted themselves to a sessile habit of life (*festsitzende Lebensweise*), this adaptation leading, as in so many other cases, to a U-shaped alimentary canal. In many cases, e. g. *Pyrosoma*, &c., the sessile habit has been secondarily exchanged for a pelagic one.



As shown by Harmer (17) the resemblance between the organisation of *Cephalodiscus* and *Balanoglossus* is an astonishingly close one, the main essential difference being in the shape of the alimentary canal in the two forms, but it has not yet been suggested that the intestine of *Cephalodiscus* is not homologous with that of *Balanoglossus*. In the familiar instance of *Phoronis* we have a straight intestine in the larva and a V-shaped one in the adult, the transition from the one condition to the other being readily observable.

The relationship of the Ascidians to *Amphioxus* seems to me to be perfectly analogous to that between *Cephalodiscus* and *Balanoglossus*, as the tabular scheme given below will show.

The homology of the intestine of the Ascidians with that of *Amphioxus* having now been established, at least on a basis of probability, it is interesting to note that there is also a caecal diverticulum of the former which would correspond with the so-called hepatic caecum of the latter. The origin of this caecum was first described by Krohn (23) in the case of *Phallusia mammillata*, but without figures, and he made the singular mistake of supposing that it was at first solid. He says (p. 331), "Sehr früh . . . zeigt sich am Anfange des Darmes gleich hinter dem Magen ein cylindrischer, gegen sein freies Ende hin etwas keulenförmig verdickter, durchweg homogener Fortsatz [later on he uses the term solid] der quer zur linken Seite bis in die Nähe der hier gelegenen Endportion des Darmes sich erstreckt." It then begins to branch dichotomously, and becomes the pyloric gland of the adult.

In *Ciona*, as a matter of fact, this caecum arises as a simple blind hollow outgrowth from the stomach, just at the point where the intestine leaves the latter. It probably commences to grow out at the stage represented in fig. 1, but at any rate is clearly visible in the succeeding stages (figs. 2—5). Fig. 19 is a ventral view showing the caecum growing out as a diverticulum of the stomach, with a distinct lumen lined by a columnar epithelium. In the next stage (figs. 3 and 4) the caecum, which, as stated by Krohn, follows the course of the

intestine, bifurcates at its distal extremity, this being the introduction to an extremely complicated system of branching, which occurs at first to a certain extent dichotomously, but the mode of branching is marked at a later stage by the occurrence of numerous anastomoses between the various branches. The epithelium of the cæcum, or, as it is called after it has commenced to ramify, pyloric gland, soon loses its original columnar character, and the wall of the gland then consists of a thin transparent membrane which is presumably lined by a flat epithelium. The branches of the gland grow in such a way as to embrace in a finger-like fashion the intestine throughout its whole course from the stomach to near the level of the anus.

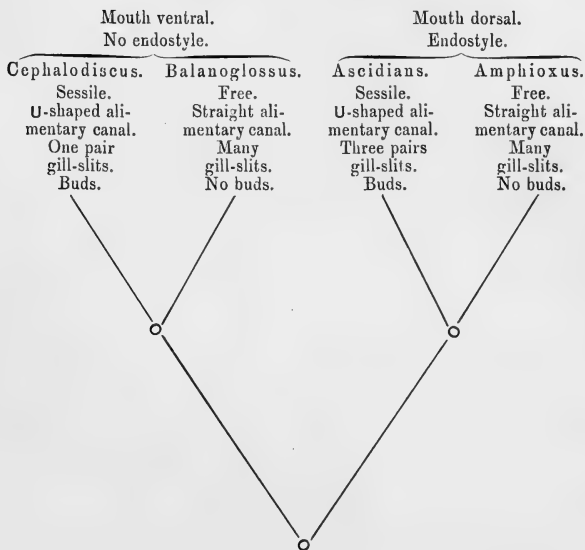
The topographical relations of the cæcum or pyloric gland of Ascidians are different from those of the cæcum of *Amphioxus*,—with the point of agreement, however, that they both lie on the left side and are directed forwards.

If now the intestine of *Amphioxus* be imagined to be doubled upon itself, the topographical relations of the cæca in the two cases would be essentially identical.

In view of these considerations, and remembering what has been said above as to the curvature of the intestine in the Ascidians, I think it may be stated categorically that the pyloric gland of the Ascidians is homologous with the hepatic cæcum of *Amphioxus*.

## 7. Scheme of the Relations of the Protochordata, with Remarks on Appendicularia.

The following diagram will give a bird's-eye view of the relations which I imagine to exist between the various groups of the Protochordata.



The form which might appear at first sight to interfere with the harmony of the above scheme is Appendicularia. Most authors (see Seeliger, 31, and Herdman, 18) agree in regarding Appendicularia as representing more or less the ancestor of the Ascidians.

From what has been said above, however, about the U-shaped alimentary canal, it would follow that Appendicularia came into existence after the acquisition of this curved intestine; in other words, that Appendicularia is at any rate less primitive than the most primitive sessile Ascidians. Seeliger agrees with van Beneden and Julin in regarding the atrial cavities of the fixed Ascidians as homologous with the two branchial tube-like apertures or atrial canals of Appendicularia, and this is undoubtedly correct. In Appendicularia, as is well known, there is a pair of tubular gill-slits but no

atrial expansions. But, as we have seen above, the atrial cavities of the Ascidians are special structures, and not merely parts of a primary pair of gill-slits, just as is the atrial chamber of *Amphioxus*, with which, as I have shown, the former are probably homologous.

The condition of the atrial cavities in *Appendicularia* points therefore, rather to a reduction from a more highly developed condition. There are many other points in the anatomy of *Appendicularia* which show a reduced rather than a primitive character. For instance, the condition of the hypophysis, consisting as it does of a simple funnel-shaped pit extending from the pharynx to the base of the brain, is an undeniable indication of secondary reduction which will be appreciated from an account of the nervous system, which will form the second of "these Studies," and is closely paralleled by what occurs in many compound Ascidians, where the reduction is never doubted. Again, the heart of *Appendicularia* has more the appearance of a reduced than of a primitive organ. Finally, the so-called vertebration of the tail of *Appendicularia* (Langerhans, 26, and Lankester, 27) presents nothing that is not readily intelligible on the view that *Appendicularia* has acquired its pelagic life secondarily, when one would expect to find the muscular and nervous system of the tail, which has now become a permanent organ, in a higher state of elaboration than in the tails of the true larvæ which only last for a few hours.

It results from these considerations, therefore, that *Appendicularia* is probably not a primitive form, but represents a larval Ascidian which has secondarily become pelagic and progenetic.

#### 8. The Longitudinal Muscles of *Ciona*.

The longitudinal muscles of *Ciona* have apparently the same primary characteristics as those of *Clavelina*, as described by Seeliger, but they appear at a much later stage.

Seeliger says (*loc. cit.*, p. 43), "Interessant ist das Auftreten der Längsmuskulatur noch im freischwimmenden Lar-

venstadium, wenn also von einer Rückbildung im Schwanze keine Spur ist."

In *Ciona* I have noticed the first rudiment of the longitudinal musculature at a stage a trifle later than that represented in figs. 2 and 3. The first muscular band proceeds from the base of the atrial siphon of each side, and seems to be at first continuous with a portion of the sphincter muscle of the siphon.

Very soon, however, it becomes quite independent of the latter and extends in length, and finally consists of a single longitudinal band bifurcated anteriorly, one branch proceeding to the region of the buccal siphon, and the other to the anterior region of the atrial cavity (fig. 5). Later on new muscular bands arise, and at a stage with six transverse rows of stigmata the longitudinal bands, about seven in number, are distributed over the body-wall on each side in a spreading, tree-like fashion; but posteriorly they all converge together, to be inserted at a definite point on each side of the stolon of fixation, which was the præoral lobe before the change of axis, near to its base of attachment to the body of the Ascidian.

By means of these longitudinal muscles the young *Ciona* can bend itself double; that is to say, it can contract itself ventralwards, so as to lie approximately at right angles to the fixing stolon. The formation of these longitudinal muscles is the first commencement of the muscular mantle of the adult.

#### 9. Pericardium and Heart of *Ciona intestinalis* and *Clavelina lepadiformis*.

I am able to confirm van Beneden's and Julin's account of the endodermal origin of the pericardium in Ascidians, and of the absence of an endothelium in the wall of the heart.

In *Ciona* the pericardium arises at a later period than in *Clavelina*, and it is only with a knowledge of what occurs in *Clavelina* that the endodermal origin of the pericardium could be affirmed for *Ciona*. I have seen the epicardium in *Clavelina* which was described by van Beneden and Julin, but no trace

of such an organ in *Ciona*, although it was held as probable by these authors that it occurred in all Tunicates (7, p. 300).

Figs. 25 and 27 show the first origin of the pericardium in *Clavelina lepadiformis*. From the ventral wall of the pharynx in the pericardial region a single layer of cells is produced by some sort of delamination, but whether through special cell divisions or through the separating out of individual cells I could not exactly determine, but incline to regard the latter as the method. Its endodermic origin is, therefore, undoubted, since it arises at a stage before the ectoderm has sprung away from the endoderm to give rise to the body-cavity between these two layers. The mesoderm, therefore, which, as shown in fig. 25, lies dorsally on each side of the nerve-tube, can have no part in the origin of the pericardium.

In *Ciona* the first appearance of the pericardium presents an essentially similar aspect to that described for *Clavelina*, but on a much smaller scale, and at a later period of the development, when a body-cavity is already present. As for the actual double nature of the pericardial "ébauche" at the very first, I am not able to confirm van Beneden and Julin, as my figures will show; but I may point out that their figure (7, pl. ix, fig. 1) representing the earliest stage of the pericardium is drawn from an optical section. For the further development of the pericardium and heart in *Clavelina* I have nothing essential to add to the account given by van Beneden and Julin.

The first sign of the pericardium in *Clavelina* occurs at a very early stage of development, before any trace of the atrial involutions is present, and before the appearance of pigment in the cerebral vesicle; and the statement of Seeliger (31) that it arises at a comparatively late period, after the formation of the atrial involutions and the appearance of pigment in the brain as a hollow evagination from the ventral wall of the branchial sac, is quite erroneous. Later on, the at first solid "ébauche" of the pericardium acquires a double lumen, but the septum between the two lumina is apparently never complete, and soon disappears, and the heart then arises as an

invagination of the dorsal wall of the pericardium (cf. van Beneden and Julin, 7).

In *Ciona*, on the contrary, the septum dividing the two halves of the pericardium is quite complete, and does not break down, and the heart forms by a splitting apart of the two layers composing the septum (figs. 12 and 30). Later on striated muscular fibres make their appearance on the inner surface of the cellular membrane which constitutes the wall of the heart, being apparently the product of the cells composing it. The dilated portions of these myo-epithelial cells containing the nuclei project towards the cavity of the pericardium, while the actual lumen of the heart is bounded by muscle-fibres alone, with no trace of an endothelium.

In view of the origin and structure of the heart of the Tunicata, as well as on account of its remarkable and universal recurrent action and the absence of a heart and pericardium in *Amphioxus*, I am disposed to agree with van Beneden and Julin that it is a special organ in the group of the Urochorda, and is not homologous with the heart of the higher Vertebrates.

#### 10. Summary of Principal Results.

(1) The first four primary stigmata of *Ciona intestinalis* are developed from one primitive gill-slit; II and III are formed by constriction from I and IV; and the latter represent the two halves of one slit separated by the precocious development of a tongue-bar.

(2) Three pairs of gill-slits, in the guise of six primary stigmata, are represented in *Ciona* and other simple Ascidians.

In *Ciona* the innumerable branchial stigmata of the adult are derived by subdivision from these six primary stigmata, and not by new perforations.

(3) The endostyle of *Ciona* is at first quite anterior in position, lies in a dorso-ventral direction in front of the mouth, and its primary long axis is at right angles to its definitive long axis.

(4) The cavity in the fixing stolon is the præoral or anterior

body-cavity, and contains loose mesoderm-cells derived from the two lateral mesodermic bands.

(5) The position of the præoral lobe (fixing stolon), which, as the name indicates, is at first quite anterior, becomes reversed by the rotation of the body of the Ascidian through an angle of  $90^{\circ}$ .

(6) In *Clavelina* it can be observed that the atrial involutions occur at the hinder extremity of a longitudinal groove on each side, the groove being of a very appreciable length, and gradually flattening out from behind forwards.

(7) The walls of the atrial cavities of Ascidians are essentially ectodermic, there being no difference in this respect between the somatic and visceral walls.

(8) The pyloric gland of Ascidians arises as a simple hollow cæcal diverticulum from the stomach at the point of junction between stomach and intestine, and is at first lined by a columnar or cubical epithelium.

(9) The pericardium of Ascidians (in confirmation of van Beneden and Julin) arises from the endoderm of the branchial sac, and the heart has no endothelium.

(10) The heart of *Ciona* arises by the splitting apart of the two layers of the septum which primarily divided the pericardium into two halves.

(11) The præoral lobe (fixing stolon) serves for the common insertion of all the longitudinal muscles of *Ciona*.

(12) The development of *Clavelina* as a whole, in comparison with that of *Ciona*, is greatly modified in the direction of abbreviation. This is to be correlated with the facts that the embryonic development of *Clavelina* takes place in the peribranchial cavity, and that the eggs contain a great deal more yolk than those of *Ciona*.



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## EXPLANATION OF PLATES XXX &amp; XXXI,

Illustrating Mr. Arthur Willey's paper, "Studies on the Protochordata."

*List of Reference Letters.*

*a. d.* Adhering disc. *a. g.* Atrial groove. *ant. b. c.* Anterior body-cavity. *at. c.* Atrial cavity. *atp.* Atriopore. *br.* Brain. *br. c.* Branchial cavity. *br. t.* Branchial tract. *cer. ves.* Cerebral vesicle. *cer. ves. res.* Histolytic residua of cerebral vesicle. *cor. c.* Coronal circlet at base of buccal tube. *ect.* Ectoderm. *end.* Endostyle. *h.* Heart. *hyp.* Hypophysis. *int.* Intestine. *l. m.* Longitudinal muscle. *m.* Mouth. *mes. b.* Mesodermic band. *n. c.* Nerve-cord. *nch.* Notochord. *n. hy. p.* Neuro-hypophysial pore. *n. hyp. c.* Neuro-hypophysial canal. *æs.* Œsophagus. *p. d.* Posterior dilatation of nerve-cord, or "Rumpganglion" of Kowalevsky. *pc.* Pericardium. *pr. g.* Pericoronal groove. *pr. l.* Præoral lobe. *py. g.* Pyloric gland. *st.* Stomach. *st'. st''.* Stigmata. *tr.* Remains of tale. *t. b.* Tongue-bar. *t. b. v.* Transverse blood-vessel. *I, II, III, IV.* First four primary stigmata of *Ciona*.

## PLATE XXX.

All the figures on this plate relate to *Ciona intestinalis*.

FIG. 1.—Left side of larva just before fixation. The anterior body-cavity between the three adhering papillæ and the endostyle, is filled with mesoderm. At the base of the tail are also masses of mesoderm which are partly composed of cells produced by transformation of the endodermic cells of the tail. In the middle of the body the lumen of the branchial sac is reduced almost to nothing by the pressure upon it of the large cerebral vesicle containing the eye and otolith. Drawn from living object. Zeiss, 2, D.

FIG. 2.—Right side of young *Ciona* just after fixation. The two apertures which are present in the branchial tract are very indistinct at this stage, and are represented by the two dark lines towards the centre of the branchial tract. This is the most important stage for becoming acquainted with the primary topographical relations of the various parts. Drawn from a preparation. Zeiss, 3, C.

FIG. 3.—Left side of young *Ciona* in which the rotation of the body about the præoral lobe has commenced. The transition from the larval to the adult condition of the nervous system will be fully discussed in a succeeding "Study." From a preparation. Zeiss, 2, D.

FIG. 4.—Right side of young *Ciona* of same age as preceding. At *py. g.* and *int.* are seen the openings of the pyloric gland and intestine into the stomach. Preparation. Zeiss, 2, D.

FIG. 5.—Left side of young *Ciona* in which the change of axis is completed. A small intermediate slit is being constricted off from *IV*. The branching of the pyloric gland should be noted. From a preparation. Zeiss, 2, C.

FIGS. 6—10.—Different stages in the formation of the intermediate stigmata *II* and *III*. All from living object.

FIG. 6.—Stigmata of left side before the appearance of the intermediate stigmata. Zeiss, 4, B.

FIG. 7.—Ventral extremities (i. e. nearest endostyle) of stigmata of left side at a slightly later stage than preceding. The two stigmata are in connection with one another. Zeiss, 4, D.

FIG. 8.—Similar view to preceding at still later stage. Zeiss, 3, C.

FIG. 9.—Stigmata of right side at the stage of the actual formation of the intermediate stigmata. *III* has already become independent, while *II* is still a part of *I*. Zeiss, 4, B.

FIG. 10.—Stigmata of left side of same individual as preceding. Same magnification.

FIGS. 11 and 12.—Oblique transverse sections through branchial sac of young *Ciona* of the stage shown in Fig. 2 to show the primary relations of the two first-formed branchial apertures. In Fig. 12 the atrial aperture is cut tangentially. In the same Fig. the pericardium is included in the section where it is seen to lie to the left of the middle line in the section, that is, on the right side of the body of the larva. Zeiss, 3, D.

FIG. 13.—Horizontal section through young *Ciona* of the stage of Figs. 3 and 4. The section only passes through the actual atriopore on the right side (left of the section). On the other side the atriopore is cut tangentially, as also is the branchial aperture (*IV*) on each side. The section is slightly oblique, and is of value from a topographical point of view. Zeiss, 3, D.

FIG. 14.—Stigmata of left side showing the addition by fresh perforation of No. 5. Zeiss, 4, B.

FIG. 15.—Transverse section through the præoral region of a tadpole of *Ciona* of the stage represented in Fig. 1. The endostyle is cut vertically and longitudinally, since its long axis at this and the next stage is dorso-ventral. Zeiss, 3, E.

FIG. 16.—An abnormal case in which the primary stigmata (*I* and *IV* of the left side) had fused together at their ventral ends, i. e. the ends towards the endostyle. The two stigmata of the right side of this individual were independent of one another. From living object. Zeiss, 3, C.

## PLATE XXXI.

FIG. 17.—Secondary stigmata of the right side of young *Ciona* illustrating their production by subdivision of the primary stigmata. From living object. Zeiss, 2, B.

FIG. 18.—One transverse row of secondary stigmata at a later stage than preceding to illustrate their change of axis. From living object.

FIG. 19.—Ventral view of stomach, intestine, and pyloric gland, in optical section, at a stage intermediate between Figs. 2 and 3, to show that the primary nature of the pyloric gland is that of a cæcal diverticulum of the pyloric region of the stomach. Zeiss, 3, D.

Figs. 20—24 and Fig. 30 relate to *Ciona intestinalis*, and are all drawn from living object, and Figs. 25—29 to *Clavelina lepadiformis*.

FIG. 20.—Stigmata of right side in an abnormal specimen in which *II* and *III* had fused together and were represented by one peculiarly shaped aperture. Between *I* and *IV* are also shown two papillæ (*x, y*) which project into the branchial cavity, and from which the formation of the longitudinal and transverse blood-vessels proceeds. Zeiss, 3, C.

FIG. 21.—Stigmata of left side of a young *Ciona* showing addition by fresh perforation of No. 6. Zeiss, 4, B.

FIG. 22.—Portion of two transverse rows from the branchial sac of a young adult *Ciona* with eleven rows of stigmata, showing the origin of the successive transverse rows by subdivision from pre-existing rows, and not by fresh perforations. Zeiss, 2, C.

FIGS. 23 and 24.—Two stigmata from the branchial sac of same individual as preceding, exhibiting unequal division. In Fig. 24, when the constriction at the lower end of the slit is completed, the resulting smaller aperture might be thought to have arisen by fresh perforation, but it does not do so, as the figure shows. Zeiss, 2, C.

FIG. 25.—Transverse section through branchial region of a very early larva of *Clavelina* before the appearance of the atrial involutions or of pigment in the brain, and while the neuroporus is still present, to show first origin of pericardium. Zeiss, 2, D.

FIGS. 26 and 27.—Transverse sections through a rather older larva of *Clavelina*, to show the atrial grooves, pericardium, and body-cavity, as compared with Fig. 25. Fig. 26 passes through the first rudiment of the eye in the brain, and Fig. 27 passes through the so-called post-vesicular ganglion, in which the ventral wall of the neural canal is much thickened. Zeiss, 2, D.

FIG. 28.—Rather oblique transverse section through a still older larva of *Clavelina*, showing on the left side (right of the section) the opening of the neuro-hypophysial canal into the branchial sac, and on the other side the

relations of the atrial cavity to the stigmatic region of the branchial sac. Zeiss, 2, D.

FIG. 29.—Transverse section through a larva of *Clavelina* older than the preceding. The neuro-hypophysial canal lies closely applied against the left wall (right of the section) of the cerebral vesicle. The two atrial cavities are shown lying against the folds into which the stigmatic region of the branchial sac is thrown. The endostyle here and in preceding figure is also cut transversely. Zeiss, 2, D.

FIG. 30.—Optical section, showing mode of formation of the heart in *Ciona* by a splitting apart of the layers of the pericardial septum. Zeiss, 4, D.

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A NEW SPECIES OF MONILIGASTER FROM INDIA. 361

## Description of a New Species of *Moniligaster* from India.

By

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Oxford.

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With Plate XXXII.

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IN June of the present year, 1892, my friend Professor Bell sent me a specimen of a worm collected on the Nilgiris by Mr. T. R. Henderson, which forms a new species of the genus *Moniligaster*, Perrier, and for which I propose the name *M. indicus*.

At first I imagined that it would be one of Dr. Bourne's species, but it agrees with none of them in the few—the very few—characters given by him; he practically only gives the position of the gizzard in his seven species, and even this in such a way as is scarcely sufficient for identification; for he does not state how many constrictions are present, i.e. whether there is a separate portion of gizzard to each somite passed through. We await impatiently a more detailed description of the several interesting species, especially of *M. sapphirinaoides*, which has been so long promised to us.

The position of the various genital pores in *Moniligaster* by the repeated contributions of Mr. Beddard (1, 2, 3, 4, 5), as well as by those of Rosa, Bourne, and Michaelsen, has now become definitely ascertained; and I much regret that my figure representing the genital organs of this genus, published in my "Attempt to classify Earthworms," on p. 295, is

wrong, owing to my having followed Dr. Horst's account of *M. Houtenii*, which appears to have the organs posterior to their position in the other species.

This octochætous, meganephric genus is distinguished, as has been pointed out by recent writers, by the following external characters:

- (a) The male pores (a single pair) between Somites x and xi.
- (b) A single pair of spermathecal pores between Somites vii/viii.
- (c) A pair of oviducal pores between Somites xi and xii.
- (d) Nephridiopores in line with the dorsal (or outer) couple of chætæ.

Internally the following features may be taken as characteristic:

- (e) The gizzard constricted by one to four narrow, fibrous, annular bands at the septa, giving the "moniliform" appearance indicated by the generic name.
- (f) Absence of calciferous or other enteric diverticula.
- (g) A single pair of spermathecæ in Somite viii, with very long, narrow ducts.<sup>1</sup>
- (h) A single pair of sperm-sacs, supported by the septum between Somites ix and x, but belonging to the former; the sacs are independent, and each encloses the testis and the spermiducal funnel.
- (i) A single pair of atria (prostates), of varied size and shape.
- (j) A large ovisac, which may extend through several somites.

*M. indicus*, n. sp., which forms the subject of the present paper, may be diagnosed as follows:

- (a) Length  $5\frac{1}{2}$  inches (13.75 centimetres).
- (b) Body consists of about 150 somites.
- (c) Ventral intersetal space is rather wider than the lateral space (or, as a formula, I—I > II—III).

<sup>1</sup> The apparent exception in *M. japonicus*, Mich., requires further investigation.



- (d) The septa VI/VII, VII/VIII, VIII/IX are thick, but not so thick as in other species.
- (e) Gizzard occupies Somites XIII, XIV, XV, XVI, with annular bands separating the four muscular regions.
- (f) Atrium (prostate) large, spherical, lying in Somite XI.
- (g) Spermatheca nearly spherical; the duct opens to the exterior through a muscular sac, subdivided into an anterior and a posterior lobe by the septum VII/VIII.

DESCRIPTION OF *M. INDICUS*, N. SP.

I. External Anatomy.

The size of the present species has just been stated, and it appears to be of some importance, as there is a great range amongst the species; for example, *M. japonicus* and *M. Barwelli* is only 28 mm., *M. Deshayesi* 150 mm., whilst *M. Houtenii* attains the length of one and a half metres. Of Bourne's seven species, only *M. ruber* is definitely measured, its length being 100 mm.

As in all other species, with the exception of *M. sapphirinaoides*, no clitellum was present; the worm was evidently not quite sexually mature, as deduced from the condition of the genital organs. As Beddard (5) and myself (6) have previously suggested, the clitellum may be a more transient structure than in other macrodrilous Oligochæta; and it would be very interesting, and even important for systematic purposes, to know the minute structure of the clitellum in Bourne's species. Does it agree more closely with the microdrilous clitellum, or is it several cells thick, as in *Lumbricus*, &c.?

The colour of the worm during life is unknown to me. In the spirit specimens the dorsal surface is very much darker—a greeny brown—than the ventral and lateral surfaces; there is a very sharply marked line of separation between the two colourings, and not a gradual paling out as in many other worms.

The worm is rather flattened, and the posterior end, which is lighter in colour, tapers off to a point, apparently in the same sort of way as in *M. robustus*, A. G. B., for which species I at first took it; but in that species the gizzard differs in extent and position.

The prostomium is rounded, not embedded in the peristomium at all, but is retracted in the same sort of way as Beddard (5) found in his species.

The somites are separated by deep intersegmental grooves; the first and second, as Beddard points out in his last contribution (5) to the anatomy of *M. Barwelli*, are very short, the two together barely reaching the length of the third somite.

The chætæ are of the normal shape (fig. 2), and do not agree with those figured by Horst for *M. Houtenii*, nor with those figured by Beddard (5); they are small, as in the other species, measuring 2 mm.; the free end is rather more hooked than in *M. Barwelli*. All four couples of chætæ in the present species are on the ventral surface, so that none are visible from above. Their arrangement, as I have inferred above, is of some specific importance. In all species of *Moniligaster* the individuals of each couple are very close together, and the space between the two ventral couples—i. e. the ventral space—may be equal to, greater than, or less than the lateral space or distance between the dorsal and ventral couples of either side (see fig. 1).

Thus in *M. japonicus*, Mich., *M. Beddardii*, Rosa, the ventral space (V) = the lateral space (L); in *M. Barwelli*, *M. unicus*, A. G. B.,  $V < L$ ; in *M. grandis*, A. G. B., as in the present species,  $V > L$ ; whilst in *M. Houtenii*  $V = 2L$ .

In the remainder of Bourne's species no reference is made to this point.

The nephridiopores appear to commence in Somite VI, but on dissection I find nephridia anterior to this.

I failed to discover any dorsal pores, either by means of a lens or by mounting a piece of the body-wall in Canada

balsam; but in other species they are apparent, viz. in *M. Barwelli* and *M. Beddardii*.

The genital pores have the position normal for the genus, and I found it quite easy to recognise all three pairs (fig. 1); with regard to the male pores, however, I was at first deceived by an apparent slit in the hinder part of Somite x; this turned out to be merely a groove (fig. 1, *x*), due, no doubt, to the shrinkage of the large mass of muscle attached here around the atrium. The groove is bounded anteriorly by a fairly prominent ridge, and presented the appearance figured by Beddard (5, fig. 1), and indicated by him as the male pore itself. I find, however, that the true pore does not correspond with the position assigned to it by him for *M. Barwelli*; and in this point I am in agreement with Michaelsen's description of *M. japonicus* (9), where the pore is at the apex of a small tubercle, in front of which is a transverse groove. It is probably a matter of preservation whether the tubercle is prominent or not. My own specimen was very soft and ill-preserved.

The position of the atriopore (fig. 1, ♂) between the dorsal and ventral couples of chætæ agrees with that ascribed to it by previous writers.

The oviducal pores are small but distinct slits in the groove between Somites XI and XII, in line with the ventral couple of chætæ.

The spermathecal pores are larger, and, as in other species, are in line with the dorsal couple of chætæ; in *M. Deshayesi*, however, the pore is stated to be in line with the "inferior chætæ."

## II. Internal Anatomy.

It is to the generative organs that the lumbricologist first turns his attention in opening, or otherwise examining, a worm, and naturally these organs are more engaging, so to speak, in a genus about which such diversity of statement exists, or has till quite recently existed, as to the position of

the various constituents. I have already referred to the uncertainty as to the precise somites to which the different organs belong, which has resulted from the descriptions of Perrier, Beddard, and Horst. But now that a greater number of species are known, some of them of fairly large size, we find Perrier's original statements are correct with regard to the position of most of the genital organs, and that Horst's numbers alone differ by being greater by a single unit. Beddard's original description has been modified by his discovery that his apparent first somite really consists of Somites I and II. The positions attributed to the organs in the species examined by Rosa and Michaelsen, and in the present one, all agree with Beddard's amended and Perrier's original numbers. But nevertheless there still remain certain points on which some discrepancy or uncertainty exists, both with regard to exact position and minute structure. Some of these I hope to clear up, or at any rate to advance, though, owing to the poor condition of the worm, my contribution to the histology of *Moniligaster*—of which we know very little indeed—is very imperfect.

The single pair of sperm-sacs (figs. 3—5) occupies partly Somite IX and partly X. On the animal's left side the sac appeared to be strung up by the Septum IX/X attached round its equator. In reality the septum is pouched, and the sperm-sac, as figs. 3 and 4 will show, projects into Somite IX through the wide aperture of this pouch.

On the right side, however, the pouch was deeper, so that at first sight the sac appeared to lie entirely in Somite X; but I could trace the Septum IX/X behind the sac, and sections show me that the sperm-sac belongs, as Beddard has already suggested, to Somite IX.

Each sperm-sac is nearly spherical, and is not so simple as in *M. Barwelli*, for I find that the cavity is not undivided, as Beddard figures and states, but is traversed by bundles of muscular fibres in different directions (fig. 5, *trab.*), between which lie the groups of developing spermatozoa. The trabecular structure is certainly not so highly developed as

in *Perichæta*, *Lumbricus*, and other genera, but it is as certainly not entirely absent.

Beddard has laid great stress on the simplicity of the sperm-sac in associating *Moniligaster* with the *Microdrili* or "Limicoline section" of the *Oligochæta*. Here, then, we have still another apparent distinctive character between "aquatic" and "terrestrial" *Oligochæta* breaking down, and that within the limits of one and the same genus; and it is gradually becoming more and more impossible to characterise differentially the two groups, for in fact they verge into one another at almost every point.

The two sperm-sacs are entirely independent of one another. Each contains a testis and spermiducal funnel.

The testis (fig. 5) is digitate and attached to the hinder wall of the sac, i. e. to the Septum IX/X. The funnel—we cannot call it a "rosette"—of the sperm-duct is a simple, wide, ciliated tract of the hinder wall of the sac (fig. 5). The cells are tall, and thus readily distinguishable from the flattened cells which elsewhere form the wall around it.

This flat funnel can be seen through the thin wall on dissection, and the sperm-ducts can be seen passing away from it (fig. 4).

As to the point of attachment of the testis, I find that it is independent of the funnel. Rosa figures it, both for *Moniligaster Beddardii* and for *Desmogaster*, attached to the funnel near to its centre. Beddard also in one figure (fig. 8) represents the testis arising from the funnel, whilst in fig. 9 he shows it at its side. In my own sections the testis lies nearer the middle line of the body than the funnel, so that the two structures are not at their best in any one given section. Perhaps Rosa's diagram is in this point merely diagrammatic.

The sperm-duct is very delicate and very greatly convoluted (fig. 4), much more so than is indicated by either Beddard's or Rosa's figures; it more nearly approaches the condition represented by Perrier (pl. iv, figs. 81, 83), though this zoologist appears to have been disinclined to regard the

“*feuilletts blancs*” as forming part of the sperm-duct, for it would, says he, give such an enormous length to it.

I may mention that in Perrier's species the sperm-duct, which is represented as a comparatively thin coiled duct, appears to pass through a mass of isolated white leaf-like structures set round the duct as an axis. A microscopical examination of these “*feuilletts*” showed that they consist of a very fine coiled duct surrounded by a thin membrane (his fig. 83), and I think there can be no doubt, from the condition present in *M. indicus*, that this duct in the “*feuillet*” is part of the sperm-duct itself, and not an appendix thereto. In other species, so far as descriptions go, the duct is not of so great a length. The cells lining the duct are striated as in other worms (fig. 12), but I have never been able to detect hitherto the boundaries of the cells; here, however, they are very plain, and the cells large. In many earthworms the nuclei are flattened, but here, as in aquatic forms also, they are spherical.

In *M. indicus* the greater part—nearly the entire length—of this fine, convoluted sperm-duct lies in Somite IX below the sperm-sac (figs. 4, 5). It passes through the septum near the body-wall, which it enters, traverses the short distance between this septum and the prostate, embedded in the longitudinal muscle, and enters the atrial wall (prostate) at its anterior end (fig. 5); passes along the dorsal wall of the prostate, perforates the glandular coat, and opens into the atrial cavity at the apex of a slight prominence in the wall (figs. 5, 8). This condition of the duct is very similar to that described by Rosa for *Desmogaster doriae*, and so far as the præseptal portion is concerned agrees with Michaelsen's description of *M. japonicus*.

The prostate is a hemispherical structure occupying the greater part of the length of Somite XI, at the anterior margin of which it opens to the exterior; it also encroaches to a slight extent on to Somite X, to which it probably belongs morphologically.

It is about half (linear) the size of the sperm-sac, larger

than the ovoid prostate of *M. Barwelli* and *M. Beddardii*, and unlike these is bound down to the body-wall by special muscles; if it were placed on end with its morphologically dorsal (its actual posterior) end upwards it would resemble the condition in *Beddard's* species. The hemispherical glandular part is seen in sections to be provided with a duct dorso-laterally compressed and underlying the glandular part. In the other species, so far as is described, the prostate is elongated, and is very large and extensive in *M. Deshayesi*.

We have no information as to its shape, which is apparently a good specific character, in any of *Bourne's* species.

There is a very peculiar arrangement of muscles in connection with the atrium which has not hitherto been recorded in any earthworm.

A sheet of muscles, or rather a series of flattened bundles of muscle-fibres, passes obliquely across the body-cavity from their origin in the body-wall above the lateral line to their insertion in the wall of the prostate. On dissection, when the sides of the body are pinned down, this sheet is of course horizontal; in the natural position, however, it is an oblique, transverse sheet, such as exists almost universally in the *Polychæta*, where, however, it is generally in relation with the *chætophores* at its outer end.

In *Somite x*, immediately in front of the atrium, a similar sheet of muscles exists, reaching nearly to the level of the inner *chæta* ventrally, and having the same origin as that in *Somite xi*. In *Somites vii, viii, ix* quite a similar arrangement obtains, though, as we get forwards, the muscle bundles are smaller and smaller.

These recall the "arciform muscles" recently described by *Cerfontaine*<sup>1</sup> in *Lumbricus*, but which pass, not from the lateral to the ventral surfaces, but from one side to the other, inserted at each end at the level of the ventral *chæta*. Another point of difference there is, in that in *Lumbricus* these muscles do not traverse the body-cavity—they are embedded

<sup>1</sup> 'Arch. de Biol.,' x, 1890: "Rech. sur le syst. cutané et sur le syst. musculaire du *Lombric* terrestre."

in the longitudinal muscles of the body-wall. The "arciform muscles" are confined to those somites between the male pore on Somite xv and the hinder end of the clitellum at Somite xxxvii, and serve to produce during copulation the groove on the ventral surface, along which the spermatozoa travel from the male pore of one worm to the spermathecæ (?) of the other.

Now in *Moniligaster*, though we have no knowledge of the mode of copulation, yet there can be little doubt that these oblique muscles are connected with that process. By their contraction they would raise the ventral surface of the body between the male pores and the spermathecal pores, not, as I believe, for the passage of spermatozoa, but to help in holding the two worms together.

The minute structure of the prostate of *M. Barwelli*<sup>1</sup> has been dealt with by Beddard in more than one contribution; in one of these (4, p. 121, pl. xii, fig. 11) he figures a transverse section of this structure, and it will be convenient to refer to this briefly before passing to a consideration of what I find to be the condition in the present species. In *M. Barwelli*, then, the cavity of the prostate (or atrium) is lined by columnar granular cells; outside this is a layer of muscles; this, again, is surrounded by "an external covering composed of large granular cells, which are separated into groups by partitions. Each cell is prolonged into a fine process, which extends at least as far as the muscular wall; indeed, it is difficult to believe that the cells do not in some way or other reach the lumen of the atrium, and there discharge their glandular secretion."

In *M. indicus* the hemispherical glandular portion of the atrium, which portion may be termed the prostate, has a structure differing from that of the more compressed duct leading to the external aperture. The latter is provided with an irregular lumen, lined by a low columnar, non-glandular epithelium, the nuclei of which are oval and occupy the

<sup>1</sup> I shall use the word "prostate" to refer to the glandular wall of the organ, the word "atrium" being employed for the chamber into which the gland-cells and sperm-duct open.



middle of the cell (fig. 10); outside this is a thick coating of muscles in various directions, with of course numerous blood-vessels. But after a short course this simple epithelium gives way to a glandular coat (fig. 11), recalling the structure of the "prostate."

The "prostate" or glandular wall of the atrium (fig. 9), however, is lined by a layer of tall, thin, glandular cells, with nuclei (? at any rate deeply stained structures) placed at the sides of the cells, as if compressed; somewhat similar to, though much narrower than, the epithelium figured and described by Beddard.

The muscular coat, consisting of circular, longitudinal, and oblique fibres, does not immediately surround this epithelium as in *M. Barwelli*, but the two are separated by a considerable area, about twice as deep as the epithelium itself, which appears to be occupied partly by certain longer cells (*gl.*) than the lining epithelium, and partly by the necks of the extra-muscular multicellular glands (see figs. 8, 9).

In a foot-note on p. 573 of his memoir on *Ocnerodrilus*,<sup>1</sup> Beddard refers to the fact, as observed in *M. Barwelli*, that there is "hardly any distinction between a glandular and non-glandular section of the atrium." In the present species, as is shown, there is such a distinction very well marked.

Outside the muscular coat are the groups of glandular cells figured by Beddard. Each group (fig. 9) consists in a section of some eight to ten club-shaped cells, the narrow necks of which pass through the muscular coat, and can be traced in bundles nearly up to the epithelium. Each group is, in fact, a multicellular gland. This arrangement is quite evident in my sections, and the necks or ducts of the glands are quite noticeable, though I have been unable to trace the necks right up to the epithelium; the latter, however, is traversed by narrow clear tubes, resembling ducts, and which differ from the epithelial cells in having no inner boundary (as at *a*, fig. 9). The nucleus of each cell of the multicellular gland is naturally at the bottom, the widest part

<sup>1</sup> 'Trans. Roy. Soc. Edin.,' xxxvi, part 2.

of the cell. But I can give no detailed description of the finer histology owing to the ill-preservation of my material; I can detect granules, as if arranged around vacuoles, but very indistinctly. Outside the glands is a very delicate membrane (*cæ. ep.*), sparsely provided with flattened nuclei (*n. per.*), which I take to be the cœlomic epithelium, and which dips down, for some distance at any rate, between the groups of cells.

In Beddard's figure the muscular coat is made to be continuous, and no indication of "ducts" or communication between the gland-cells and the lumen is represented, though, as the above quotation shows, Beddard expected to find such "ducts." My description of *M. indicus* agrees pretty closely with Rosa's description of the prostate of *M. Beddardii*, and figure relating to the prostate of *Desmogaster*.

Beddard has already (4, p. 125) pointed out the resemblance between the gland (cement-drüse, prostate) attached to the atrium of *Tubificidæ* and the glandular lining of the atrium of *Perichæta* and other earthworms; at the same time he has denied the homology of the gland-cells of *Moniligaster* with those of *Acanthodrilus*, *Perichæta*, and other worms, chiefly, if not entirely, on the ground that in *Moniligaster* and in *Rhynchelmis* there is (according to his observations) no peritoneal membrane surrounding the glands; whilst the position of the gland-cells outside the muscular coat led him to regard these cells as representing the peritoneal membrane. But I have seen what I believe to be the peritoneal membrane both in *M. indicus* and in *Rhynchelmis*; and further, the prolongation of the extra-muscular gland-cells up to the epithelium of the atrium in *Moniligaster* and *Desmogaster* seems to me to point conclusively to the derivation of those gland-cells from that epithelium, in the same way that the "cement-drüse" of *Tubificidæ* has been shown by *Vejdovsky* to be developed as an outgrowth from the lining of the atrium. Therefore probably the "prostate" of *Tubifex* is homologous with the "prostate" (using the word in a narrow sense to mean the glandular cells) of *Moniligaster*.

*Telmatodrilus*, Eisen,<sup>1</sup> one of the Tubificidæ, presents an intermediate condition between the arrangement met with in *Tubifex* and that in *Moniligaster*; for in this worm, instead of the single group of gland-cells communicating with the atrium, as in *Tubifex* and other of its allies, there are eight or ten such isolated groups (fig. 16, *b*) arranged around the upper part of the atrium, that is the "glandular part of the atrium," as I have called it in my description of *Heterochæta*.<sup>2</sup>

If now the atrium were to shrink, so to speak, these isolated groups of gland-cells would be approximated, and there would result a continuous coating of gland-cells, communicating here and there through the muscular coat with the cavity of the atrium, as we find in *Moniligaster* and *Rhynchelmis*.

In other earthworms, such as *Acanthodrilus*, *Perichæta*, &c., the structure of the prostate has been dealt with by Beddard (4); the chief difference from *Moniligaster* being, as I believe, due to the restriction of the muscular coat to the neck of the gland, and the consequently greater compression of gland-cells against one another (fig. 16, *e*).

In the "intermediate condition" (fig. 16, *d*) I have imagined the muscular coat becoming more definitely confined to the "duct," though some of the glands still perforate it; whilst others are in a condition similar to that in *Deinodrilus*, &c.

The spermatheca presents certain interesting features. The nearly spherical or slightly pyriform sac, lying above the œsophagus in Somite VIII, is provided with a very long delicate, shining duct,<sup>3</sup> several times coiled, which passes downwards to reach the body-wall in the anterior of the somite

<sup>1</sup> 'Report of Commissioner of Fish and Fisheries for 1883,' p. 880, pl. i, fig. 1.

<sup>2</sup> "Note on Aquatic Oligochæta," 'Quart. Journ. Mic. Sci.,' xxxiii.

<sup>3</sup> In *M. japonicus* Michaelsen mentions that he found only one "Samentasche" on the left side attached to the body-wall between Somites IX/X. If this is a spermatheca, it differs from the remaining species in being without the very characteristic long duct, as well as in its position.

in a line with the lateral chætæ (fig. 3). On dissection there appears to be an accessory gland in front and one behind the point of entrance of the duct into the body-wall, similar to that in many Perichætæ and others; but in reality, as sections show, these two ovoid structures are due to the constriction, by Septum VII/VIII, of a single sac, with thick muscular walls, which opens externally in the intersegmental groove (figs. 5, 13, *cop. sac.*). This sac is lined by a columnar glandular epithelium, the nuclei of the cells being at their inner ends (fig. 14) similar to that of the spermatheca itself. The spermathecal duct perforates the dorsal wall of this sac at about its central point, where it is nipped by the septum, and owing to its cubical epithelium can readily be traced; the wall of the duct is very thick, being provided with a circular coat of muscles (fig. 15). It appears to me that possibly this sac is a copulatory sac in the true sense of the word, and that the muscular duct of the atrium is to some slight extent eversible, and is received into the copulatory sac.

Amongst the other species, in which the genital organs have been described, an arrangement at all comparable to this occurs only in *M. Deshayesi*. All recent authors agree that Perrier's interpretation of the organs lying in Somite VII as "prostates" connected with an anterior pair of testes is erroneous. Horst regarded these pyramidal glandular organs as "spermathecæ," the ducts of which unite to form a short common duct, receiving a more delicate "vas deferens" (Perrier). But Beddard has conjectured, rightly as it appears to me, that these glands are comparable to such accessories of the spermatheca as are usual amongst the Perichætidæ.

Perrier's fig. 79, pl. iv, represents a section through one of the pyramidal organs of Somite VII, which shows its glandular character, but an absence of muscle in its wall. In the present species the glandular lining is relatively thin, the muscular coat being very greatly developed. But in *M. indicus* no ducts such as Perrier figures exist. I would suggest that the wide bilobed sac in my worm corresponds to these pyramidal organs. In *M. Deshayesi* a greater differentiation has occurred, the

glandular portion being distinctly marked off from the muscular duct, whereas in *M. indicus* no such separation exists. If the bilobed structure of my worm were to be drawn out in such a way as to produce a couple of glands communicating by short ducts with a common duct, much the same arrangement would be produced.

The ovary closely resembles that represented by Rosa for *M. Beddardii*, and occupies the space between the displaced septum  $x/xi$  and that between Somite  $xi$  and  $xii$ , being therefore in Somite  $xi$ .

The oviduct is provided with a wide expanded funnel (fig. 8), very much as Perrier describes it; it is quite independent of the ovisac—that is, this latter structure opens into the cœlom outside the edge of the funnel, and not through it, as in some earthworms. Nor is there any reflected portion of the funnel entering the sac, as I have recently described in *Sparganophilus*.<sup>1</sup>

The ovisac is not so extensive as it is in several of the species, e. g. in *M. minutus*, A. G. B., where it traverses Somites  $xii$ — $xv$ , but it is readily visible in dissection as a narrow white structure lying in Somite  $xii$ , and attached to its anterior septum.

The worm was not fully mature. I find no spermatozoa in the spermathecæ; those in the sperm-sacs are none of them fully formed, except some attached to the funnel of the duct. At first I took the muscular trabeculæ for spermatozoa, but by following their course from section to section I soon ascertained that this was not the case.

The ova in the ovary are quite small, and there are none in the ovisac.

I will now pass to the consideration of a few other points in the anatomy of *M. indicus*.

The Body-wall.—The usual muscular coats are present, but they show a feature which has hitherto not been noticed; the lateral regions both of the circular and the longitudinal layers are very much thicker than the dorsal and ventral

<sup>1</sup> "A British Aquatic Rhinodrilid," this Journal, November, 1892.

regions. In *Plutellus Perrieri*<sup>1</sup> I have noticed a somewhat similar thickening of the ventral body-wall, due, however, to the greater development of only the longitudinal coat. The longitudinal coat is, in *Moniligaster indicus*, interrupted by four continuous grooves, visible on simple dissection. It is in these grooves—marked *i. ch.* and *o. ch.* in fig. 7—that the chætophores are situated. On the ventral side of the lower groove is a special bundle of longitudinal muscles (*v. long. mus.*) which appears to run throughout the greater part of the worm, though I am not certain whether it extends forwards into the genital region, for I cut only longitudinal sections of this part. The longitudinal muscles exhibit a pinnate arrangement so well known in the group, but only in its thicker portions; it gradually merges into an irregular arrangement dorsally and ventrally (fig. 7).

In some of the anterior somites peculiar bundles of muscles traverse the body-cavity in an obliquely vertical direction, attached at one extremity just within the ventral chætophoral groove, and at the other to the outer part of the dorsal surface (fig. 6). These muscles I have referred to in speaking of the generative apparatus, and they are represented as seen in a dissected specimen in fig. 3. These oblique muscles are limited to Somites VII to X, for those which lie apparently in Somite XI, morphologically, as I believe, belong, like the atrium with which they are connected, to the preceding somite. I have referred above to the suggested purpose of these muscles.

The septa present the same variability in thickness which has been remarked in so many worms. In the present species the three septa, VI/VII, VII/VIII, VIII/IX, are thick and muscular, the remainder thin (figs. 3, 5). In other species of *Moniligaster* we find the same three, or an additional one in front thickened.

I believe none of the septa are absent, as Bourne states is the case for some of his species. Certainly on dissection

<sup>1</sup> "Description of Three New Species of Earthworm," 'Proc. Zool. Soc.,' 1892, p. 136.

some of the septa appear to have been lost; this is due to the peculiar shifting of the septa first pointed out by Horst and by Rosa.

The three thickened septa are nearly in their normal position, but are inserted in the body-wall slightly behind the inter-segmental groove. The same is true for Septum IX/X, which is bagged out by the sperm-sac. Septum X/XI is, however, thrown back a whole somite; it is confluent with the Septum XI/XII along a certain part of its course laterally (fig. 5), but becomes separate towards the middle of the body, and is there inserted into the body-wall just in front of the groove XI/XII. At the level of the atrium, however, it can be traced below this organ to its insertion just behind the groove X/XI; that is, in a position corresponding to that of the preceding septa (fig. 8). The Septum XI/XII, again, is inserted in a normal position above the groove. There are, then, no septa absent in the present species.

Rosa's diagram of the arrangement in *M. Beddardii* shows it to be much less abnormal than in the present species.

In *M. Houtenii*, allowing for the fact that the various organs are situated one (testes, spermathecae) or two (ovary, ovisacs) somites further back, the arrangement is the same; i. e. Septum X/XI is attached to body-wall about the middle of Somite XI, Septum XI/XII to the body-wall near the hinder part of Somite XII, Septum XII/XIII close to hinder boundary of Somite XIII and immediately in front of Septum XIII/XIV, which has almost the normal position.

Neither Beddard nor Michaelsen makes any remarks about this shifting of the septa, which may turn out to be a normal feature for the genus; and as it occurs too in *Desmogaster*, perhaps even for the family.

The nephridia closely agree with those of *M. Houtenii*; they commence in Somite IV, and are continued in each somite in a regular manner, and the fact that only one pair of nephridia occur in the wide stretch between Septum IX/X and that which I have referred to as Septum X/XI confirms me in this interpretation.

The nephridia in Somite iv are slightly larger than those immediately following, as Beddard has noted for *M. Barwelli*, the convoluted tube being thicker and whiter. I have not been able to assure myself as to the external opening, whether it is in the body-wall or in the stomodæal wall, but I believe the former.

The nephridia are provided, as in other species, with a very large muscular duct, forming a diverticulum. The coiled tube is embedded in tissue, as in *Lumbricus*, and a fairly extensive plexus of blood-vessels can be detected around the tube, as in all other "earthworms" except *Ocnerodrilus*, as opposed to "waterworms."

With regard to the vascular system I may merely state that the dorsal vessel is single, and is not accompanied by a supra-intestinal vessel. Four pairs of lateral hearts lie in Somites vi, vii, viii, and ix; they are dilated and twisted, but are not moniliform. The lateral hearts in *M. Deshayesi* are in Somites vi, viii, and ix; in *M. Barwelli* in vi—xiv.

In *M. Houtenii* the dorsal vessel is doubled as in *Acanthodrilus*, and hearts in Somites vi—xi. A subneural vessel exists, as Rosa has already stated; this has not yet been observed in any Microdrilid, but as it is frequently absent in *Microchæta*, *Photodrilus*, and others amongst the Macrodrili, no great stress can be laid upon its absence or presence.

The alimentary canal is constructed on the plan described by previous authors. The gizzards, of which there are four, lie in Somites xiii—xvi; they increase in size from before backwards, the fourth being nearly twice the width of the first (fig. 3); they are very distinct, but are not so deeply marked off from one another as Beddard figures (5, fig. 5) for *M. Barwelli*. Behind each gizzard is an annular fibrous band, apparently of connective tissue, for it appears white, and not glistening, as do the gizzards. Perrier and Horst mention them. Similar fibrous bands occur at the hinder end of Somites xi and xii in front of the septum, and the wall of the gut in Somite xii is distinctly more muscular than that of xi,



but very much less so than that of XIII, and not sufficiently muscular to be called a "gizzard." There is thus a transition between œsophagus and gizzard; and it may possibly be that the gut in these somites has been or is in near allies or varieties of this species more muscular than is the case with the single specimen which I have had the opportunity of examining; in fact, these regions may be potential gizzards. In other species the gizzards are either more or less extensive.

The position and extent of the gizzards appear to be one of the chief specific characters of the genus, and *M. indicus* differs from *M. robustus*, A. G. B., in this point, for in Bourne's species the gizzard occupies Somites XI—XV, presumably five in number; so that, as this is the only anatomical feature mentioned by Dr. Bourne, and notwithstanding the external resemblance with regard to the tail, I am justified in creating a new species.

There are no œsophageal glands nor other diverticula of the gut. In *M. japonicus* Michaelsen finds that the wall of the "œsophagus in Segments XV—XVIII (?)"—i. e. behind the gizzard—is much folded and very vascular. In the cavities of the folds he found a granular mass, which "must be regarded as concretions of carbonate of lime;" but he gives no evidence that this is the case. In none of the other species is any mention made of the presence of lime, though of course there is no reason why it should not occur.

The "tubular intestine" immediately behind the gizzard is narrow and cylindrical, remaining thus through Somites XVII to about XX. It then commences to enlarge till it attains its full diameter in about Somite XXX, where it occupies nearly the whole width of the cœlom. At each septum the "sacculated intestine" is very deeply constricted, so that quite a narrow neck connects the thin-walled dilated regions.

There is no typhlosole; the walls of the gut are very thin, and provided with a dense network of longitudinal and circularly disposed blood-vessels.

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## EXPLANATION OF PLATE XXXII,

Illustrating Mr. W. Blaxland Benham’s paper, “Description of a New Species of Moniligaster from India.”

FIGS. 1—15.—*Moniligaster indicus*.

FIG. 1.—The body-wall of six segments, cut through along the dorsal line and spread out. Viewed ventrally.  $\times 5$ . *d.* Dorsal line. *v.* Ventral mid-line. *i. ch.* Inner series of chætæ. *o. ch.* Outer series. *neo.* nephridiopore. *sph.* Spermathecal pore. ♂. Male pore. ♀. Oviducal pore. *x.* Groove in front of male pore.

FIG. 2.—One of the chætæ.

FIG. 3.—A dissection of the left half of the animal, to illustrate the arrangement of the genital organs, and the position of the gizzards and the oblique muscles. Enlarged about 10 times. The somites are numbered, as also are some of the septa. Note the shifting of Septum x/xi. *cop. sac.* Bilobed copulatory sac, through which the spermathecal duct opens to exterior (see Fig. 5). *ann. band.* Annular bands between the gizzards. *giz.* 1, 2, 3, 4. The four gizzards. *obl. m.* Oblique muscles (see Fig. 6) in certain of the somites. *o. ch.* Groove, due to interruption in longitudinal muscles throughout the body, along the line of the outer chætæ (a similar groove exists in connection with the inner chætæ). *æs.* Œsophagus. *ovd.* Funnel of oviduct. *sp. d.* Sperm-duct. *sp. sac.* Sperm-sac, lying in a pouch formed by Septum ix/x. *spth.* Spermatheca.

FIG. 4.—View of male organs on a smaller scale. The pouch of Septum ix/x is removed, and the sperm-sac (*sp. sac*) turned forwards, showing the greatly convoluted sperm-duct (*sp. d.*) lying in Somite ix. The spermiducal funnel is seen by transparency through the thin wall of the sperm-sac. *obl. m.* Oblique muscles attached to prostate, the duct of which is now seen. *o. ch.* The groove in line of outer chætæ.

FIG. 5.—A semi-diagrammatic longitudinal section through the genital somites. It is diagrammatic in so far as it shows both spermathecal pore and atriopore, the entire ovary, and other features which really exist in neighbouring sections. The external rings are labelled with Roman numerals, the cavities of the somites with Arabic numerals; the septa are lettered. *at. o.* Male pore, or atriopore. *circ.* Circular muscles of the body-wall. *cop. sac.* Copulatory sac, showing entrance of spermathecal duct. *lg. m.* Longitudinal muscles of the body-wall. *neph.* Portions of nephridial tube. *neph. bl.* Cæcal bladder of nephridium. *obl. mus.* Oblique muscles cut across. *sp. d. o.* Aperture of sperm-duct into atrial cavity; its course is shown from the septum, backwards in the longitudinal muscles of body-wall, and through the prostate. *sp. funnel.* Funnel of sperm-duct, which does not actually occur in the same section as the testis. *spos.* Spermatozoa in sperm-sac; some are seen attached to funnel. *spth.* Spermatheca. *spth. d.* Spermathecal duct. *spth. o.* Aperture of spermatheca.

FIG. 6.—Diagrammatic transverse section through half the body in anterior region, to show position of oblique muscles. *i. ch.* Groove, along which are inserted the inner chætæ. *o. ch.* Similar groove for outer chætæ. *n. c.* Nerve-cord. *sub. n. v.* Subneural vessel.

FIG. 7.—Half a transverse section through the intestinal region, in order to show the peculiar band of longitudinal muscle (*v. long. mus.*) which traverses this region of the body. The lateral thickening of the body-wall is also seen in these two sections.

FIG. 8.—A longitudinal section of the atrium and neighbouring parts. The Septum x/xi is seen passing forwards underneath the atrium to be inserted near anterior boundary of the somite (cf. Fig. 5) where this septum coalesces with Septum xi/xii. *circ. m.* Circular muscles of the body-wall. *cœ. ep.* Cœlomic epithelium outside the prostate. *gl.* The glandular region of the duct of the atrium. *long. m.* Longitudinal muscles of the body-wall, a portion of which is continuous with the muscular wall of the atrial duct. *multicell. gl.* Pyriform groups of gland-cells projecting outside the muscular coat (*mus. coat*) of the atrium, and whose necks traverse this coat. *neph.* Portion of nephridium in Somite xi. *obl. m.* Oblique muscles, some amongst the longitudinal and others amongst the muscles of the atrial wall. *ov.* Portion of ovary. *ovd.* Edge of the funnel of the oviduct. *p.* Prominence of the lining of the atrium, on the apex of which (in another section) the sperm-duct opens. *sp. d.* Portion of sperm-duct in the wall of the atrium.

FIG. 9.—A portion of the prostate (wall of the atrium) greatly magnified. One group of gland-cells is represented in detail; the necks of the cells are readily traced through the muscular coat (*mus.*), but not so readily traced up to the epithelium (*ep.*). The latter is, however, traversed by narrow ducts (as at *a*), which are, no doubt, the necks of the gland-cells. Between the epithelium and the muscular coat are large pyriform glands, the details of which could not be made out owing to the preservation of the material. *b. v.* Blood-vessels. *n. per.* Nucleus of flat cœlomic epithelial cells, which surround the multicellular glands and dip inwards between them.

FIG. 10.—A portion of the epithelium of the atrial duct. *m.* Muscles. *b. v.* Blood-vessel.

FIG. 11.—A portion of the glandular region of the atrial duct (see Fig. 8, *gl.*). *ep.* Epithelium. *gl.* Gland-cells. *m.* Muscles.

FIG. 12.—Transverse section of sperm-duct. *ep.* Large striated epithelial cells. *mus.* Muscles. *spos.* Spermatozoa.

FIG. 13.—Longitudinal section of the copulatory sac, showing its constriction by Septum vii/viii, and the entrance into it of the spermathecal duct (*spth. duct*). *ep.* Epithelium. *mus.* Muscular coat.

FIG. 14.—A portion of the epithelium of the copulatory sac.

FIG. 15.—Section of spermathecal duct, to show the very thick coat of circularly disposed muscles.

FIG. 16.—A series of diagrammatic sections illustrating my view as to the development of the prostate in earthworms from the condition in *Tubifex*. The lining epithelium of the atrium is represented as consisting of cubical cells, the muscular coat by thick lines, the cœlomic epithelium by interrupted lines.

## Note on a New Species of the Genus Nais.

By

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With Plate XXXIII.

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IN a gathering from a ditch in the neighbourhood of Oxford I found several specimens of a species of *Nais*, which present features differing from those recorded for any species of which I have been able to find a recognisable description.

*Nais heterochæta*, n. sp., is a small worm about a quarter of an inch in length, of a dull brownish colour. I have not yet come across any sexually mature forms, or specimens exhibiting zones of budding; the number of somites varies from about thirty-one to about forty-one in specimens which I have observed from this point of view.

The dorsal bundles of chætæ have a characteristic composition, which the specific name is intended to indicate. Normally there are only two chætæ to a bundle—cases with three being very rare. These two chætæ are of different shape and size. (*a*) One is capilliform, but comparatively short, being  $\cdot 165$  mm. in length, not as long as the body is broad; (*b*) is a small furcate or "crochet," measuring  $\cdot 045$  mm. (fig. 2).

The length of the capilliform chætæ varies slightly in different regions of the body; those of the Somites VI and VII being shorter than the above length, and those of Somite XII exceeding it to a slight extent. They gradually increase in

length then up to Somite XII, then decrease for a few somites, and retain a normal length to the end of the body. In one or two specimens I noted that the dorsal chætæ of Somite VI consisted only of crochets, one on one side, two on the other side; in Somite VII there were two furcates and a short capilliform, only slightly exceeding them in length. It is, perhaps, needless to remark that the dorsal bundles are absent in the first five somites.

A comparison of my figure of these dorsal chætæ with those of Vejdovsky<sup>1</sup> shows that the shape of the chætæ does not agree with those of either of the species, *N. barbata*, *N. elinguis*, or *N. josinæ*, described by him.

In the last species, however, the dorsal bundles do contain crochets in addition to capilliforms; but not only do these differ from those of *N. heterochæta* in position of the "node," but also in the fact that two of them and two capilliform exist in a bundle, and in the relative size of the two.

Another point of difference—if the above be not sufficient—is the presence of eyes in my species, whereas they are absent in *N. josinæ*.

The ventral chætæ (fig. 3) are of the usual Naid shape; usually there are four in a bundle, rarely three or five. Those of Somites II, III, IV, and V differ slightly from the remainder in that the distal prong is rather longer than the proximal; whilst in the normal chætæ the two prongs are, as nearly as I can make out, equal in length, though the proximal prong is distinctly the stronger.

The blood is yellow, and the connections between the dorsal and ventral trunks (fig. 1) are peculiar. The two lateral branches into which the dorsal vessel divides in the prostomium, in front of the brain, unite in Somite V to form the ventral trunk; these are connected with the dorsal trunk by four pairs of vessels, each of which branches more or less irregularly, as will be understood better by a reference to the figure than by a description.<sup>2</sup> The arrangement is

<sup>1</sup> 'System und Morphologie d. Oligochäten,' pl. ii, figs. 18, 19, 26.

<sup>2</sup> These branches are accompanied by irregular patches of brown pigment

less regular than in *N. elinguis*, or *Bohemilla*, or *Paranais*, but more regular than in *N. josinæ*. One very peculiar feature, hitherto unrecorded, I believe, is the connection which exists between the branch *d*, in Somite *v*, and the "commissural" vessel *e* in Somite *vi*, which connects the dorsal and ventral trunks; the branching of this commissural vessel is also peculiar. The shape of the brain is utilised by Vejdovsky for determining species, therefore I have appended a figure of this organ in *N. heterochæta* (fig. 5); it will be seen to resemble somewhat the brain of *N. josinæ* (Vej., Taf. ii, fig. 28) in the constriction of the anterior lobes from the posterior, but in *N. heterochæta* this is more marked, and at the same time the shape of the posterior lobes is different.

With regard to the gut, the "stomach," or dilatation in Somite *viii*, is not nearly as marked as in other species, and more nearly resembles that in *Paranais littoralis*.<sup>1</sup>

The pigmented covering of chloragogenic cells commences in Somite *vi*, and is continuous thence throughout the body till quite near the posterior end.

The nephridia present the peculiarity which has scarcely been sufficiently insisted upon by recent writers, though it has been recorded by Carter<sup>2</sup> and by Timm,<sup>3</sup> that very usually there is in Naids only a single nephridium in some or all the somites. In the present species there is never more than one nephridium per somite; the nephridium is very long, and frequently the coiling tube occupies two somites, communicating by means of a funnel with a third somite (fig. 4). In this case, then, there is one nephridium in the place of four (a pair in Somite *xi* and a pair in Somite *xii*). In most of the somites the nephridium lies on the animal's right side. So far as I have been able to observe, in the living animal there

<sup>1</sup> See A. G. Bourne, "Notes on Naidiform Oligochæta," 'Quart. Journ. Micr. Sci.,' xxxii, Pl. XXVI, fig. 2.

<sup>2</sup> "Spermatology of New Species of Nais," 'Ann. Mag. Nat. Hist.,' ii, 1858, p. 1.

<sup>3</sup> "Beob. üb. Phreoryctes und Nais," 'Arb. aus Zool. Inst. Wurzburg,' vi, 1883.

is no trace of the other nephridia. It will be an interesting point to look for in the developmental history of the genus—the suppression of nephridia; for Michaelsen has described certain earthworms, *Kynotus*, in which the nephridia are stated to occur in alternate somites. I have suggested elsewhere that an error in observation may perhaps have occurred, and that the external markings indicating “somites” are in reality annuli. But in *Nais*, of course, there is no question of annuli.

The first nephridium lies in Somite VII; the arrangement in following somites is subject to a good deal of variation.

The post-septal glandular region of the tube is of a different shape from that figured by Vejdovsky for *N. elinguis*, and more nearly resembles therein *N. josinæ* (Vej., pl. iii, fig. 4, *a*); but with regard to the terminal dilatation this species differs considerably from *N. heterochæta* (cf. my fig. 4).

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### EXPLANATION OF PLATE XXXIII,

Illustrating Mr. W. Blaxland Benham's “Note on a New Species of the Genus *Nais*.”

FIGS. 1—5 illustrate specific characters of *Nais heterochæta*, n. sp.

FIG. 1.—The vascular system of the anterior somites. *D. v.* Dorsal trunk. *lat.* The two branches from the dorsal trunk which unite to form the ventral trunk (*V. v.*). *a, b, c, d.* Vessels more or less branched, passing from dorsal to lateral vessel. *e.* A commissural vessel from dorsal to ventral trunk, also branched.

FIG. 2.—A dorsal bundle of chætæ, consisting of one capilliform and one furcate chætæ.

FIG. 3.—A ventral chætæ.

FIG. 4.—A nephridium, showing its extension into two somites. *sept.* Septum. *a.* Granular post-septal region. *b.* Muscular (?) duct. *f.* Funnel.

FIG. 5.—Brain. *com.* Origin of œsophageal commissure.



On a New Organ in the Lycoridea, and on the  
Nephridium in *Nereis diversicolor*, O.  
F. Müll.

By

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With Plates XXXIV & XXXV.

ABOUT two years ago, while examining some sections of a *Nereis* (probably *N. diversicolor*, O. F. Müll.) which I had cut in the Zoological Laboratory at University College, London, I discovered an interesting organ, which appears to have hitherto escaped the notice of those naturalists who have studied the anatomy of the Nereids. Since then I have from time to time continued my observations, both in London and in the Oxford Museum, always hoping to be able to obtain the stages in the development of *Nereis*, the study of which alone can give a real clue to the homology and functions of these organs. This unfortunately has not been possible, owing chiefly to the fact that I have not been able to go myself to the sea-side to pursue my researches. It has therefore been thought advisable to publish the facts as they stand, and this paper amounts to little more than a mere description of this new organ. Some notes on the minute structure of the nephridium of the Nereids have also been added.

Various genera and species were examined, but most of the observations were made on *Nereis diversicolor*, which occurs in abundance at Plymouth, whence I have obtained

my specimens alive. A detailed description will, therefore, be first given of the organ in this species, which will then be compared with some other members of the family.

If the fresh worm be killed, laid out, and slit up on the dorsal surface on each side along the bases of the parapodia, and a piece of the strip so obtained be placed with the inner surface upwards on a slide and examined under the microscope, there will be seen running transversely on either side, and curving round the outer edge of the great longitudinal muscles, faint lines made by a folded area of the cœlomic epithelium, bounded in front by a lateral blood-vessel coming from the dorsal vessel. This folded and thickened patch of epithelium extends over the dorsal longitudinal muscles in the posterior half of each segment, and its surface is covered with delicate cilia. If now the strip be examined from the upper surface the folded ciliated area is seen to extend transversely across the middle of each segment, becoming narrower and narrower, and reaching to near the mid-dorsal line. I propose to call this organ the dorsal ciliated organ until we know more about its functions; the portion which lies on the outer surface of the muscles may be called the outer limb, and the portion which lies on the inside of the muscles the inner limb. Little more can be seen in the fresh condition; the exact position and structure of the organ can only be ascertained by means of sections.

For the preservation of *Nereis diversicolor* hot corrosive has, on the whole, given the best results. The worms were chloroformed, then opened up here and there, and the hot preservative poured on them. Hæmatoxylin and borax carmine were used as stains.

In a transverse section through the middle of a segment of an adult *N. diversicolor* (Pl. XXXIV, fig. 5) we see a covering of ciliated epithelium extending on the outer surface of the dorsal longitudinal muscle (figs. 1 and 5, *dors. long. m.*), and round its ventral border on to the lateral tegumentary blood-vessel (figs. 1 and 5, *dors. teg. v.*) which communicates with the dorsal vessel (figs. 1 and 5, *dors. v.*). This is the outer limb of the

dorsal ciliated organ (Pl. XXXIV, figs. 1, 2, 5, *o. limb*; Pl. XXXV, figs. 15, 17, *o. limb*). Fig. 15 represents a transverse section through the dorsal muscle of another specimen, taken rather farther back in the segment than that in fig. 5, thus avoiding the blood-vessel. The ciliated organ curls round the edge of the muscle, and ascends on its inner side nearly as high as the slight angle formed where this muscle leaves the body-wall. It will be seen that the inner limb (fig. 1, and figs. 15, 17, *i. limb*) does not adhere closely to the muscle, but to a fold of the septum which is bounded anteriorly by the dorsal tegumentary vessel (figs. 1, 4, 15, 17). The septum, in fact, is not attached to the inner face of the longitudinal muscle, and its free edge bends forward at right angles (fig. 4, *fl. sept.*), and proceeds upwards, leaving a space between itself and the muscle (figs. 1, 4, 5, 15, 17); it is on the inner side of this flap, which faces slightly backwards, that is situated the inner limb of the dorsal ciliated organ (figs. 1, 4, 5, and figs. 15, 17, *i. limb*). The outer and dorsal limb varies somewhat in its extension, sometimes reaching quite near the median dorsal line, as I have already mentioned. In this region blind prolongations of the cœlom run up between the longitudinal muscles and the body-wall (figs. 1, 5, 7, *dors. cœl.*); they are separated from each other by connective-tissue walls. Small blood-vessels (fig. 7, *bl. ves.*) and bundles of circular muscle-fibres run along the cœlomic spaces (fig. 7, *circ. m.*). The end of the outer limb of the dorsal ciliated organ (fig. 7, *o. limb*) extends up the largest of these spaces (which is situated almost exactly in the middle of each segment), being continuous with the cœlomic epithelium which lines the space and covers its anterior side. A branch of the tegumentary vessel follows it closely during its course. I first expected that this dorsal tubular prolongation of the cœlom would, with the outer limb of the ciliated organ, lead to an external aperture; but I have looked in vain for such a pore in numerous sections—transverse, sagittal, and horizontal. Both cœlomic space and ciliated organ gradually dwindle away until they disappear altogether some little way from the median

dorsal line. As for the extension of the organ at its ventral border, fig. 4, which represents the middle portion of the sagittal section through two segments, shows that it reaches halfway across the segment from near its posterior limit (figs. 2, 4, *dors. cil. org.*). The surface of the organ is much folded, especially the outer limb.

The finer structure is shown in figs. 4 and 6. In the former, which was taken from a section stained in borax carmine, the cells are seen to have indistinct walls and to be somewhat striated on the outer edge, which is very darkly staining. The nuclei are large and more or less oval in shape. Fig. 6 represents a small portion of the organ, taken from a section very similar to the right side of that shown in fig. 5. This section has been stained with hæmatoxylin, and shows no distinct cell outlines. The protoplasm in which the nuclei are embedded is slightly granular within, and under a high power (Z. 2 mm. hom. oil im. and oc. 8) appears to be divided up into chambers, as it were, by the minutest ramifications of a network of darkly staining substance very similar to that described below in the nephridium. Towards the inside this substance forms the thin limiting membrane (Pl. XXXIV, fig. 6, *l. mb.*) which lies on the muscle, while towards the free surface it forms a dark zone (fig. 6, *d. z.*), and then the dark lines which give the outer edge of the organ its striated appearance. Outside this striated layer, at the very surface, the darkly staining substance forms a cuticular layer (fig. 6, *cut.*). The surface is beset with fine cilia (fig. 6, *cil.*), the bases of which, perhaps, are continuous with the light portions of the striæ in the underlying substance. On every side the epithelium forming the organ is continuous with the cœlomic epithelium, of which it is, in the adult at all events, a highly modified patch. It is quite clear from these descriptions, I think, that the dorsal ciliated organ shows no trace of a glandular structure.

In conclusion, I may say that this organ is present in every segment of the body from the tenth, except the last two, in which the nephridia appear to be also absent. It occurs in both sexes, and I have found it in every member of the family which

I have had the opportunity of examining—namely, *Nereis diversicolor*, *N. macropus*, Clp.,<sup>1</sup> *N. cultrifera*, Gr., *Alitta virens*, Sars, and *Nereilepas fucata*, Sav. In all these species the organ resembles that described in *N. diversicolor* in every particular, as far as I was able to ascertain; but in some cases the specimens were not very well preserved. It is a somewhat remarkable fact that I have failed to find it in two Heteronereid forms (the ♀ Heteronereid of *N. pelagica*, and a small ♂ Heteronereid which I have not yet been able to identify).

Of other genera, both nearly related to, and far removed from, the Lycoridea, I have examined the following species: *Aricia fœtida*, *Nephtys scolopendroides*, *Eunice* sp., *Lumbriconereis impatiens*, *Staurocephalus Rudolphi*, *Sthenelais dendrolepis*, *Polynoë elegans*, *Rhynchobolus convolutus*, and *R. siphonostoma*. In none of these forms has any trace of the dorsal ciliated organ been found, and it is to be noticed that all these species have nephridia provided with large and widely open funnels, and short, more or less straight, ducts.<sup>2</sup>

A short time ago Professor Lankester directed my attention to a very interesting paper by Professor A. Kowalevsky (7) on excretory organs, in which certain segmentally arranged organs, occurring in *N. cultrifera*, are shortly described. I shall quote the passage in full from p. 71: “Das Indigokarmin [which the animals had taken in] wird meistens von den Blutkörperchen aufgenommen, und zum Teil färbt es in jedem Segmente besondere Organe, welche an der Rückenseite der Segmente liegen und aus drüsenartigen Zellen der Haut bestehen, unter denen man immer eine grosse Anhäufung der Blutkörperchen sieht. Die Stellen, welche so das Indigokarmin bei *Nereis* aufspeichern, sind auch an normalen Tieren zu sehen; dies sind Stellen mit Anhäufungen von braunen

<sup>1</sup> I am much indebted to Signor Lo Bianco, of the Naples Zool. Station, for collecting and sending me several species of *Nereis*.

<sup>2</sup> I hope soon to be able to give a description of the minute structure of the nephridia of some of the genera mentioned above.

oder gelben Körpern, die in jedem Segmente und besonders in den hintern liegen. Diese Stellen nun speichern auch das Indigokarmin auf. Tötet man mit Alkohol eine so bearbeitete Nereide und spannt sie dann auf oder nimmt nur die Haut der Rückenseite, so gewinnt man ein Präparat wo diese blauen Organe in jedem Segmente sich metamerisch wiederholen und den Eindruck besonderer regelmässiger Segmentarbildung machen." It seems evident that this excretory organ is not the same as the dorsal organ I have described, which is not glandular, and is not situated in the skin. Also Kowalevsky makes no mention of cilia. On the other hand, it appears not improbable that the "grosse Anhäufungen der Blutkörperchen" seen below the excretory organ are the accumulations of cœlomic corpuscles, which seem to be collected together by the cilia of the dorsal organ near the top of the outer limb (Pl. XXXIV, figs. 5, 7, *cœl. corp.*); it also frequently happens that a large number of ova are collected in this region.

When I first discovered the dorsal ciliated organ in Nereis, I was immediately struck with its remarkable resemblance to the genital ducts (Genitalschläuche) described in the Capitellids in Dr. Eisig's beautiful monograph (6). I have obtained sections of Nereis showing the organ in question almost exactly like Eisig's figs. 1, 2, and 14, pl. xiv. It seems to me, therefore, very likely that we have here a "genital duct," which has not yet acquired an opening to the exterior. My inability to show such an opening may, perhaps, be explained by the fact that it has never been my good fortune to obtain a perfectly mature Nereid. The acquiring at maturity by the duct of an opening would be a fact by no means unparalleled in nature; in the Capitellids themselves it only occurs late (6). It may be remarked, also, that the dorsal organ of Nereis and the genital ducts of the Capitellids show many points of resemblance in histological detail.

Mr. Cunningham (4) argues that it would be quite impossible for the genital products in Nereids to be discharged by means of the nephridia; in this I entirely agree with him. Not only would it be impossible for the ova to escape by the

nephridial canal, owing to their size; but their nuclei alone could not pass down its tortuous and narrow lumen. The genital products must therefore escape either by dehiscence, as held by Mr. Cunningham (4), or by means of genital ducts (ducts such as we know to be formed at maturity in the Nemertines).<sup>1</sup> The former method would be neither agreeable nor advantageous to the parent; the latter, on the contrary, would seem to be the natural one.

The fact that no dorsal organs were found in the two Heteronereids I have examined, does not appear unnatural when we consider that these forms are much modified for the purpose of dispersing the ova, and are in many respects degenerate and unfitted for a long life.<sup>2</sup> Probably, in this case, dehiscence takes place, followed by the death of the individual.

#### THE NEPHRIDIA.

Although many naturalists have examined the nephridia of various members of the family Lycoridea, these organs are still but incompletely known.

One of the chief difficulties we meet with in studying the nephridia of the Nereids, is owing to the small size of most of these worms (except *Alitta virens* and *Nereis pelagica*, which unfortunately I have not been able to obtain alive). However, if a *N. diversicolor* be carefully dissected under a powerful lens, the nephridia may sometimes be seen as small yellowish or whitish bodies at the base of each parapodium. On removing these with the septa, the whole organ, both body and funnel, may occasionally be obtained. It is then seen to consist, as described by Mr. Cunningham (4), of an opaque, massive body, containing a convoluted tube, which leads to a long canal terminating by a small funnel, the internal opening.

<sup>1</sup> Should future observations establish the fact that the dorsal ciliated organ is a genital duct, it might well be compared with the metameric genital canals of the Nemertines.

<sup>2</sup> Not only is the alimentary canal much reduced (according to Claparède [2] the Heteronereids take no food), but the nephridia also seem to be degenerate and in some cases even absent. I have not, however, yet been able to examine sufficient material to say anything definite on this latter point.

The whole nephridium is covered with cœlomic epithelium. I have not attempted to follow out the complicated coils of the nephridial tube in series of sections; but fig. 8, Pl. XXXIV, is a diagram showing the main features of the system greatly simplified. The nephridial canal may, for convenience' sake, in description be divided into four regions; it will be understood that the transition in structure between the regions is gradual. The ventral tegumentary vessel (fig. 1, *vent. teg. v.*) sends branches over the nephridium. The small nephrostome is attached to the lower edge of the septum (figs. 1, 2, *neph. fun.*; fig. 9 *a*), which is in this region free from the ventral longitudinal muscle. Cunningham (4) was unable to ascertain definitely whether it opens into the segment in front of that containing the main body of the nephridium and the external pore; while Cosmovici (3) says, "Pour moi, chaque paire d'organes segmentaires n'est en communication qu'avec l'anneau qui la contient." Claparède, on the other hand, figured the funnel opening into the next segment (2, pl. vi, fig. 5); horizontal and sagittal sections clearly show that he was right. Frequently, however, being only suspended to the border of the septum, the nephrostome seems to swing round and open into the segment which contains the nephridium; but this is not its normal position. In its general structure it is very similar to the nephrostome of *Alitta virens* (4); it has, however, a nearly straight margin to its internal opening, and possesses no trace of an internal septum, as described by Cunningham in the above species. In *N. diversicolor* the edge or lip of the funnel is closely folded back over the outside of the organ (fig. 4, *lip of fun.*; fig. 9, *dors. lip, vent. lip*), and from this reflected surface and the margin of the internal opening (fig. 9, *int. op.*) spring long delicate processes (fig. 9, *cil. proc.*), just as in *A. virens*. These processes contain no nuclei, are formed of very granular protoplasm covered with long waving cilia, and must be regarded as mere outgrowths from the underlying cells. Occasionally the processes branch (fig. 3). In the nephrostome of *Nereilepas fucata* (fig. 9 *a*)



the lip of the funnel is not reflected, and the processes, which are longer and more delicate, spring from the margin only. The inner wall of the funnel is formed of large vesicular cells (figs. 9 and 9 *a*, *w. fun.*) with round nuclei and deeply staining inner borders; they bear numerous strong cilia (figs. 9 and 9 *a*, *int. cil.*), which beat very rapidly.

From the funnel we pass to a short, narrow, glandular region, which is not ciliated (fig. 9 *a*, *n. can.*; not shown in fig. 9), leading into the first region, the long post-septal canal (fig. 8, *p. s. can.*). The wall of this canal is composed of many glandular cells, and becomes ciliated towards the nephridial body. On entering the main compact body of the nephridium the second region of the nephridial canal becomes much convoluted, but scarcely differs in structure from the next region, except in having more nuclei round the tube, and a few cilia distributed all round the lumen.

The third region is chiefly distinguished by having a very narrow lumen, and the cilia situated only on one side of the tube (figs. 11, 16, *cil.*). The cilia may not be in a single row, but the arrangement is essentially similar to that described by Dr. Benham in *Lumbricus* (1); and the peculiar sinuous, wave-like effect produced by the motion of the cilia in the nephridia of most *Oligochætes* is visible here also.

In a transverse section of this region of the canal, one (fig. 11, *n.*) or two nuclei are generally present; I cannot say for certain whether the tube should be considered as inter- or intra-cellular. No doubt a hard and fast line of distinction cannot be drawn between the two varieties. The narrow tube which constitutes the third region of the nephridial canal is chiefly situated in the distal half of the nephridium, and leads into the fourth and last region (fig. 8).

This region is shorter and less convoluted than the last, and is situated on the under surface of the nephridium (fig. 8). Its lumen is moderately wide, and not provided with cilia (figs. 12—14); at more or less regular distances along the tube are two nuclei, situated opposite each other on either side of the lumen (figs. 12 and 15, *n.*). The nuclei in this and

other regions possess, as a rule, one large nucleolus, and sometimes some small ones in addition.

The fourth region of the nephridial canal leads directly to the exterior by means of the nephridiopore (figs. 1 and 2; fig. 10, *neph. p.*), which opens on the ventral surface of each segment, about halfway between the ventral cirrus and the longitudinal muscles. In fig. 10 it is seen that the wall of the tube pierces the epidermis (fig. 10, *ep.*), and reaches the cuticle itself: near the pore are a pair of nuclei, one on either side of the canal.

The sections through the wall of the nephridial canal show that it is lined by a more or less definite layer (figs. 11—14, *b. l.*), which is formed of an apparently denser material than that which lies outside. This boundary layer is very well developed in the last region (fig. 14, *b. l.*). Running throughout the substance of the nephridial mass is a delicate network of some denser cuticular substance, which stains darkly with hæmatoxylin (figs. 11, 12, 12*a*, *b*, 13, 14, 16, *net.*). The boundary layer is pierced by the network, which thus reaches the lumen of the tube, and forms a close network round it. The cut ends of the threads of this network can be seen in the longitudinal section of the lumen drawn in fig. 14. Dr. Eisig describes in the Capitellids a somewhat similar though coarser mesh-work, as continuous with a boundary layer which he believes to be cuticular. In *Nereis* there appears to be a supporting network, and a distinct boundary layer, which is probably formed, not of cuticle, but of dense protoplasm, filled with minute granules. In some sections of a specimen preserved in Hermann's fluid (fig. 12 *a*, *ves.*) little vesicles or vacuoles can be seen piercing this layer and opening into the lumen, presumably between the meshes of the network; these vesicles probably contain some excretory products.

Fig. 12 *b* represents a small portion of the supporting network, situated between the coils of the canal, in which are seen some connective-tissue cells. These cells do not belong to the wall of the canal, and their nuclei are smaller than those of the lining cells.

The nephridium may, therefore, be described as a mass of connective tissue, in which is embedded an excretory canal, the wall of which has a small number of nuclei in it, but no distinct cell outlines.

It is well known that Ehlers (5) described the nephridium of *N. cultrifera* as having a long duct leading to the exterior, and a crescent-shaped internal opening. Schröder (9), who seems to have copied Ehlers' errors as carefully as his correct observations, gives a similar figure and description of the nephridium in *N. diversicolor*. I feel convinced that these observers, examining the nephridium after its removal from the worm, have simply mistaken the post-septal canal for the duct to the exterior, and that their internal opening is the scar left on tearing the organ away from its attachment to the body-wall at the nephridiopore. This interpretation is confirmed by the fact that Ehlers states that "die Richtung der Flimmerbewegung ging an der äusseren Mündung nach innen."

#### SUMMARY AND CONCLUSIONS.

We may sum up the main facts set forth above as follows:

*Nereis diversicolor* has in every segment, except the first and last few, a pair of large, highly differentiated, ciliated patches of cœlomic epithelium—the dorsal ciliated organs. These organs seem to occur throughout the Lycoridea, as they have been found in all the genera of that family which I have examined.

The nephridium of *Nereis diversicolor* consists of a compact mass, perforated by a convoluted canal, which can be distinguished into several regions, and communicating with the exterior by a short duct leading to a nephridiopore on the ventral surface. A long canal springs from the main body of the nephridium, and ends in front by a nephrostome which opens into the next segment. The nephrostome is provided with long ciliated processes. The nephridium of *Nereilepas fucata* is of essentially similar structure.

Reasons have been given above for considering the dorsal ciliated organ as a genital duct not fully developed. It would be premature, however, to try to come to any definite conclusion on the subject of its functions and homology until we know both its development and its fate. But I should like to point out that the Capitellidæ, the only other Polychætes possessing a nephridium described in detail which resembles that of *Nereis*, also have in many segments a large ciliated patch of cœlomic epithelium, which becomes funnel-shaped and functions as a genital duct (Eisig, 6). Most of the Polychæta, however, have large-funnelled nephridia which may function as carriers of the genital products. On the other hand, the latest researches on the development of the nephridia in the Polychætes (Meyer, 8) and in the Oligochætes (Vejdovsky, 10) seem to show most conclusively that these organs were developed phylogenetically from nephridia similar to those of the Planarians, which were provided with flame-cells, and did not open internally. Now Meyer has shown (8) that the large funnels in the tubicolous worms which he studied are developed independently and as outpushings of the cœlomic epithelium which join and fuse with the blind end of the nephridium. May not this funnel be the same as the genital ducts of the Capitellids and other worms (Oligochætes)? I should consider, then, that in most Polychætes the nephridium is a compound organ formed from the fusion of a tube with an outpushing of the cœlomic epithelium, as Meyer holds; and further, that in the Capitellids this funnel is partly nipped off as the genital duct, while in the Oligochætes, and perhaps in the Lycoridea also, this cœlomic funnel either has never joined the nephridium at all (most of the lower Oligochæta, Enchytræids, Naids, &c.), or that it is afterwards mostly or entirely separated off as a genital duct.

It must be remembered that if we assume that in the Chætopods the genital ducts are simply modified nephridia, and at the same time consider that their nephridia, which open into the cœlom, were derived from nephridia without internal nephrostome, but provided with flame-cells;—if we assume

this, then we must be prepared to explain what has become of the genital ducts with which the ancestors of these Chætopods were provided before their nephridia opened inwards, and why these ducts have disappeared leaving no trace behind them. On the other hand, I think that this difficulty may be avoided if we consider the original genital duct to have been a simple outpushing of the cœlomic epithelium which opened to the exterior, and afterwards became more or less grafted on to the nephridium.<sup>1</sup> Whether the cœlom in the Chætopods was primitively ciliated all over—as, for instance, in *Rhynchobolus*—is a very interesting question suggested to me by Professor Lankester. If this was the case the ciliated organs might have been formed by the restriction of the cilia to a definite area, bringing with it the specialisation of the epithelium and the development of a definite organ for a particular function.

In conclusion, I wish to express my thanks to Professor Lankester and Dr. Benham for their constant help and advice throughout my investigations.

## LIST OF WORKS REFERRED TO.

1. BENHAM.—“The Nephridium of *Lumbricus*,” ‘*Quart. Journ. Micr. Sci.*,’ xxxii, 1891.
2. CLAPARÈDE.—‘*Les Annélides Chétopodes du Golfe de Naples*,’ Suppl., 1870.
3. COSMOVICI.—“Glandes génitales et organes segmentaires des Annélides Polychètes,” ‘*Arch. de Zool. exp. et gén.*,’ viii, 1879–80.
4. CUNNINGHAM.—“Some Points in the Anatomy of Polychæta,” ‘*Quart. Journ. Micr. Sci.*,’ xxviii, 1887.
5. EHLERS.—“Die Borstenwürmer,” Leipzig, 1864–8.
6. EISIG.—‘*Die Capitelliden des Golfes von Neapel*,’ Berlin, 1887.
7. KOWALEVSKY.—“Ein Beitrag zur Kenntniss der Exkretionsorgane,” ‘*Biol. Centralblatt*,’ ix, 1889.
8. MEYER.—“Studien über den Körperbau der Anneliden,” ‘*Mittheil. Zool. Station Neapel*,’ vii and viii, 1887–9.

<sup>1</sup> Since this was printed I have found that E. Meyer put forth very much the same theory in 1890 (“*Die Abstammung der Anneliden*,” ‘*Biol. Central.*,’ x).

9. SCHRÖDER.—“Anatomisch-histologische Untersuchung von *Nereis diversicolor*, O. Fr. Müll.,” ‘Inaug.-Diss. Kiel,’ 1886.
10. VEJDOVSKY.—“Entwicklungsgeschichtliche Untersuchungen,” 3rd part, Prague, 1886.

### EXPLANATION OF PLATES XXXIV & XXXV,

Illustrating Mr. E. S. Goodrich's paper “On a New Organ in the *Lycoridea*, and the Nephridium in *Nereis diversicolor*, O. F. Müll.”

All the figures, except Fig. 9*a*, are from *Nereis diversicolor*, O. F. Müll.

#### *List of Reference Letters.*

*ap.* Aperture through the septum leading from one segment to the other.  
*b. l.* Boundary layer. *bl. v.* Blood-vessel. *c. b. w.* Cut body-wall. *cil.* Cilia. *cil. proc.* Ciliated processes. *circ. m.* Circular muscles. *cæl.* Cælom. *cæl. ep.* Cælomic epithelium. *cæl. corp.* Cælomic corpuscles. *cut.* Cuticle.  
*d. z.* Dark zone. *dors. cil. org.* Dorsal ciliated organ. *dors. cæl.* Dorsal extension of the cælom. *dors. long. m.* Dorsal longitudinal muscle. *dors. lip.* Dorsal lip of the funnel. *dors. marg. fun.* Dorsal margin of the funnel. *dors. teg. v.* Dorsal tegumentary vessel. *dors. v.* Dorsal vessel. *ep.* Epidermis. *excr.* Excretory products. *ext. cil.* External cilia. *fl. sept.* Flap of the septum. *i. limb.* Inner limb of the dorsal ciliated organ. *int.* Intestine. *int. cil.* Internal cilia. *int. op.* Internal opening. *l. mb.* Limiting membrane. *l. neph. can.* Lumen of the nephridial canal. *lip of fun.* Lip of the funnel. *lu. fun.* Lumen of the funnel. *n.* Nucleus. *n'.* Nucleus of a connective-tissue cell. *n. can.* Narrow canal. *net.* Network of supporting substance. *neph.* Nephridium. *neph. fun.* Nephridial funnel. *neph. p.* Nephridiopore. *o. limb.* Outer limb of the dorsal ciliated organ. *obl. m.* Oblique muscles. *p. s. can.* Post-septal canal. *par.* Parapodium. *sept.* Septum. *sp. m.* Sperm-morulae. *v. marg. fun.* Ventral margin of the funnel. *vent. lip.* Ventral lip of the funnel. *vent. long. m.* Ventral longitudinal muscle. *vent. teg. v.* Ventral tegumentary vessel. *vent. v.* Ventral vessel. *ves.* Vesicles of excretory fluid. *w. fun.* Wall of the funnel. *w. neph. can.* Wall of the nephridial canal. *1st, 2nd, 3rd, 4th reg.* First, second, third, and fourth region of the nephridial canal.

FIG. 1.—Diagram of a transverse section, showing the posterior half of a segment as seen from in front. For the sake of clearness the smaller blood-vessels, setæ, and all the muscles except the four main longitudinal muscles have been omitted. The larger blood-vessels are shown on the left-hand side of the figure.

FIG. 2.—Diagrammatic side view of three segments from which the body-wall and parapodia have been removed from the left side. Only the dorsal and ventral blood-vessels are indicated.

FIG. 3.—A branching ciliated process of the nephrostome.

FIG. 4.—Portion of sagittal section through two segments—above the ventral edge of the dorsal muscle, below the dorsal edge of the ventral muscle, between the two the cœlomic cavity. The mass of fatty tissue which fills the cœlom is not represented. The anterior segment is to the right. Corrosive borax carm. Zeiss B., detail with high power.

FIG. 5.—Upper part of a slightly oblique transverse section through the middle of a segment. Corr. bor. car. Zeiss A., oc. 2, camera.

FIG. 6.—Transverse section through the edge of the dorsal ciliated organ. Corr. hæmat. Zeiss apochr. 4 mm., oc. 3, camera.

FIG. 7.—Sagittal section cutting across the dorsal extension of the cœlom. The cuticle is not represented. Corr. bor. car. Zeiss D., oc. 3, camera.

FIG. 8.—Diagrammatic sketch of the nephridium and its canal, which is subdivided into four regions.

FIG. 9.—Optical section through the nephridial funnel, drawn from the fresh, and completed from a stained specimen. Zeiss F., oc. 4.

FIG. 9*a*.—Optical section through the nephridial funnel of *Nereilepas fucata*, Sav., drawn from the fresh, and completed after staining with alum carmine. Zeiss apochr. 4 mm., oc. 4, camera.

FIG. 10.—Portion of a transverse section, showing the nephridiopore. Corr. bor. car. Zeiss apochr. 4 mm., oc. 8, camera.

FIG. 11.—Transverse section through the third region of the nephridial canal. Corr. hæmat. Zeiss 2 mm. oil im., oc. 8.

FIG. 12.—Transverse section through the fourth region of the nephridial canal. Corr. hæmat. Zeiss apochr. 4 mm., oc. 8.

FIG. 12*a*.—Transverse section through the third region of the nephridial canal. Hermann, hæmat. Zeiss 2 mm. oil im., comp. oc. 4.

FIG. 12*b*.—Section through the tissue between the coils of the nephridium, showing network and connective-tissue cells. Hermann, hæmat. Zeiss 2 mm. oil im., comp. oc. 4.

FIG. 13.—Transverse section, slightly oblique, through the fourth region of the nephridial canal. Corr. hæmat. Zeiss 2 mm. oil im., oc. 8.

FIG. 14.—Section through the fourth region of the nephridial canal. The lumen not being straight, the wall of the canal is cut through here and there. Corr. hæmat. Zeiss apochr. 4 mm., oc. 4, camera.

FIG. 15.—Portion of a transverse section, showing the dorsal muscle and dorsal ciliated organ cut through. Corr. hæmat. Zeiss B., oc. 4, camera.

FIG. 16.—Longitudinal section through a piece of the third region of the nephridial canal. Corr. hæmat. Zeiss apochr. 4 mm., oc. 4, camera.

FIG. 17.—Portion of a horizontal section, about midway through the intestine. Corr. bor. car. Zeiss A., oc. 3, camera.



**Nephridia and Body-cavity of some Decapod  
Crustacea.**

By

**Edgar J. Allen, B.Sc.,**  
University College, London.

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With Plates XXXVI, XXXVII, & XXXVIII.

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THE following paper contains the results of researches carried on at the Plymouth Laboratory of the Marine Biological Association, where, by appointment of the British Association Committee, I occupied a table for six weeks during the summer of last year (1892), my stay being prolonged for an additional month through the kindness of Mr. Robert Bayly, one of the Governors of the Association, who furnished me with an additional nomination.

The observations were made chiefly upon larvæ of *Palæmonetes varians*, but they were subsequently extended to the adult of this form, as well as to larvæ and adults of allied species, the latter part of the work having been done in Professor Weldon's laboratory at University College, London.

*Palæmonetes varians* is found in the brackish waters of certain ditches and pools near the estuary of the Plym, which are subject to the influence of the tides.

The larvæ were at first obtained by keeping gravid females, whose eggs were in an advanced stage of development, in separate vessels in a mixture of one part of sea water to two of fresh (this mixture having about the same density as the water in which the animals were captured). They were after-

wards found to hatch equally well in a stream of running sea water, and this method was then chiefly used.

Towards the end of the summer, larvæ in all stages of development were obtained in large numbers by fishing with a fine net in certain sheltered pools, and further breeding in captivity became unnecessary.

The larvæ were preserved in Flemming's fluid (both the weak and strong mixtures gave good results), washed in water, and hardened in alcohol. The sections were stained with Delafield's hæmatoxylin.

### I. THE NEPHRIDIA.

During the greater part of the larval life two pairs of nephridia are present; the green glands, which open at the bases of the second antennæ, and the shell-glands, which open at the bases of the second maxillæ.

**THE GREEN GLAND.**—A horizontal longitudinal section through the green gland of a *Palæmonetes* larva, which is three or four days old, is represented in fig. 1. At this stage the gland has a form which is similar to that described by Weldon (No. 20) and Marchal (No. 17) as persisting in the adult of *Virbius*, *Pandalus*, and *Crangon*, excepting that there is as yet no trace of the remarkable enlargement of the bladder which the former author designates as "nephro-peritoneal sac."

The end-sac (fig. 1, *e. s.*) communicates by means of a U-shaped tube (*tu.*) with the bladder (*bl.*), which is in reality merely the enlarged distal portion of the tube. (The dotted lines in the figure [fig. 1] indicate the way in which tube and bladder join each other, as determined by the following sections of the series.) The bladder is placed in communication with the exterior by means of a very short ureter, which opens in the region indicated by the letter *O* in fig. 1.

It is not necessary for me to give an account of the histological structure of the various portions of the gland, as it has

been so fully and accurately described for this and other species by Grobben (No. 10), Marchal (No. 17), and Weldon (No. 20). The only point upon which there appears to be a division of opinion is as to the nature of the most internal layer of the tube (*cut.*), which Grobben considers to be a cuticle pierced by fine pores, whilst Marchal regards it as made up of rows of minute vesicles, which subsequently enlarge and break away from the cells. Without expressing an opinion as to the latter point, I can say that Marchal's figures (No. 17), especially his fig. 8, pl. v, represent much more nearly the appearance of this layer, as I have observed it, than the figures given by Grobben (No. 10).

The condition of the green gland represented in fig. 1 occurs, as I have stated, in larvæ which are a few days old. At the time of hatching, however, a more primitive condition is found, for when this event takes place the gland is entirely without a lumen, although the ureter and external opening are present. A transverse section through it at this stage is represented in fig. 2. The gland has the same general shape as in the later stage, and the end-sac (*e. s.*) and bladder (*bl.*) are easily distinguished. They consist, however, of solid masses of cells, in which as yet no cavity has appeared. A few hours after the larva is hatched the cells begin to separate, and so give rise to the lumen of the gland. A transverse section at this time is shown in fig. 3.

The striation of the protoplasm of the bladder can be indistinctly seen in these early stages, but from the appearance of the gland I should not judge that it was yet functional.

The later development of the green gland consists chiefly in the enlargement of the bladder. The latter commences to grow in the region indicated by the letter *E* in fig. 1. At the end of a week after hatching its enlargement has already passed out of the basal joint of the second antenna, and by the end of a fortnight it has grown inwards beneath the circum-oesophageal nerve-commissure as far as the mid-ventral line. A still later stage is represented in fig. 4. Here the bladder has commenced to grow in a dorsal direction, anterior to the

oesophagus, and between the two nerve-commissures. In the stage figured, it has reached a point which is at a distance from the ventral surface about a quarter as great as the height of the body in this region.

In a young *Palæmonetes*, which has apparently just assumed adult characters, the enlarged portions of the bladders of the two green glands are seen in sections (fig. 5, *bl.*) to lie side by side above the stomach in the position occupied by the single unpaired sac of the adult. The latter sac is formed by the fusion of the enlargements of the bladders of the two sides, and in the series from which fig. 5 was drawn this fusion had already commenced in the most posterior portions of the two enlargements.

The mode of development of this nephro-peritoneal sac ("vessie sus-stomacale impaire"—Marchal) proves it to be in reality derived from the fusion of the greatly enlarged bladders of opposite sides, a conclusion which has been already arrived at by Weldon (No. 20) and Marchal (No. 17) from a comparative study of the renal organs of the Decapods.

With regard to the plexus of tubules found in the adult between the end-sac and the bladder, I can only say that it is derived from the single short renal tube which in the larva connects the end-sac with the bladder; that is to say, the portion between the opening of the end-sac and the point indicated by the letter *E* in fig. 1. This tube enlarges considerably in size, but remains single until a late stage of larval life; whilst in the youngest adult of which I possess sections there are already several smaller tubules, which have obviously been derived by the splitting up of the single tube, but exactly how the process has taken place I do not know. What has in all probability happened is simply that opposite walls of the large tube have grown together along certain lines, and thus given rise to the complicated plexus of smaller ones.

THE SHELL-GLAND.—As long ago as 1876, Claus (No. 2) predicted that a rudiment of the shell-gland would in all

probability be found in Malacostraca larvæ, and he figures what he takes to be this gland in a stomatopod larva (No. 2, pl. iv, fig. 8). He has subsequently shown that the gland exists in Anisopods and Isopods (No. 7). In a figure of a *Callianassa* larva in the mysis stage, Claus also inserts and names the shell-gland, opening on the posterior surface of the second maxilla (No. 5, pl. v, fig. 42). I believe that this is the only recorded instance of the gland having been recognised in a Decapod at any stage. It occurs, however, in the larvæ both of *Palæmonetes* and of *Palæmon*, and at the time of hatching is in a much more highly developed state than the green gland. It is, in fact, at this time the functional renal organ of the animal, the green gland being still without a lumen, and only showing very faintly the characteristic striation of the protoplasm.

The shell-gland of *Palæmonetes* has the typical structure of a crustacean nephridium (fig. 6, *sh. gl.*; figs. 7 and 8). It consists of a comparatively short renal tube (*tu.*), with a considerable lumen, which communicates internally with the end-sac (*e. s.*), and opens externally at the base of the second maxilla (fig. 8, B, *ex. o.*). Fig. 6, *sh. gl.*, and fig. 7 represent transverse sections through the gland; whilst fig. 8, A, B, and C, shows three of a series of sagittal sections, of which A is more internal and C more external than B. The general form of the tube may be expressed by saying that it is Y-shaped, the two arms of the Y being in a horizontal plane, with the end-sac attached to the internal one, whilst the leg of the Y is curved in a vertical plane, the concavity looking downwards and backwards. Fig. 6, *sh. gl.*, and fig. 7 both pass through the two arms of the Y, and through the point of attachment of the end-sac.

The end-sac (*e. s.*), which is suspended from the body-wall by bands of connective tissue, has a similar structure to the end-sacs of the green glands of *Estheria* and *Mysis* as figured by Grobben (No. 10), and to those of the green gland and shell-gland of *Branchipus* as figured by Claus (No. 6). It will be observed, however, that in all my figures the cavity of

the end-sac is not in free communication with that of the tube, the entrance from the one to the other being guarded by certain elongated cells of the end-sac which project into the lumen of the tube. Two such cells appear in each section. This arrangement of cells is invariably found at the point where the end-sac joins the tube, and appears to constitute a valve which would allow fluid to pass out of the end-sac, but would prevent it from returning in the opposite direction. The structure of the walls of the renal tube of the shell-gland is the same as that of the corresponding parts of the green gland.

In his account of the development of *Eriphya spinifrons*, Lebedinski (No. 16) describes a pair of "segmental organs" which develop as evaginations of the somatopleure, and which, according to him, communicate directly with the body-cavity, and open at the bases of the first pair of maxillipedes. Korschelt and Heider (No. 14) have already suggested that this organ may be the shell-gland. If this suggestion be correct, Lebedinski must either have mistaken the appendage on which the gland opens and overlooked the end-sac, or the arrangement in the species examined by him must vary from that which exists in *Palæmonetes* and *Palæmon*, and which upon theoretical grounds appears the more probable.

It is a fact of interest, and one which is of some importance in a consideration of the phylogeny of the various groups of Crustacea, that in the Entomostraca (*Branchipus*, Claus, No. 6; *Cetochilus*, Grobben, No. 11) the green gland is the first of the two pairs of nephridia to become functional, the full development and activity of the shell-gland being deferred to the post-larval period when the green gland has almost disappeared, whilst among the Decapods the periods of development of the two glands are reversed.

The shell-gland is, I believe, functional in *Palæmonetes* even before hatching, as I have observed it in sections of embryos, some time before this event, with a well-developed lumen, with the characteristic striation of the protoplasm, with a definite external opening, and with a mass of yellowish

concretion in the distal portion of the tube. On the other hand, in young specimens which have attained adult characters no trace of this gland has been detected. In them the green gland, which did not appear to be functional at the time of hatching, has become remarkably developed, its activity having increased as that of the shell-gland diminished.

Claus has shown that shell-gland and green gland are developed in the same order in *Nebalia* as that which occurs in Decapods, and the union of that animal with the Thoracostraca rather than with the Entomostraca is favoured (cf. Claus, No. 8, p. 100).

The different behaviour of the two pairs of nephridia in Entomostraca and Malacostraca renders it unlikely that the latter have descended directly from the former. We should rather suppose that the two groups possessed a common ancestor, in which both pairs of nephridia were equally developed.

## II. THE BODY-CAVITY.

THE ANTERIOR REGION OF THE THORAX.—Fig. 6 represents a transverse section through the region of the second maxillæ of a *Palæmonetes* larva which is ten days old. The body of the animal is surrounded by a layer of thin chitin, beneath which the ectoderm lies. The latter consists of a layer of flattened cells with oval nuclei. A considerable thickening of the ectoderm is generally found in the middle dorsal line (figs. 9, 16), whilst along the ventral surface the layer presents a peculiar granular appearance (figs. 6, 18, 19, *ect.*) which I have been unable to account for. The cavity enclosed by the chitin and ectoderm may be divided into four regions: a dorsal sac (*c.*) surrounded by a definite layer of epithelium, and in which the cephalic aorta (Claus; “*artère ophthalmique*”—Milne Edwards) lies ( *Ao. c.*), but which does not itself contain blood; a central cavity (*b. c.*), in which the liver, intestine, and nerve-cord are found; two lateral cavities (*b. lat.*), separated from the central cavity by masses of muscle and bands of connective tissue, and which

in the region of the second maxillæ contain the proximal ends of the shell-glands; and fourthly, the cavities of the limbs, which contain the distal ends of the same organs. The cavities of the limbs communicate with the lateral cavities, and the latter frequently communicate with the central cavity by the disappearance of the connective-tissue bands. The three latter cavities all contain blood. The intestine, the liver lobes, the nerve-cord, and the muscles are each surrounded by a definite layer of mesoderm. That surrounding the liver is strongly muscular, the lobes in the living larva being often seen to vigorously contract. Around the shell-gland I have been unable to detect any similar mesodermal investment.

In the parts of the thorax anterior to the region of Maxilla II a similar condition of things occurs (fig. 9), except that the central cavity is somewhat broken up by the masses of muscle which move the mandibles. No trace of nephridia has been seen in the segments between Antenna II and Maxilla II, but a section through the region of the first maxillæ (fig. 9) shows in the lateral cavities a single pair of large glands (*rt. gl.*), which have the same structure as the spherical glands which I have recently described in the axis of the gill of the adult *Palæmonetes* (No. 1). These glands open by short ducts at the bases of the first maxillæ, and they, together with the smaller salivary glands (*sal. gl.*), which are present in considerable numbers in the upper lip, the paragnaths, and the maxillæ, have a great affinity for hæmatoxylin, and assume a much brighter tint when that stain is used than the surrounding tissues.

**THE DORSAL SAC.**—I have found the dorsal sac in *Palæmon serratus*, *Palæmonetes varians*, and *Cragon vulgaris*, and in the adult it attains a considerable size. If a dissection be made of an adult *Palæmon* the sac is readily seen (fig. 10). Anteriorly it appears as a long cylindrical tube (*c.*) lying upon the dorsal enlargement of the bladder (*bl.*), and containing within it the cephalic aorta ( *Ao. c.*). Posteriorly it is very



much enlarged, covering the front part of the ovaries, and running downwards on either side into the cavity which surrounds the intestine and liver. The sac extends backwards to near the front end of the pericardial cavity, but it is completely closed, and has no communication with the latter.

By means of a series of sections through a fully grown adult specimen of *Palæmonetes varians*, I have ascertained that exactly similar relations exist in that form, and the sections entirely confirm the results of dissection.

The position of the sac in larvæ is also similar to that which it occupies in adults. It is seen in transverse section in figs. 6 and 9, *c.*, and in sagittal section in fig. 11, *c.* It extends from the base of the rostrum to a point in front of the anterior end of the pericardial septum. The sac appears to be completely closed, and in preserved specimens contains a clot, which can generally be distinguished from the surrounding blood-clot, and which contains no corpuscles.

I have only met with one reference to the existence of this sac. Weldon (No. 20) describes the nephro-peritoneal sac of *Palæmon* as lying "ventral to the ophthalmic artery and to the median dorsal blood-sinus." The dorsal sac above described is what is here referred to as the "median dorsal blood-sinus." It does not, however, contain blood. I have been led to this conclusion for the following reasons:—(1) In a large number of series of sections, both of larvæ and adults, I have never seen a blood-corpuscle within the sac. (2) The sac is closed, and has no communication with the blood-sinuses of the body. This point can be definitely established for larvæ. With regard to adults I cannot make such a positive statement, on account of the difficulty of obtaining a perfect series of undamaged sections, but I have seen nothing which would suggest a contrary conclusion. (3) I have observed carefully and for a long time living larvæ under the microscope. If the larvæ are lying upon their sides blood-corpuscles are readily seen passing along the cephalic aorta, and corpuscles returning from the head are also observed; but the latter keep always quite close to the anterior lobes of the liver. The space occu-

ped by the dorsal sac—that is to say, the space between the cephalic aorta and the row of corpuscles close to the liver—is absolutely free from corpuscles.

At its anterior end the dorsal sac is surrounded by a curious mass of tissue, which is seen in transverse section in fig. 12 (compare also figs. 10, 11, and 15, *l. g.*). Before commencing this research, Professor Weldon, to whom the existence of this mass of cells was known, and who has indicated it in his figures (No. 20, pl. i, figs. 1—3), suggested to me that blood-corpuscles were being budded off by the tissue, and my preparations certainly tend to support this view. In fig. 12 I have endeavoured to represent as nearly as possible the appearance presented by a section, and it is difficult to account for it in any other way than that which Professor Weldon suggests, since the outlying cells cannot be distinguished from blood-corpuscles found in other parts of the body.

A pair of muscles must also be mentioned, which run on either side of the cephalic aorta in the anterior portion of the dorsal sac. These muscles (figs. 11, 12, 15, *c. m.*) run, in the adult, from the median dorsal surface of the carapace to points just below the angle made by the inferior surface of the rostrum with the front end of the head. What their function is in *Palæmonetes* is not apparent, but they would seem to be homologous with the muscles which move the rostrum in other forms.

DEVELOPMENT OF DORSAL SAC.—According to Reichenbach for *Astacus* (No. 18), and Kingsley for *Crangon* (No. 13), the cephalic aorta of Decapods is formed from mesoderm-cells which have broken away from the ventral bands and wandered to the dorsal surface, where they unite to form a tube. Although I have not specially studied these stages, I may say that one series of sections which I have made tends to confirm the view that these cells travel up on either side between the liver lobes and the ectoderm; and the mode of development of the heart of Branchipus, as described by Claus (No. 6), in which animal solid masses of mesoderm grow up on both

sides, appears to be a more primitive form of the same process.

In embryos of *Palæmonetes*, in which the cephalic aorta is already formed, the latter is not surrounded by a single layer of cells, but the nuclei are in reality arranged in two layers, an internal and an external. This may be seen from fig. 13, A and B, which are drawn from a late embryo of *Palæmonetes*; but the arrangement in two layers becomes even more obvious when a series of sections is examined. Fig. 13, B, represents the condition of things along the greater part of the length of the aorta, but a few anterior sections appear as in fig. 13, A, where a tongue of mesoderm extends downwards between the liver lobes. This condition of things will be explained at a later stage. In both figures (fig. 13, A and B) the nuclei *n'* belong to the internal layer, the nuclei *n''* to the external.

Before the time of hatching arrives, the cells which surround the aorta become considerably enlarged, and give rise to the appearance of solid masses of mesoderm upon either side. Fig. 14, E, may be taken to represent the condition of things throughout the greater part of the length of the aorta just before the larva leaves the egg. In this figure the blood is coloured black, the central mass ( *Ao. c.*) being in the cavity of the aorta, the remainder being in the cavity of the body which lies between the liver lobes (*li.*) and the ectoderm (*ect.*); *mes.* represents the mass of mesoderm on either side of the aorta.

Soon after hatching a change takes place, which leads to the formation of the dorsal sac. Fig. 14 represents sections through different regions of the thorax of a larva very soon after it has become free. The second section drawn (fig. 14, B) passes through the region of the paragnaths. The cells of the external layer (cf. fig. 13, B) are here seen to have drawn away from those of the internal layer which form the walls of the aorta, leaving a clear space (*c*), which extends almost completely around the latter. A few sections further back this cavity begins to close, until the condition represented in fig. 14, C, is reached. A comparison of this section with those which pre-

cede and follow it renders it highly probable that there is a complete closing of the cavity at this point, which is situated in the anterior portion of the segment of the first maxillæ. Behind this point sections similar to that seen in fig. 14, D, are met with, and this stage is specially important and interesting. Two distinct cavities have here formed in the masses of mesoderm-cells, and these cavities are separated from each other by the cephalic aorta. After persisting throughout the region of the first maxillæ these cavities close, and the sections appear as in fig. 14, E; that is to say, solid masses of mesoderm still lie on either side of the aorta. This condition of things continues through the region of the second maxillæ until the point is reached at which, in the following stages, the dorsal sac is found to end. This point is easily determined, because the intestine is there attached by bands of connective tissue to the dorsal surface of the carapace, the bands passing close to the cephalic aorta.

The most anterior region of the aorta and sac remains to be considered. A transverse section through the parts, which is nearly at the level of the mouth, is shown in fig. 14, A. The appearance here presented is explained by fig. 15, which represents a horizontal section through the front part of the head. The cephalic aorta, which has run horizontally from the heart, suddenly bends downwards, and runs almost perpendicularly towards the brain. It is surrounded during this part of its course by the cells already described (fig. 12) as giving rise to blood-corpuscles (*l. g.*), and has upon either side of it the two muscles (*c. m.*) which are also found in the adult. The dorsal sac is already open behind the aorta (fig. 15, c), and the transverse section (fig. 14, A, c) passes along its length.

The following numbers, obtained from the series of which figs. 14, A—E, represent selected sections, will give an idea of the extent of the different regions. The cavity of the sac is seen below the aorta as in fig. 14, A, in three sections at the level of the mouth, this condition passing into that of fig. 14, B, where the cavity is below and on both sides of the aorta, which continues for six sections. The next section is

represented in fig. 14, c. The condition with two lateral cavities (fig. 14, d) then appears, and persists in eleven sections in the region of the first maxillæ. The appearance seen in fig. 14, b, in which no cavity is yet formed, runs through the next nine sections in the region of the second maxillæ to the point where the bands of connective tissue suspend the intestine.

In a larva only a few hours older than the one just described, what appears at first sight to be a very considerable development has taken place. From the region of the mouth to that of the second maxillæ the parts under consideration have the appearance represented in fig. 16, A, a few sections only at the posterior end presenting that shown in fig. 16, B. There is now one cavity, which surrounds three sides of the aorta and extends along its whole length. But no great rapidity of growth has been necessary to produce this marked result. By comparing the sections of fig. 14 with those of fig. 16 it will be seen that what has taken place is that the protoplasm of the cells, instead of being gathered into masses around the nuclei, has spread out into a thin sheet, thereby enlarging considerably the cavity, and drawing its walls away from the wall of the aorta.

The sections at the posterior end of the sac in this and the following stages are of special interest, because in them the cavity is divided by a vertical septum (fig. 16, B, s.) into two lateral portions. This fact tends to confirm what is already apparent from fig. 14, d, of the previous stage, that the cavity of the dorsal sac is formed by the union of two lateral cavities, which lie on either side of the cephalic aorta.

The further development of the dorsal sac consists mainly of an increase in its size. Later stages are seen in fig. 9 and fig. 6, c. Its walls are very thin, and the nuclei spindle-shaped. At its posterior end the sac grows backwards as a pair of lobes, which are not attached to the wall of the aorta, and which extend as far as the front end of the pericardium. A section through these lobes is seen in fig. 17. This posterior portion of the dorsal sac becomes very much enlarged in

the adult, as has already been shown, and lies upon the front end of the ovary (fig. 10).

**THE POSTERIOR REGION OF THE THORAX.**—The condition of the body-cavity in this region may be gathered from figs. 18 and 19. The central and lateral cavities (*bc.*, *b. lat.*) are similar to those in the anterior region, whilst dorsal to these the pericardial chamber lies (*per.*). This chamber is separated from the central body-cavity, as is already well known, by the pericardial septum (*p. sep.*), and it contains the heart. In the larva the pericardial cavity appears to be bounded dorsally by the ectoderm, but I consider it probable that a layer of mesoderm lies within the ectoderm, although I have been unable to detect it. Such a layer is undoubtedly present in the adult, although it is even then very thin, and has extremely small nuclei.

At the front end of the pericardial cavity, immediately beneath the pericardial septum, the genital organs are situated (fig. 18, *gen.*). In the just hatched larva and in late embryos these consist of two masses of cells with large nuclei, each mass being enclosed in a sheath of mesoderm. At this stage the presence of the latter, on account of the extreme tenuity of the layer, can only be ascertained by the presence of occasional spindle-shaped nuclei which lie outside the larger cells, but in later stages this mesodermal investment becomes much more marked. Bobretzky (see No. 14, p. 379) has already stated that the genital organs originate in the region in which they are found in the larva.

I have not been able to find any trace of the genital ducts in young larvæ, and can give no information as to how these organs originate.

**THE ABDOMEN.**—With regard to the abdomen I have no new facts to add, but my sections confirm the accounts given by Milne Edwards (No. 9) and Claus (No. 4). There are two principal sinuses which run along its whole length—a dorsal sinus in which the intestine lies, and a ventral one which con-

tains the nerve-cord. These two sinuses are generally separated by masses of muscle, but they communicate at intervals by means of lateral sinuses.

**THEORETICAL CONSIDERATIONS.**—We may seek for an explanation of the relations above described by comparing them with the condition of the body-cavity, as described by Sedgwick (No. 19) and von Kennel (No. 12), during the development of *Peripatus*. Briefly stated, the course of events in the latter animal is as follows:—The hollow mesoblastic somites which form in the ventral bands of mesoderm divide into two portions, which are distinguished as dorsal and lateral. The lateral portions of the somites are transformed into nephridia, whilst the cavity of the lateral sinus of the body originates as a hollowing out in their thickened external walls. The dorsal portions of the somites enlarge upwards, but those of opposite sides do not meet in the dorsal middle line. A space is left between them, which becomes the cavity of the heart. At this stage the dorsal portions of the somites may be said to have attained their maximum state of development. By the diminution of their cavities they then cause the formation of spaces external to themselves, which become lined by wandering mesoderm-cells, and form the pericardial chamber and central body-cavity of the adult. These two cavities are separated by the pericardial septum, which is apparently formed in a more direct way from the walls of the diminishing somites. In certain regions of the body the remnants of the dorsal portions of the somites persist, according to Sedgwick, as the external membrane of the genital glands; whilst, according to v. Kennel, they give rise both to the internal and external cells of these organs. The condition in the adult *Peripatus* is described by Sedgwick (No. 19, pt. 4, p. 385) as follows:—“The hæmocœle is divided into five main chambers: (1) the central compartment of the body-cavity; (2) the heart; (3) the pericardial cavity; (4) the two lateral compartments or lateral sinuses (in which the nerve-cord and salivary glands lie). In addition to these there are the

leg-cavities, which contain the nephridia and communicate with (4)."

We are now in a position to compare the body-cavities of *Palæmonetes* and *Peripatus*. Considering first the anterior region of the thorax of the former animal, as shown in figs. 6 and 9, we may compare it with the condition of things in *Peripatus* at the time when the dorsal portions of the mesoblastic somites have attained their maximum development. Bearing in mind that the dorsal sac of *Palæmonetes* has been formed by the union of two lateral cavities, which lay on either side of the aorta (cf. figs. 14, D, and 16, B), the differences between the two forms are very slight. The dorsal sac represents the two dorsal portions of the mesoblastic somites, whilst the central cavity, the lateral cavities, and the nephridia agree, with the one exception that the two lateral portions of the nerve-cord of *Peripatus* have united in the middle line in *Palæmonetes*, and in the process have passed out of the lateral cavities. The fact that the internal end of the nephridium lies in the lateral cavity, and not in the cavity of the leg, which, as already stated, contains the greater part of its tube, appears to agree with the condition of things figured by Sedgwick for certain parts of *Peripatus* (No. 19, pt. 4, pl. xxvii, fig. 11).

The agreement is so close that it appears to me to be fully justifiable to homologise the various parts. If this be so, it follows that the dorsal sac of *Palæmonetes* is homologous with the dorsal portions of the mesoblastic somites of *Peripatus*, and that its cavity is a true coelom (enterocoel). The central and lateral cavities, together with the cavities of the legs, will represent the pseudocoel, and, being filled with blood, may be termed with Lankester hæmocœle.

Passing now to the posterior part of the thorax, the region of the heart (figs. 18 and 19), we find that the different cavities correspond with those which persist in the adult *Peripatus*. Heart, pericardium, and pericardial septum of *Palæmonetes* present exactly the same relations as in *Peripatus*, and are clearly homologous structures in the two animals.



The central and lateral cavities only differ with regard to the relative position of the nervous system, and this difference has already been accounted for. In the leg-cavities of *Palæmonetes* in this region no nephridia have been developed.

Beneath the anterior end of the pericardial septum are found, as has been already stated, the genital organs (fig. 18, *gen.*), and here also the comparison with *Peripatus* may be instituted. We find a similar agreement to that which existed in the other regions compared, and we may with a considerable degree of probability again homologise corresponding parts of the two forms. The genital organs of *Palæmonetes* must then be regarded as the representatives in this region of the cœlom.

It is worthy also of note that the genital ducts, as seen in young adults of *Palæmonetes*, agree in all their relations with those of *Peripatus*, and the probability of their being derived from nephridia, as suggested by Lankester (No. 15), is very great.

If the homologies here suggested are valid, the body-cavity relations of the Crustaceans under consideration may be stated briefly thus :—Both enterocœle (true cœlom) and pseudocœle are present, the enterocœle consisting of the dorsal sac, the green gland and shell-gland, together with the genital organs and their ducts, whilst the pericardial septum may be regarded as equivalent to the fused walls of another portion of the same structure (cf. Korschelt u. Heider, No. 14, p. 901). The pseudocœle consists of the heart and arteries, the pericardial cavity, the central cavity of the thorax, with the lateral cavities and the cavities of the limbs, and the various sinuses of the abdomen. The whole of the pseudocœle is filled with blood, and hence can be termed a hæmocœle.

A few considerations may now be added with regard to that portion of the cœlom which persists as the dorsal sac. The most striking feature of this cœlom is the late period of development at which it opens; but it may be pointed out that the cavity of the green gland (both of its tube and end-sac), which we also regard as cœlomic in nature, begins to appear

at precisely the same time, the two cases differing, however, in all probability, in the fact that in the former the cells which subsequently form the walls of the cavity have been through a wandering stage (mesenchyme), whilst those of the latter, so far as we can judge, have not. This does not, however, I believe, alter the conclusions which have been arrived at by the comparison with *Peripatus*, and which are also supported by what is known of corresponding parts in Arachnids and insects.

The question suggests itself, what effect has the presence of this persistent cœlom in the anterior part of the thorax upon our views as to the nature of the heart of these animals? The view held by Claus, and which is generally accepted, is that the short heart of Decapods has been reduced from a heart similar to that of *Branchipus*, which extends throughout almost the whole length of the body. Claus (No. 3) further considers that the Decapod heart represents the anterior portion of the heart of Stomatopods, and the evidence which he brings forward in support of this view is very convincing. How are we to account for the fact that in the region of the body anterior to the heart of these Decapods a more primitive condition of things persists than is found even in the adult *Peripatus*? There appear to me to be two alternatives: either the heart and pericardium have at one time been differentiated along the whole length of the body, and there has been subsequent degeneration in the anterior portion to the more primitive condition, or we must assume that in the ancestor of the Crustacea the differentiation into heart and pericardium had never taken place at all in this anterior region. What evidence I have been able to gather appears on the whole to favour the latter view, although it is by no means conclusive, and the question can only be settled by further research. The following facts, however, have a bearing on the matter. In *Branchipus* the cephalic aorta is present, it has no ostia, and does not pulsate. It extends through the region of the maxillæ to the second segment of the body (Claus, No. 6, p. 71). In the larva of *Artemia* the heart ends anteriorly

at about the level of the shell-gland—that is to say, in the region of the second maxillæ (ib., pl. iv, fig. 1). In *Nebalia* Claus figures a section which passes through the valves which separate the heart from the aorta, and this also passes through the point where the nerves of the second maxillæ are given off from the nerve-cord (No. 8, pl. xi, fig. 11). Claus, however, states that this section is somewhat oblique, sloping downwards and backwards, so that we must place the anterior end of the heart at least as far forwards as the front end of the segment of Maxillæ II.

In a Stomatopod larva (No. 2, pl. iv, fig. 8) the front end of the heart is figured as being slightly anterior to the shell-gland.

In young larvæ of *Palæmonetes*, as I have already shown, the dorsal sac ends in the posterior part of the region of the second maxillæ; but in all these cases it must be borne in mind that, owing to the moving forward of the appendages towards the mouth, the actual segment to which any part of the cephalic aorta or heart belongs can only be very approximately determined. Considering, however, the facts adduced, we may, I think, fairly say that in no Crustacean does the heart extend in front beyond the region of the second maxillæ, and that there is therefore no evidence to show that heart and pericardium have ever been differentiated in segments anterior to this.

#### SUMMARY OF CONCLUSIONS.

1. The green gland of *Palæmonetes* (and *Palæmon*) at the time of hatching of the larva has not developed a lumen, although the external opening can be detected. When the larva leaves the egg the lumen commences to open, and the gland consists of an end-sac and a U-shaped tube, of which the distal portion gives rise to the bladder. The bladder then enlarges greatly, growing at first inwards towards the middle ventral line, then upwards, within the œsophageal nerve-ring and anterior to the œsophagus, to the middle dorsal line,

where it meets its fellow of the opposite side. The two bladders grow backwards over the stomach and beneath the dorsal sac, subsequently fusing together in the middle line to form the unpaired nephro-peritoneal sac.

2. The shell-glands are the functional excretory organs at the time of hatching and during the latter part of the embryonal period. They open at the bases of the second maxillæ, and each consists of an end-sac and a Y-shaped renal tube, which have the typical structure of a crustacean nephridium.

3. A dorsal sac, which is completely enclosed by an epithelial lining, persists in adults of *Palæmon*, *Palæmonetes*, and *Crangon*. This sac, which does not contain blood, lies upon the nephro-peritoneal sac and the front end of the ovary, being much enlarged at its posterior end. The cephalic aorta (ophthalmic artery) lies within the dorsal sac.

4. At its anterior end the dorsal sac is surrounded by a mass of tissue which appears to be producing blood-corpuscles.

5. The dorsal sac is formed as a hollowing out in masses of mesoderm-cells, which lie on either side of the cephalic aorta. Two lateral cavities are thus formed, which increase in size and unite below the aorta. Taking into account this mode of development, a comparison with *Peripatus* shows that the dorsal sac is homologous with the dorsal portions of the mesoblastic somites of that animal, and must therefore be regarded as a true cœlom.

6. The body-cavity of these Crustaceans varies in different regions.

(a) In the anterior part of the thorax it consists of a true cœlom (the dorsal sac and nephridia) and a hæmocœle. The hæmocœle consists of (1) a central cavity, in which the stomach and intestine, the liver and the nerve-cord lie; (2) two lateral cavities, which contain the end-sac and proximal end of the tube of the shell-gland, and which communicate with the central cavity and with the cavities of the legs; and (3) these leg-cavities, which, in the second maxillæ, contain the tube of the shell-gland.

(b) In the posterior part of the thorax the body-cavity is entirely a hæmocœle. It consists of (1) the pericardial cavity, in which lies (2) the heart, and which is separated by the pericardial septum from (3) the central cavity of the body, which contains the genital organs, liver, intestine, and nerve-cord; (4) the lateral cavities, which communicate with the central cavity and with (5) the cavities of the legs.

(c) In the abdomen the body-cavity is entirely a hæmocœle. It consists of a dorsal and a ventral sinus, which communicate with one another by lateral sinuses.

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## EXPLANATION OF PLATES XXXVI, XXXVII, and XXXVIII,

Illustrating Mr. Edgar J. Allen's paper on “Nephridia and Body-cavity of some Decapod Crustacea.”

### LIST OF REFERENCE LETTERS.

*Ant. a.* Antennary artery.  *Ao. c.* Cephalic aorta.  *b. c.* Central body-cavity.  *bl.* Bladder of green gland.  *b. lat.* Lateral cavity of body.  *c.* Dorsal sac (cœlom).  *car.* Carapace.  *c. m.* Cephalic muscle.  *con. t.* Connective tissue.  *cor.* Blood-corpuscle.  *cut.* Cuticular layer of renal tube.  *E.* Point at which bladder enlarges.  *ect.* Ectoderm.  *e. s.* End-sac.  *ex. o.* External opening.  *gen.* Genital organs.  *ht.* Heart.  *int.* Intestine.  *l. g.* Tissue where blood-corpuscles are formed (lymphatic gland).  *li.* Liver lobe.  *mes.* Mass of cells from which dorsal sac develops.  *mus.* Muscle.  *Mx. II.* Maxilla II.  *n. c.* Nerve-cord.  *O.* Point where bladder of green gland joins ureter and opens.  *o. es.* Opening of end-sac into tube.  *per.* Pericardium.

*p. sep.* Pericardial septum. *rt. gl.* Reticulate gland. *s.* Septum dividing dorsal sac. *sal. gl.* Salivary gland. *sh. gl.* Shell-gland. *st.* Stomach. *st. a.* Sternal artery. *tu.* Renal tube. *u. l.* Upper lip.

## EXPLANATION OF FIGURES.

All the figures were drawn with the aid of the camera lucida.

FIG. 1.—Horizontal longitudinal section through the green gland of a larva of *Palæmonetes varians* three or four days old.  $\times 420$ .

FIG. 2.—Transverse section of green gland of *Palæmonetes* at the time of hatching.  $\times 770$ .

FIG. 3.—Ditto, a few hours after hatching.  $\times 770$ .

FIG. 4.—Somewhat diagrammatic transverse section through green gland of old larva of *Palæmonetes*.  $\times 240$ .

FIG. 5.—Transverse section of young adult *Palæmonetes*, just behind mouth.  $\times 240$ .

FIG. 6.—Transverse section of *Palæmonetes* larva, ten days old, through the region of Maxilla II.  $\times 240$ .

FIG. 7.—Transverse section through shell-gland of a recently hatched *Palæmonetes* larva. (The figure is combined from two sections.)  $\times 240$ .

FIG. 8, A, B, C.—Three sagittal sections of ditto, of which A is the most internal, B the most external.  $\times 240$ .

FIG. 9.—Transverse section of *Palæmonetes* larva, about twenty-four hours old, through the region of Maxilla I.  $\times 240$ .

FIG. 10.—*Palæmon serratus* dissected from the dorsal surface.

FIG. 11.—Sagittal section of larva of *Palæmonetes*, ten days old.  $\times 100$ .

FIG. 12.—Transverse section through anterior end of dorsal sac of young adult *Palæmonetes*, showing the tissue from which blood-corpuscles are budded off.  $\times 240$ .

FIG. 13, A, B.—Two sections through the region of cephalic aorta of a *Palæmonetes* embryo. A represents the condition at anterior end, whilst B represents the condition further back. *n'* = nucleus of internal layer, *n''* = nucleus of external layer.  $\times 240$ .

FIG. 14.—Transverse sections through cephalic aorta of *Palæmonetes* larva, within a few hours of hatching.  $\times 240$ .

- A. About level of mouth.
- B. Region of paragnaths.
- C. Ditto.
- D. Region of Maxilla I.
- E. Region of Maxilla II.

FIG. 15.—Horizontal section through anterior end of cephalic aorta of larva slightly older than that of Fig. 14.  $\times 240$ .

FIG. 16, A, B.—Transverse sections of dorsal sac and aorta of *Palæmonetes* larva, a few hours old.  $\times 240$ .

FIG. 17.—Transverse section through posterior portion of dorsal sac of *Palæmonetes* larva, three weeks old.  $\times 240$ .

FIG. 18.—Transverse section of just-hatched larva of *Palæmonetes*, through front end of pericardium.  $\times 240$ .

FIG. 19.—Ditto through middle of pericardium.  $\times 240$ .



## Note on the Cœlom and Vascular System of Mollusca and Arthropoda.

By

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THE reference by Mr. Allen in his memoir published in this number of the Journal to a note by me appended to Dr. Gulland's paper in 1885 on "The Coxal Gland of *Limulus*" induces me to reprint here the report of a paper which I read to Section D at the Manchester meeting of the British Association in 1887. This report was furnished by me to 'Nature,' and printed in that journal in March, 1888 (p. 498). Professor Julin, of Liège, also published—in a report made by him to the Belgian Academy on the proceedings at Manchester—an abstract of the same paper. The report printed in 'Nature' is as follows :

"The object of the author was to establish the fact that the system of blood-containing spaces pervading the body in Mollusca and in Arthropoda was not, as sometimes (and indeed usually) supposed, equivalent to the cœlom or perivisceral space of such animals as the Chætopoda and the Vertebrata, but was in reality a distended and irregularly swollen vascular system—the equivalent of the blood-vascular system of Chætopoda and Vertebrata. Hence he proposed to call the body-spaces of Mollusca and Arthropoda 'hæmocœl,' in contradistinction to 'cœlom.' It had been held by previous investigators that in Mollusca and Arthropoda the cœlom and the vascular system were united into one set of spaces—whether by a process of gradual fusion, or owing to the fact that the two systems had never been differentiated from a common

original space representing them both in the ancestors of these two great phyla. The author stated that he had been led to the view which he now formulated by his discovery of distinct spaces in both Mollusca and Arthropoda, which appear to be the true cœlom, and are separate from the swollen vascular system.

“ In Mollusca the pericardial space is the chief representative of cœlom. It is usually taught that the pericardium of Molluscs contains blood, and is in free communication with veins; but the author had succeeded in showing by observations on the red-blooded *Solen legumen* (already published, ‘*Zoolog. Anzeiger*,’ No. 170, 1884), and by more recent careful investigation of *Anodonta cygnea*, *Patella vulgata*, and *Helix aspersa*, that the pericardium has no communication with the vascular system, and does not contain blood. The perigonadial spaces (so-called generative glands) and the pericardial space (which has arborescent tubular outgrowths in some Lamellibranchs forming Keber’s organ) are, then, the cœlom of the Mollusca. It is quite distinct from the hæmocœl. In Cephalopods, and in the archaic Gastropod *Neomenia*, the pericardial and perigonadial cœlomic remnants are continuous, and form one cavity. There is strong reason to believe that in ancestral Molluscs the hæmocœl was more completely tubular and truly vasiform than it is in living Molluscs. In the later Molluscs the walls of the vessels have swollen out in many regions (especially the veins), and have obliterated the cœlom, which has shrunk to the small dimensions of pericardium and perigonadium. There are, however, many Molluscs with complete capillaries, arteries, and veins, in certain regions of the body. These had been recently studied by the author by means of injections, and by silver impregnation, and drawings illustrative of them were exhibited to the Section.

“ With regard to the Arthropoda, Professor Lankester formulated the same view, viz. that the ancestral blood-vessels have swollen and enlarged, especially the veins, so as to form large irregular spaces, which have blocked up and so obliterated the

previously existing cœlom. Nevertheless the cœlom still persists in some parts of the Arthropod body quite separate from the swollen blood-vascular system. It persists as the tubular generative glands (perigonadium), and also as a system of small spaces (lymph-system) in the connective tissue of *Astacus* and of *Limulus*, and as the internal terminal vesicle of the green glands and other nephridia present in various Arthropoda. Professor Lankester stated that he had been led to this view with regard to the vascular system and cœlom of the Arthropoda by the results of his histological investigations on the vascular system and connective tissues of *Astacus* and *Limulus*, and by the results obtained in his laboratory by Mr. Gulland in studying the development of the nephridial 'coxal gland' of *Limulus* (already published, with note by Professor Lankester, in the 'Quart. Journ. Micr. Sci.,' 1885, vol. xxv, p. 515). He had also been led to this view by the attempt to explain theoretically the origin of the peculiar structure of the Arthropod's heart and blood-holding pericardium.

"The Arthropod's heart and pericardium are absolutely peculiar to the group, and characteristic of all its members, even of *Peripatus*. The author had asked himself how the existence of a tubular heart with paired valvular apertures in each segment of the body, lying within a blood-holding sac, could be explained. He conceived that it might best be explained by that tendency of the veins to dilate and to form irregular large blood-sinuses, which on other grounds we have reason to consider as a structural tendency of Arthropods. Each pair of valvular apertures in the Arthropod's heart represents a pair of distinct tubular veins, which in the ancestors of the Arthropoda brought blood to the heart from the gills. These veins have dilated, and their adjacent walls have been absorbed, so that we now have, instead of a series of veins, a great continuous blood-sinus on each side of the heart or dorsal vessel.

"Capillaries of the finest dimensions were shown by Professor Lankester to exist in certain parts of *Astacus* and of *Limulus*. In studying these he had come across the remnants of cœlom.

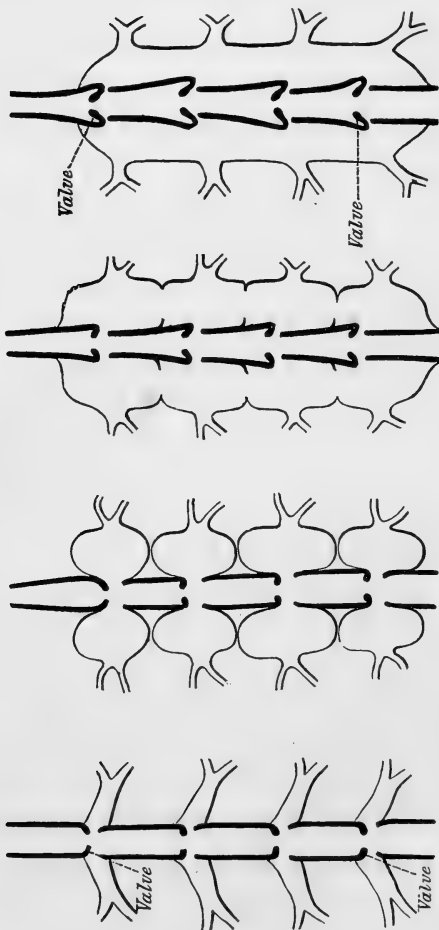


Fig. A.

Fig. B.

Fig. C.

Fig. D.

DIAGRAMS ILLUSTRATING PROFESSOR LANKESTER'S THEORY OF THE DEVELOPMENT OF THE ARTHROPOD HEART AND PERICARDIAL SINUS.

- Fig. A.—Dorsal vessel and veins with valves at their junction with the dorsal vessel. Chetopod stage.  
 Fig. B.—Hypothetical. The veins dilated.  
 Fig. C.—Hypothetical. The veins further dilated and now made confluent by the absorption of their adjacent walls.  
 Fig. D.—Arthropod heart with four pairs of ostia and a pericardial blood-sinus.

Between the capillaries and unconnected with them—in the connective tissue of both *Astacus* and *Limulus*—is a system of spaces containing a coagulable fluid. (These spaces were described and figured in *Limulus* in 1884 by Professor Lankester in the 'Quart. Journ. Micr. Sci.'). It is into this system of spaces that the tubular nephridium which becomes the coxal gland of *Limulus* opens. Hence these spaces are remnants of the cœlom, elsewhere blocked up and obliterated by the swollen veins which form the hæmocœl. The tubular generative glands of Arthropods are to be explained as perigonadial cœlom communicating with the exterior through modified nephridia. Beddard's discovery of such a condition of the ovary and oviduct in the earthworm *Eudrilus* is confirmatory of this explanation.

"The views which had been thus arrived at by Professor Lankester, and very briefly indicated in the note in the 'Quart. Journ. Micr. Sci.,' 1885, p. 515, have received a startling and demonstrative confirmation in Sedgwick's brilliant results as to the development of cœlom and hæmocœl in *Peripatus*, published in the 'Quart. Journ. Micr. Sci.,' February, 1888, and announced early in 1887 to the Cambridge Philosophical Society."

To this brief statement I may now add that it has been for some time my desire to obtain well-preserved specimens of *Lernanthropus*, the remarkable Copepod with a tubular vascular system containing hæmoglobinised blood, first described as possessing this peculiarity by Edouard van Beneden, and subsequently figured and described in detail by Heider ('Arbeiten Zool. Inst. Wien,' Bd. ii, 1879). It would be extremely important to ascertain, if possible, whether the tubular vascular system of *Lernanthropus* co-exists with spaces which can be identified with the supposed hæmocœl of other Crustacea, or whether, as should be the case if my theory is correct, the spaces in *Lernanthropus*, which are not in continuity with the red vascular system, can be identified as "cœlom," and distinguished from "hæmocœl spaces."

I have failed to obtain *Lernanthropus* either from Plymouth

or from Naples. If any naturalist reading these lines should be able and willing to furnish me with specimens he would confer a great favour on me by communicating with me.

The question in regard to *Lernanthropus* may be further stated in this way: is the tubular vascular system of that animal an heirloom from Annelid-like ancestors with the characteristic *Chætopod's* vascular system? or is it a special development *de novo* peculiar to this *Copepod*?

One of the most attractive features about the theory of dilated veins in the Arthropods is the simple explanation which it affords of an otherwise puzzling structure, namely, the Arthropod heart. I therefore venture to present here a diagram which I have made use of during the last six years in my lectures illustrating the possible—I think we may say the probable—steps by which the Arthropod heart, with its curious valvate ostia and blood-holding pericardial space, was developed from the dorsal vessel of a closed “tubular” vascular system such as that of the earthworm.

## Contributions to a Knowledge of British Marine Turbellaria.

By

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With Plates XXXIX, XL, & XLI.

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### I. INTRODUCTORY.

#### 1. Nature and Scope of the Paper.

It is usual to begin a faunistic paper on Turbellaria with the words of Oscar Schmidt, "Man braucht, wie es scheint, wo man will nur zuzugreifen und ist der Ausbeute sicher;" and although written forty years ago, they are still applicable to this group. In the northern European seas (and it was to these that Schmidt referred) many species may be found by careful examination of almost any portion of the littoral and laminarian zones. Yet, owing probably to their small size, inconspicuous appearance, perishable nature, and obscure

anatomy, few naturalists in this country have devoted much attention to them. When once a keen interest, however, is aroused, the number of new and morphologically important forms that may be found in a limited area is beyond anticipation. This has been well expressed by Jensen in the preface to his work on the Turbellaria of the west coast of Norway: "The new forms described here are only a very small part of those that occur on our coasts. A rich harvest remains behind. Indeed, one has no need to go far to find numbers of new species. Among seaweed they are frequently brought up at every haul. At greater depths, again, other new species are found; but as regards the occurrence of the smaller and more numerous forms, our fauna is still quite unknown."<sup>1</sup>

This quotation applies very appositely to the present case. As yet only a small portion of our coast has been explored. Extended observations are urgently needed. Still, from my own list, together with the records of other naturalists who have from time to time noted the occurrence of British forms, it appears that our fauna already includes fourteen Polyclads, two Triclads, and fifty-five Rhabdocœles—a total of over seventy species. It is to the description of these that I address myself. In doing so I shall try to indicate the distinctive points, structural and bionomical, that separate the various forms, reserving a more detailed account of the anatomy of new or partially known species to a future paper.

The specific descriptions (which largely confirm those of previous observers) are taken, except where otherwise stated, from my own observations.

One section of the group—the parasitic Turbellaria—is omitted. These forms undoubtedly occur on our coasts, but I have had no opportunity for their investigation.

<sup>1</sup> Preface: "De her beskrevne nye Former ere da kun en meget liden Brökdel af de ved vore Kyster forekommende. En rig Höst staar tilbage. Man behöover sandelig ikke at gaa langt for at finde en Mængde nye Arter. I Tangen i Fjæren kan man jevnlig drage saadaanne op hvert Kast . . . men Faunæn her, navnlig for de mindre og talrigste Årters Vorkommende, er endnu helt unbekjendt" (49). The numbers in brackets refer to the list of literature at the end of this paper.



## 2. Historical Account.

The history of British marine Turbellaria may be said to begin with the publication of Dalyell's octavo volume, "Observations on some Interesting Phænomena in Animal Physiology exhibited by Several Species of Planariæ" (1811 and 1814). Among the eight species there described, is a marine one, *Planaria flexilis* (now known as *Leptoplana tremellaris*), from the Firth of Forth. This animal, however, was not new. It had been discovered and carefully described by O. F. Müller, in his 'Vermium terrestrium et fluviatilium Historia,' nearly forty years before. While, therefore, Dalyell made no new discovery in *Planaria flexilis*, his study of its habits considerably increased our existing knowledge.

The merit of his work lies in the careful and patient observations, the accumulation of many years, which it records. The muddy haunts of the *flexilis*, its active behaviour when in search of food, its inordinate appetite after a period of starvation (illustrated by a case in which the bodies of three individuals burst and subsequently putrefied, owing to the quantity of food absorbed), the increase in bulk and changes of colour due to the contained nutriment, the mode of propagation by eggs laid in batches like those of molluscs, and the power of repairing serious injury,—all these points are graphically described and extended to seven fresh-water forms. In fact, this book contains even at the present time the best account that we possess of the bionomics of these animals, and well earned for Dalyell the dedication by v. Graff of his 'Monographie der Turbellarien.'

From 1814 to 1852 the work done on this group was confined, in this country, to the description of single forms, or to the records of their occurrence on our coasts. Montagu (7) in 1815 discovered *Planaria vittata* (*Prosthecercæus vittatus*) on the south coast of Devonshire. In 1821 Fleming (8) found *Planaria atomata*, *tremellaris*, and *vittata* during a voyage round Scotland. Our knowledge of this part of the British fauna was further increased by a series

of papers by Dr. George Johnson, and Wm. Thompson, of Dublin. The former, under the title 'Illustrations of British Zoology' (11 and 12), described *Planaria cornuta* (*Eurylepta cornuta*) and *Planaria subauriculata* (*Stylochoplana subauriculata*) from the shores of Berwick Bay. These accounts suffice to enable us to identify the species referred to, but give little idea of their internal anatomy. The relations of the known forms to one another were as yet quite obscure. Thompson recorded forms from various Irish localities. Forbes and Goodsir found Polyclads in the Orkneys and Shetlands in 1839 (13), and in his later dredging reports Forbes frequently enters "*Planaria* sp.?" accompanied by a lament that so little is yet known of these forms.

If we turn to work done on the Continent during this period (1830—1850) we find that v. Baer and Dugès had independently discovered the internal anatomy and especially the generative organs of the fresh-water Planariæ, and had proposed a rough scheme of classification. The corresponding discovery of the anatomy of Polyclads was made by v. Mertens.<sup>1</sup> Ehrenberg (10) had found many new forms, some of which constituted his subdivision "*Rhabdocœla*." Oersted's most important paper (16) appeared in 1844,<sup>2</sup> containing a system which included all known species, and from which later attempts originate. Our knowledge of the histology and anatomy of the *Rhabdocœles* (the small size of which usually prevented an adequate investigation being made, on account of the necessity for high magnifying powers) was immensely increased by Max Schultze's '*Beiträge zur Naturgeschichte d. Turbellarien*,' 1851. The accuracy of the descriptions and beauty of the copper plates are well known.

The following year (1852) Dalyell published the '*Powers of the Creator*,' the second volume of which contains references to a considerable number of Turbellaria. Among these,

<sup>1</sup> "Untersuchungen ü. d. Bau verschiedener in d. See lebender Planarien," '*Mém. de l'Acad. Imp. d. Sciences d. St. Pétersbourg*,' sér. 6<sup>me</sup>, t. ii, 1833.

<sup>2</sup> Reprinted with figures and additions from '*Krøyers Naturhist. Tidsskrift*,' 1843.

*Monotus lineatus* and *Convoluta paradoxa* are interesting as being the first records of British Rhabdocelida. The habits and reproduction are well described, but the anatomy is very far behind the knowledge of the time. For ten years (1852—1862) little work on these forms was done in this country, while Oscar Schmidt, Schultze, and Leuckart on the Continent were extending a monographic and systematic knowledge of the group. In 1859, however, Claparède spent August and September in the Hebrides, chiefly at Skye. In a most interesting paper (35) he describes *Convoluta paradoxa* (in which he determined successive hermaphroditism), *Mesostomum marmoratum*, *Prostomum caledonicum*, *Vortex quadrioculata*, *Enterostomum fingsalianum*, and the Polyclads *Centrostromum Mertensii* and *Eurylepta aurita*. Similar researches (36) on the coast of Normandy showed what a varied Turbellarian fauna existed there. No one, however, was found in this country to advance our knowledge of the group on similar lines.

In 1865 the 'Catalogue of Non-parasitical Worms in the British Museum' appeared. The marine Turbellaria are taken from the works of Johnston, Thompson, and Dalyell, together with a few new records.

A year later Lankester (39) issued a list of the fauna of Firman Bay, Guernsey, containing *Convoluta paradoxa*, *Leptoplana auricularis*, *L. flexilis*, and *Eurylepta cornuta*. In 1875 McIntosh (45) published his 'Marine Invertebrates and Fishes of St. Andrews,' in which several Turbellaria are mentioned. The occurrence of *Prostoma lineare*, Oe. (*Gyrator hermaphroditus*, Ehrh.), in the sea, and a short description of *Mesostoma bifidum*, n. sp. (*Pseudorhynchus bifidus*), are specially noteworthy. v. Graff paid a visit to Millport, the results of which are incorporated in his great monograph ([53,] 1882, p. 437). Twenty-four marine species of this group were found and fully described. In the summers of 1884 and 1885, Koehler explored the Channel Islands. A list of the forms obtained may be found in the 'Annals and Mag. of Nat. Hist.,' fifth

series, vol. xviii, p. 362. The most important additions to the Turbellarian fauna are *Oligocladus sanguinolentus* and *Proceros argus*.

### 3. Nomenclature.

I wish in this section to discuss certain difficulties connected with the terminology of the complicated reproductive organs of the Turbellaria.

The stages exhibited by different members of this group, by which a simple organ, producing ova capable of manufacturing the necessary food-yolk, becomes differentiated into two parts, one furnishing ova, the other yolk, and the final separation of these two parts into two distinct organs, have been pointed out by Gegenbaur, Balfour, and others. Thus in the *Acœla* the organ is quite simple, the ova elaborating their own food-yolk. To such an organ I shall apply the term ovary. Certain *Rhabdocœla*—e. g. *Prorhynchus*—exhibit the first stage in complexity. The cells are still equivalent, but are not all equally capable of becoming ova; those that are not, form yolk-cells destined for the nutrition of the ovarian part of the organ. The secretion of yolk-granules by the yolk-cells surrounding the fertilised ova, which in this form does not take place until the ova have undergone segmentation, in the *Cylindrostominae* and others occurs before the yolk is transferred to the ova. To such an organ, performing a double function, the Germans apply the term "Keimdotterstock," and as an equivalent I shall use "germ-yolk-gland," although, strictly speaking, the word "gland" should apply to the vitelline portion only.

In the great majority of Turbellaria the two parts become separate organs with distinct functions. For these I use the old terms *germarium* for the ovarian organ, and *vitellarium* or yolk-gland for the nutritive one. The term *vagina* I apply to that part of the female genital duct which forms a sheath for the penis during copulation. For the storage and nutrition of the spermatozoa various accessory organs are developed. For a single organ, serving to retain the sperm until

fertilisation is accomplished, the term *spermatheca* is a convenient equivalent for "*bursa seminalis*," used by v. Graff. In many cases (e. g. *Vorticidæ*) two organs are present, one of which receives the male products of another individual, and then passes it on to the second, from which fertilisation takes place. I retain the term *bursa copulatrix* for the former muscular structure, and *receptaculum seminis* for the latter. While the ova are being duly fertilised, provided with food-yolk, and surrounded by an egg-capsule, they are usually retained within the body of the parent during, and usually also a short time after, these changes. Consequently a certain amount of development is passed through. To the region in which this takes place the term *uterus* may be applied.

The testes offer no difficulties of terminology. *Vasa efferentia* may be applied to cases such as *Polyclads*, where a fine duct passes from each *testis-follicle*, and *vasa deferentia* to the paired canals formed by their union. These canals usually open into a *vesicula seminalis*. Accessory male glands are very commonly present, and possess fairly uniform histological characters. Hence the terms *granule-gland*, *granule-duct*, *vesicula granulorum*. The duct through which the male products reach the exterior is the *ductus ejaculatorius*, and any chitinous investment round it may be called a *copulatory organ*.

As regards the authors' names appended to the species, I have endeavoured to follow the British Association rules. Von Graff, in his 'Monograph,' has employed the name of that author who first used the definitive combination of genus and species. Thus *Vortex balticus*, M. S. Schultze, becomes *Provortex balticus*, v. Graff, whereas I write it *Provortex balticus* (M. S. Schultze).

The terminations of generic names have not hitherto been formed in an uniform way. Von Graff changed the terminations of all the older generic names, such as *Acmostomum*, to *Acmostoma*, whereas Lang retains the *-um* form. In the present paper I have followed these authors. It would, however, seem advisable in the future to adopt either one termina-

tion or the other, right through the group. Spengel's<sup>1</sup> Latinised form of "Alloiocœla" (Allœocœla) is adopted.

## II. SYSTEMATIC.

### TURBELLARIA.

#### Sub-order 1.—RHABDOCÆLIDA.

##### A. ACÆLA.

A digestive cavity absent. Mouth ventral, leading indirectly through the pharynx into the parenchyma. A "frontal gland" and otolith present. Nervous system consisting of a brain and peripheral nervous sheath. Hermaphrodite. Testes follicular, rarely compact.

##### Family PROPORIDÆ.

Acœla with a common genital pore.

Genus 1.—PROPORUS, v. Graff  
(= SCHIZOPORA, Schmidt, 28).

Proporidæ without spermotheca.<sup>2</sup>

#### 1. PROPORUS VENENOSUS (O. Schmidt, 28).

Length 1 mm. Body elongate, cylindrical, rounded at both ends. Colour bright yellow, due to diffused granular pigment. Epidermis ciliated, containing numerous rhabdites, some free, some grouped in formative cells. These pyriform groups are specially abundant towards the hinder end, giving a spinous appearance to the surface. The mouth lies just beneath the anterior end; circular at rest, it becomes slit-like during movement. The pharynx is a direct invagination of the anterior end (v. Graff, 'Acœla,' pl. x, fig. 5). It is long (one-fourth the length of the body), cylindrical, and

<sup>1</sup> 'Götting. gelehrte Anzeigen,' March 1st, 1884, p. 183, note.

<sup>2</sup> The definitions of families, sub-families, and genera are taken from v. Graff (53).

muscular. The otolith has a distinct central portion, and is radially striated. The two eyes are large, and provided each with a lens. The common genital pore lies at the hinder end of the body. It leads into a ciliated, muscular, narrow atrium, which is an invagination of the hinder extremity. Testes rounded, scattered. Vesicula seminalis spherical, opening into the pyriform muscular penis enclosed in its sheath. These organs lie at the front end of the genital atrium. The spermatozoa when mature are broad and thick, tapering at either end, the head filament shorter than the tail. Ova occur in two lateral rows, sometimes those of one side being more developed than those of the other (v. Graff).

**HABITAT.**—This active yellow form is not uncommon between tide-marks in Plymouth Sound (F. W. G.). This is, I believe, the first record of its occurrence north of the Mediterranean.

**DISTRIBUTION.**—Trieste, Naples, Messina (v. Graff), Lesina (Schmidt, 28), Sebastopol (Uljanin, 41).

Genus 2.—**MONOPORUS**, v. Graff (56)  
(= **PROPORUS**, Schmidt, 28).

Proporidæ with spermotheca.

## 2. **MONOPORUS RUBROPUNCTATUS** (O. Schmidt, 28).

Length 1 mm. Body ellipsoidal with rounded extremities. Colour white, the central parenchyma brown, owing to the presence of coloured vacuoles and food-particles. The epidermis contains clavate rhabdites, the thickened outer ends of which project beyond the surface. The mouth is mid-ventral, leading into a very short simple pharynx; the "terminal mouth" of earlier descriptions being, according to v. Graff (56, p. 57), the opening of the "frontal organ." The eyes lie right and left close to the anterior end. They are placed in the epidermis, and consist of polygonal pigment masses of a brilliant carmine colour. In his recent accounts

of the "Accela" v. Graff gives some interesting additions to our knowledge of the genital organs. The genital pore is single. The testes are compact as in no other Accelous form. The vasa deferentia are merely their posterior prolongations. The oviducts are continuous with the epithelial lining of the ovary, and unite to form a vagina. Opening into this vagina is a spermotheca, the duct of which is slightly chitinised.

HABITAT.—Among littoral algæ, Plymouth Sound (F. W. G.).

DISTRIBUTION.—Naples, Trieste, Dalmatian Islands (v. Graff, 55), Lesina (Schmidt, 28).

#### Family APHANOSTOMIDÆ.

Accela with two genital apertures, the female pore placed in front of the male. A spermotheca present.

Genus 3.—APHANOSTOMA, Oersted (21).

Spermotheca unarmed.

#### 3. APHANOSTOMA DIVERSICOLOR, Oersted (21).

Length .75—1 mm. Body somewhat fusiform, tapering gradually forwards from the posterior third, more rapidly backwards to the hinder end. The colour (which is variable in amount and intensity) is due to violet pigment-cells and yellow vacuoles in the parenchyma. These are usually disposed in a characteristic way. The yellow pigment is present at the anterior end, and extends a short distance backwards on each side, enclosing the violet pigment which occupies the median part of the body as far back as the limit of the anterior third. A small patch also occurs at the extreme hinder extremity. The violet pigment-cells are capable of altering their shape according to the state of contraction of



the body. Their most characteristic form is that of a **U**, the curved portion being much thicker than the long slender processes.

The mouth is almost mid-ventral. It leads into a funnel-shaped pharynx. Two genital apertures are present. The male pore lies a short distance in front of the hinder end, the female pore still further forward. The conical penis encloses a vesicula seminalis in its proximal part. The ovaries extend throughout the greater part of the body. A spermatheca, possessing intrinsic and extrinsic muscles, opens into the vagina. The epithelium of its duct (according to v. Graff) secretes a cuticle.

**HABITAT.**—Among stones and seaweed at the base of the littoral zone, Plymouth, Port Erin, Isle of Man (F. W. G.); Millport (v. Graff).

**DISTRIBUTION.**—Naples, Trieste, Roscoff (v. Graff); Denmark (Oersted, 21); in colonies among *Laminaria* and *Fucus*, a few feet below the surface, Bergen (Jensen).

#### 4. *APHANOSTOMA ELEGANS*, Jensen.

Length .75 mm. Body colourless, with a lobate dark green spot in the centre due to coloured parenchymatous vacuoles. Form broadly rounded in front, tapering gently posteriorly. Eyes absent. The male genital aperture lies a short distance in front of the hinder end; the female pore close behind the green spot. According to Jensen the spermatozoa are long, filiform, thicker and spirally twisted anteriorly.

**HABITAT.**—Among *Ulva*, between tide-marks, Plymouth (F. W. G.).

**DISTRIBUTION.**—Alværström and Bergen (Jensen, 49).

Jensen's description reads, "Corpus utraque extremitate rotundatum in anteriore parte latius, retrorsum sensim an-

gustus." My specimen was certainly during active motion broader in front than behind, approaching Jensen's figure of *A. rhomboides* (49, pl. i, fig. 1).

*Aphanostoma* is a distinctly northern genus. The coast of Denmark and the western shores of Norway and Greenland have furnished the bulk of the existing records. The presence of *A. elegans* at Plymouth suggests that further search will reveal localities for the remaining species on our coasts.

#### Genus 4. CONVOLUTA, Oersted (16), 1844.

*Aphanostomidæ* with a broad, flat body, the margins of which are in some forms capable of being flexed ventrally. *Spermotheca* with a chitinous mouth-piece.

#### 5. CONVOLUTA SALIENS, v. Graff, 1891.

1882. *CYRTOMORPHA SALIENS*, v. Graff (53).

Length 1 mm. Body elliptical, the dorsal surface convex, ventral surface flat. Colour is absent except in the centre, where it is due to brown food-particles among the parenchyma. Locomotion is effected thus:—From the anterior end backwards for one-third of its length the margins of the body are capable of being gradually extended outwards, so that the greatest width of these animals when in motion is a short distance in front of the centre of the body. These lappets are then flapped inwards and downwards, the animal at the following instant leaping forward. When, however, contraction occurs, it is no longer possible to define the lappets. The anterior end is at a much lower level than the rest of the dorsal surface. As the change of level is abrupt the front end appears snout-like, especially when seen from the side. This snout is moved from side to side in a sensitive manner. Short cilia and slightly irregular rhabdites are present in the epidermis, and

are disposed in alternate longitudinal rows, which converge anteriorly towards the opening of the "frontal gland." Eyes are absent. The otolith is concavo-convex, with a central "nucleus." The two genital pores are posterior, the female in front of the male. Opening to the exterior through the former is the spermotheca. The curved penis receives the contents of the seminal vesicle.

HABITAT.—In tide-pools, Millport (v. Graff). Two specimens among *Zostera* and *Corallina*, Plymouth (F. W. G.).

#### 6. CONVOLUTA PARADOXA, Oersted (16), 1844.

1777. *PLANARIA CONVOLUTA*, O. F. Müller (4).  
 1844. *CONVOLUTA PARADOXA*, Oersted (16).  
 1845. *PLANARIA MACROCEPHALA*, Johnston (20).  
 1853. " *HAUSTRUM*, Dalyell (29).  
 1855. *CONVOLUTA PARADOXA*, Gosse (30).  
 1861. " " Claparède (35).  
 1865. " " Johnston (38).  
 1866. " " Lankester (39).

Length 1—3·5 mm. Schmidt (28) found specimens up to 9 mm. in length in the Faroe Islands and other northern localities; v. Graff records equally large examples from Millport. Specimens from more southerly places are usually much smaller, and it might therefore appear that this species attains a larger size in the northern than in the southern seas. Claparède, however (35), working on the north-west coast of Skye, examined a large number of specimens, none of which exceeded 2 mm. in length; while recently (55) v. Graff has found "giant specimens" at Roscoff. It seems more likely, as Claparède suggested, that this species attains a considerable size before the reproductive organs begin to develop. Thus he found individuals 1·5—2 mm. long without a trace of gonads, and I have myself observed the same thing.

The form of the body changes with different states of contraction and expansion. When freely swimming the form is

that of (53) pl. xi, fig. 15, the sides flexed ventrally, almost touching one another except in front, where they diverge. The hinder end is produced into a finely-pointed tail. The anterior end is truncate, the angles being frequently more or less produced. It is a most actively sensitive animal, especially during creeping movements, when the "head" is converted into a funnel-shaped structure which explores the surroundings.

The general colour varies from greenish-brown to a warm chestnut-brown, which is the usual tint. The anterior margin is paler than the rest. The brown pigment is deposited in the cell of a "symbiotic alga," the nature of which has not been thoroughly investigated. Transverse, narrow white bars, 1—2 in number (v. Graff has observed three, and Claparède [35, pl. vi, fig. 2] figures four such bands), are present in large individuals (1.75 mm. and upwards). They are the expression of a large number of very small irregular granules, insoluble in acids (v. Graff). Claparède has suggested that these bars may be a "caractère sénile." This view is supported by v. Graff, since he finds that the bars become more and more distinct with the increased size and age of the animal. The epidermis contains flagella, rhabdites, and pigment. The latter forms elongate masses of rod-like granules. The mouth, which is ventral and subcentral, leads into a very short pharynx. The eyes are constantly present in this species. They are red pigmented bodies, and occur right and left of the otolith. Poison-organs ("Gift-Organ") have been discovered by v. Graff (44) in this and other species of *Convoluta* (*C. grœlandica*, *cinerea*, *flavibacillum*, *bimaculata*). They consist in *C. paradoxa* of a pair of pyriform, transparent, muscular vesicles, provided with hollow chitinous tips, and are placed at the margin of the body in such a way that when this is flexed ventrally the tips are directed towards the mouth. The contents consist of small refractive granules. At each contraction of the muscular wall the tip is moved forwards, at the same time discharging some of its contents. This oral pair of poison-

organs is constantly present in sexually mature individuals. When the male products ripen (this species is a distinctly protandrous hermaphrodite) two other pairs (according to v. Graff) arise close to the male genital pore. They differ from the oral pair in three points—their time of appearance, their variability (the hinder pair may be absent), and their disappearance after the shedding of the male products (see v. Graff, 44, p. 61). The female genital pore lies slightly in front of the centre, the male pore halfway between it and the hinder end. The testes are dorsal in position. The penis is a narrow, cylindrical, muscular tube opening into the short genital atrium, surrounded by radiating accessory glands. The spermatozoa are long ( $\cdot 22$  mm.), and consist of a finely granular central portion and hyaline borders, absent, however, on the distinct "tail." The ova are placed ventrally, and when mature are ovoid,  $\cdot 07$  mm. diameter, containing much yellow food-yolk, and surrounded by a delicate membrane. Thirty to forty fertilised eggs may be present at one time in a single example. A spermotheca is present. Its neck is produced forwards into a funnel-shaped expansion opening into the female atrium and backwards into the swollen basal portion containing spermatozoa. Round the neck chitinous plates are arranged one over another, the margins of which are thin and colourless, forming the "mouth-piece." Young specimens of *Convoluta paradoxa* differ from the adults, to which the foregoing description applies, chiefly in the absence of reflexed marginal lappets, and the small number (five to seven) of symbiotic algæ present.

**HABITAT.**—A littoral species, occurring among seaweeds in tide-pools all round our coast. Berwick Bay (Johnston); Firth of Forth (Dalyell); among Ceramixæ, Weymouth (Gosse); Skye (Claparède); Guernsey (Lankester); St. Andrews (McIntosh); Millport (v. Graff); Plymouth, Port Erin, Isle of Man (F. W. G.).

**DISTRIBUTION.**—Mediterranean, Adriatic and Black Seas, North Sea, North Atlantic, coast of Denmark.

7. *CONVOLUTA FLAVIBACILLUM*, Jensen.

Length 2—3 mm. Body stout, oval, pointed behind, dorsal surface convex, ventral surface flat. The margins are produced into thin lamellæ, flexed ventrally. Colour yellow, due to the prevalence of pigmented yellowish-green rods over irregular brown granules. Epidermis, flagella, and rhabdites are similar to those of *C. paradoxa*. Eyes two, reddish, placed on each side of the otolith. Female genital pore situated at one-third the length of the body from the hinder end; halfway between the latter and the pore is the male aperture. The chitinous mouth-piece of the spermatheca is cylindrical, and composed of a number of perforated plates placed one upon another. The spermatozoa are elongate, tapering at each end, with a granular central portion and clear lateral membranes. Penis cylindrical, muscular.

HABITAT.—Among *Laminaria*, &c., Millport (v. Graff); among sand at base of *Corallina officinalis* in tide-pools, Port Erin, Isle of Man; Plymouth (F. W. G.).

DISTRIBUTION.—Bergen (Jensen).

The stout form and yellow colour sufficiently serve to distinguish this species, which, in its anatomy, closely resembles *Convoluta paradoxa*.

B. *RHABDOCÆLA*.

Gut and parenchyma distinct. A spacious body-cavity usually present. Nervous and excretory organs present. Gonads hermaphrodite (except *Microstoma* and possibly *Stenostoma*). Testes usually compact, and ovaries, germ-yolk-gland, or separate vitellaria and germaria may be present; in all cases surrounded by a tunica propria. Pharynx present, variable. Otolith usually absent.

## Family MICROSTOMIDÆ.

Rhabdocœla with sexual and asexual reproduction.  
Female accessory apparatus absent. Pharynx simple.

Genus 5.—MICROSTOMA, O. Schmidt, 1848 ('Die rhabd. Turbellarien d. süßen Wassers').

Microstomidæ with separate sexes and compact testes. Body uniformly ciliated, provided with "ciliated grooves" and a pre-œsophageal gut-cæcum.

## 8. MICROSTOMA GRÆNLANDICUM, Levinsen (51).

Length 1.75 mm. Body composed of about eight zooids, in colour resembling *M. lineare*. Eyes absent. Ciliated grooves small. Rhabdites well developed anteriorly, more sparsely behind. No sexual organs were observed.

HABITAT.—Among *Ulva*, Plymouth Sound (F. W. G.); Millport (v. Graff).

DISTRIBUTION.—Egedesminde, Greenland (Levinsen).

I place the Plymouth specimen here, for although it does not agree exactly with Levinsen's original description (the red spot at the anterior end is wanting), it does agree with a form described by v. Graff from Millport, and placed under this species.

## Genus 6.—ALAUINA, Busch (26).

Hermaphrodite Microstomidæ, with tactile anterior "proboscis." Usually with posterior setæ; paired lateral ones sometimes present.

## 9. ALAUINA CLAPAREDII, v. Graff.

Length .3 mm. Anterior end modified to form a tactile

proboscis provided with numerous circular folds. The base of the proboscis is marked off by a tuft of cilia on each side. A single posterior group of setæ at the hinder end. The posterior sixth of the body is marked off transversely (probably an indication of fission).

HABITAT.—Coast of Skye (Claparède).

Claparède (35) described this form as a rhabdocœle larva, but it was referred to *Alaurina* by Metschnikoff (37). It is probable that this genus is not uncommon on our coasts.

#### Family MESOSTOMIDÆ.

Rhabdocœla with one or two genital apertures; yolk-glands and germaria distinct or united. Testes compact. Female accessory organs present. Pharynx ventral, rosulate (for the term "rosulate" see v. Graff, 'Monogr.', p. 80).

#### Subfamily PROMESOSTOMINÆ.

##### Genus 7.—PROMESOSTOMA, v. Graff.

Mesostomidæ with two germaria and separate yolk-glands, and a common genital aperture. Female accessory organs absent. Testes small.

#### 10. PROMESOSTOMA MARMORATUM (Schultze [27]). Pl. XXXIX, fig. 10; Pl. XL, fig. 16.

Length .5—1.5 mm. Body elongate, cylindrical, broadly rounded in front, truncate behind. Anterior end used as a tactile organ. Colour very variable. The epidermis which furnishes the ground colour is colourless, bright yellow, or yellowish-red. Black reticular pigment is almost constantly present as a small patch between the eyes; elsewhere to a variable extent, and may be entirely absent. The epidermis on the inner side of the eyes contains immense numbers of rhabdites (fifteen to twenty in a single mother-cell), forming two well-defined tracks. Elsewhere they are few in number. The posterior end is provided with adhesive papillæ.



The pharynx lies just behind the centre of the body. The commencement of the gut (as v. Graff observed) is marked by active flagellæ. The genital aperture, provided with a muscular lip, is placed behind the pharynx. Testes two, oval. The connection between the two paired vasa deferentia has not actually been traced. From their point of union (behind the genital aperture) the single duct runs forward and expands into a vesicula seminalis, which is partly filled with sperm, partly with the granule-secretion. Both these products are conveyed to the exterior by a very curious copulatory organ. The most typical form which this chitinised ejaculatory duct assumes is that of a bishop's crosier, Pl. XL, fig. 16. The variations both in the number and form of the coils, and also in the form of the tip of the organ (straight, curved, forked), are great. The limits of variation in different directions would become of specific value if intermediate forms were not known to occur. The germaria and yolk-glands are paired and lateral. The egg-capsules are stalked.

**HABITAT.**—This very active littoral species has been found at Millport (v. Graff); Kilmore, Skye (Claparède); Port Erin, Isle of Man (F. W. G.); Plymouth (F. W. G.). At Millport and Plymouth forms with "long" and "short" copulatory organs occur; at Trieste and Naples v. Graff found only forms with short ones. At Plymouth most of the specimens had little or no pigment.

**DISTRIBUTION.**—Naples, Messina, Black Sea, Baltic, North Atlantic.

#### 11. PROMESOSTOMA OVOIDEUM (O. Schmidt, 28).

Length .5 mm. Body oval. The dense black colour is due to reticular parenchymatous pigment, which forms a thick mesh-work round the internal organs. The epidermis contains large numbers of rhabdites, especially developed along the inner side of the eyes, which are reniform, and provided with a lens. v. Graff has observed trembling movements of the eyes.

I have described them as seen in *Pr. solea*. Pharynx in the posterior third of the body. Behind it lies the penis, which is pyriform, its upper part filled with spermatozoa. The duct is chitinous.

HABITAT.—This species is found rarely in 5—15 fms. Plymouth Sound (F. W. G.).

DISTRIBUTION. — Messina, Naples (v. Graff), Lesina (Schmidt), Egedesminde, Greenland (Levinsen).

## 12. PROMESOSTOMA SOLEA (O. Schmidt, 32).

Differs from the preceding species in two points. The reticular pigment is less dense, and the pigment-cup of the eye sends a hooked process over the outer surface of the lens. The latter point alone seems to me to be constant. The amount of reticular pigment varies greatly. Seen from the dorsal surface the eye has an appearance similar to a miniature pan or tobacco-pipe, the bowl being represented by the pigment-cup, and the stem or handle by the strip of pigment running over the lens. The vibratory movement of the eye is performed in the following way. Suppose the pan or pipe to vibrate through a small angle in its plane of symmetry, in such a way that the plane is horizontal, the bowl moving forwards and then backwards. The actual vibrations of the eye are of this kind. Apparently one eye commences, performs five or six vibrations in a second, and then stops; the other eye begins, and so on. I am not certain, however, that the movements are alternate for any length of time. Of the mechanism I am ignorant.

HABITAT.—This is a typical deep-water (8—20 fms.) Turbellarian. Only once have I taken it between tide-marks. When dredge-material is placed in sea water, dark oval specks (the present species) are often seen swimming actively at the surface. In a few hours they descend, and reappear only when the water begins to foul. Plymouth (F. W. G.).

DISTRIBUTION.—Naples (Schmidt and v. Graff), Messina (Graff), Sebastopol (Uljanin).

13. *PROMESOSTOMA LENTICULATUM* (Schmidt [28]). Pl. XXXIX, fig. 6; Pl. XL, figs. 13, 17.

Length .65—.7 mm. (i. e. half that of Schmidt's specimen). Body broadly truncate and slightly convex in front, the antero-lateral margins produced slightly outwards. Behind these it becomes narrower, forming a "neck;" it then widens towards the middle, diminishing again to the posterior end. The general shape is, in fact, similar to *Jensenia* (see Jensen [49], pl. iii, figs. 1, 2), but more elongate. Colour to the naked eye scarlet; this is due to the contents of the extensive gut. Movements extremely active. Epidermis very transparent. Rhabdites few, scattered. Pharynx placed slightly in front of the middle of the ventral surface. Intestine large, corresponding to the shape of the body. The eyes are provided with a large conspicuous lens, which is easily detached from the pigment-cup. The genital aperture is a short distance behind the pharynx. The testes have the usual relations, and lead at their posterior ends into the vasa deferentia, which unite to open into the base of a most remarkable copulatory organ. This is cylindrical at its proximal end, provided distally with a series of triangular chitinous plates ranged round the terminal slit. The whole resembles the tool known as a "rose-bit" or "counter-sink," and used for embedding the heads of screws in wood or metal. The base of this organ is divided into spermatid and granule portions. The germaria are placed posteriorly. On one side the germarium was normal; on the other it was composed of lenticular masses, with difficulty separable optically from one another. The paired yolk-glands occupy the greater part of the sides of the body.

HABITAT.—Two specimens from a tide-pool among corallines, Port Erin, Isle of Man (F. W. G.).

DISTRIBUTION.—Faroe Islands (Schmidt).

This species has hitherto only been seen by Schmidt, who gave no account of the genital organs. He described the form and colour, the position of the pharynx, and the eyes. Excepting the difference in size (Schmidt's specimens measured 1.5 mm.) I have no reason for doubting the identity of my specimens with his.

As regards the systematic position of this species, my observations are not perfectly conclusive. It is possible that further investigations may prove that the organ R. S. is a receptaculum seminis, and B. C. a bursa copulatrix, the transverse markings I have noted being the subspiral muscles of Jensen. At present, however, from the nature of the protoplasm, I believe it to be an ovary, while the presence of a single genital opening is evidence for a position in the genus *Promesostoma*, where v. Graff has already placed it doubtfully.<sup>1</sup>

14. *PROMESOSTOMA AGILE* (Levinsen). Pl. XL, fig. 14.

Length .5 mm. Body oval, rounded posteriorly, tapering forwards in front of the hinder third. Colour light red. Movements very active. Eyes placed close together, triangular, the apex being formed by the pigment-cup, directed inwards and backwards, the lens outwards and forwards. Pharynx subcentral. Intestine reddish, occupying the space between the pharynx and the lateral yolk-glands. The genital aperture is placed about halfway between the pharynx and the posterior end. The testes are two oval sacs behind the pharynx; they communicate by short ducts with the penis, the base of which is spherical, and contains the secretion of a granule-gland, while its distal portion is produced into a long, narrow, slightly curved copulatory organ. A pair of ovaries are placed at the posterior end of the body, their ducts running forwards to the genital aperture.

<sup>1</sup> A second genital pore might have easily been overlooked. If further examination should demonstrate a second aperture, the species would have to be transferred to the genus *Byrsophleps*.

The yolk-glands are lateral, uniting behind the brain. A small muscular sac placed behind the penis appears to be a receptaculum granulorum.

**HABITAT.**—Two specimens among littoral weeds, Plymouth (F. W. G.).

**DISTRIBUTION.**—West coast of Greenland (Levinsen).

Levinsen's description (according to v. Graff) left this form indeterminate. The two pyriform bodies that he called "Samenblasen," and which v. Graff suggested might be local swellings of the vasa deferentia, I take to be the true testes. They have all the structure of such an organ, but occupy a more posterior position than usual. The ova did not appear to Levinsen to be distinguishable into two fairly distinct ovaries as in my specimens.

#### Subfamily BYRSOPHLEBINÆ.

Mesostomidæ with two genital apertures, the male in front of the female. Germarium single. Vitellaria distinct. Accessory organs absent or present. Testes small, rounded.

Genus 8.—BYRSOPHLEBS, Jensen (49).

(With the diagnosis of the subfamily.)

#### 15. BYRSOPHLEBS GRAFFI, Jensen.

Length .45 mm. Body cylindrical, tapering gradually posteriorly. Colourless, the gut brownish-yellow. Pharynx central, male genital aperture immediately behind it, female aperture close to the hinder end. Penis composed of a proximal cylindrical portion, strengthened by spiral and longitudinal muscles, and a distal chitinous funnel-shaped duct. The terminal aperture of this duct is provided with a short triangular projection on one side. Opening through the female genital aperture is a receptaculum seminis placed at the base of the ovary, and a muscular bursa copulatrix

at its side. Yolk-glands unbranched, lateral. (For further account with figures see Jensen (49), pl. ii, figs. 8—12.)

HABITAT.—Among algæ, Drake's Island, Plymouth Sound (F. W. G.); among *Ulva* and *Fucus*, Millport (v. Graff).

DISTRIBUTION.—Bergen and Sund, West Norway (Jensen).

#### 16. BYRSOPHLEBS INTERMEDIA, v. Graff.

Resembles the former species in most characters, differing in the arrangement of the genital organs. The penis is elongate, cylindrical, the spiral muscular fibres surrounding the united vasa deferentia. The chitinous portion is narrow, funnel-shaped, its tip partly surrounded by a curved process, similar to the "spur" in *Macrorhynchus Nægeli*. The yolk-glands are branched.

HABITAT.—In tide-pools. Port Erin, Isle of Man (F. W. G.); Millport (v. Graff).

#### Subfamily PROXENETINÆ.

Mesostomidæ with one common genital aperture and two germ-yolk-glands. Spermatheca provided at its blind end with chitinous appendages. Testes small, rounded. Copulatory organ complicated.

#### Genus 9.—PROXENETES, Jensen (49).

#### 17. PROXENETES FLABELLIFER, Jensen.

Length 1—1.5 mm. Body cylindrical, abruptly rounded in front, narrowing posteriorly to a short "tail," colourless. Flagella are everywhere present between the cilia. Long, sharply-pointed rods are present in great numbers in the epidermis, forming two well-defined tracks between the eyes and supplying the anterior end. Smaller rods occur over the rest of the surface. The hinder end is provided with adhesive cells. Pharynx large, placed in the posterior third. Between

it and the hinder end is the genital aperture. The large testes occupy the middle of the sides of the body. The vasa deferentia are swollen just before uniting at the base of the retort-shaped penis which receives the secretion of granule-glands. The copulatory organ is a complicated mechanism of chitinous pieces separating the granule-secretion from the spermatozoa. The nutrient part of the germ-yolk-gland extends along the sides of the body; the ovarian portion develops behind the pharynx. The two oviducts unite, and the common duct runs to the genital pore. Opening into the atrium, close to the pore, is the large spermotheca, which is directed forwards towards the pharynx, and then bends back upon itself. Its blind end receives chitinous ducts conveying granule-secretion. The point of connection with the genital atrium is armed with five to six triangular chitinous teeth, freely hinged at their bases. A further account of these structures will be found in v. Graff (pp. 277—279) and Jensen (49). The above are points I have verified myself.

**HABITAT.**—Several feet below surface and in tide-pools. Millport (v. Graff); Plymouth (F. W. G.); common among *Ptilota plumosa* and other red and green algæ, low spring tide, Port Erin, Isle of Man (F. W. G.).

**DISTRIBUTION.**—West coast of Norway (Jensen).

#### 18. PROXENETES COCHLEAR, v. Graff.

The four or five chitinous ducts of an accessory gland, which open into the blind end of the bursa in *P. flabellifer*, are, in this species, reduced to a single spiral one; the triangular "teeth," arming the duct of the bursa, being here represented by a series of small chitinous processes. The copulatory organ consists of three spoon-shaped pieces fitting into one another. The spaces between them constitute the passages for the seminal and granule fluids.

**HABITAT.**—Millport, one specimen (v. Graff).

## Subfamily EUMESOSTOMINÆ.

Mesostomidæ with one common genital pore, a single germarium, two vitellaria and accessory organs. Testes long. Excretory vessels opening into the pharyngeal sheath.

## Genus 10.—MESOSTOMA, Dugès.

Without otolith. Copulatory organ traversed throughout its entire length by the ducts of male secretions.

## 19. ? MESOSTOMA NEAPOLITANUM, v. Graff.

Length .5 mm. Body flattened behind, bluntly pointed in front, white. Between the eyes are two tracks formed by masses of large curved rhabdites. Smaller ones are present elsewhere. Pharynx small, in front of the centre. Intestine large, filling up the greater part of the body. Eyes two, with lenses. Genital pore close to the hinder end. Testes lateral. The penis bears a funnel-shaped terminal portion which receives the contents of the vesicula granulorum, and in front of this lies the semi-lunar vesicula seminalis. The atrium did not appear to be so large as in v. Graff's specimen.

HABITAT.—Among Fucus, Plymouth Breakwater (F. W. G.).

DISTRIBUTION.—Naples (v. Graff).

I append a query to this species, since my observations were made on one specimen, and agreed more closely (but not entirely) with *M. neapolitanum* than with any other species. More specimens of this marine *Mesostoma* are greatly needed, as its position is not thoroughly defined.

## Family PROBOSCIDÆ.

Rhabdocœla with tactile proboscis; one or two genital pores. Germaria and vitellaria distinct.



Testes compact. A spermatheca present. Mouth ventral. Gut discontinuous in the adult, owing to the development of the gonads. Copulatory organ complicated, chitinous (v. Graff, p. 315).

Subfamily PSEUDORHYNCHINÆ.

Proboscis without sheath or muscular cone. Retractors represented by short muscular bundles. Pharynx rosulate. One genital pore. Two germaria. Yolk-glands reticular. Testes paired, rounded.

Genus 11.—PSEUDORHYNCHUS, v. Graff.

20. PSEUDORHYNCHUS BIFIDUS (McIntosh).

1875. MESOSTOMUM BIFIDUM, McIntosh (45).

Length 1.3 mm. Body convex dorsally, flat on the ventral surface, slightly expanded towards the posterior end, which is bifid. The conical anterior extremity (proboscis) is devoid of cilia. Colour pale orange with darker spots, the proboscis colourless. Rhabdites are well developed and of three kinds (Jensen)—straight, ovoid, and needle-shaped. Strong adhesive papillæ occur at the bifid hinder end. Pharynx subcentral. The genital pore is placed behind the middle. Testes small, rounded. Vasa deferentia unite in a vesicula, which opens, along with the ducts of "granule-glands," into the proximal swollen part of the penis. The distal portion is muscular, and contains the copulatory organ. The latter is a conical chitinous tube, the outer wall of which is produced into a series of spiral ridges running from the base to the apex in a screw-like manner. The usual direction appears to be "right-handed." von Graff notes an interesting "left-handed" variety. The germaria are large lateral oval sacs, placed opposite the centre, and directed forwards. The spermatheca is finger-shaped with muscular walls. It contains the granular secretion of a large number of glands.

HABITAT.—On half-decayed *Laminaria* and *Ulva*, Millport

(v. Graff); under stones between tide-marks, St. Andrews (McIntosh, 45); among decaying *Ceramia*, &c., Port Erin, Isle of Man (F. W. G.).

DISTRIBUTION.—Egedesminde, West Greenland (Levinsen), Faroe Islands (Schmidt), Bergen (Jensen).

#### Sub-family ACORRHYNCHINÆ.

Proboscis at the anterior end provided with a sheath opening in front, with muscular cone and four long retractors. Pharynx rosulate. Yolk-glands reticular (v. Graff [53], p. 318).

#### Genus 12.—ACORRHYNCHUS, v. Graff.

*Acorrhynchinæ* with a common genital pore. Two germaria and elongate testes. Vesiculæ seminales and granulorum distinct, but enclosed in a common muscular penial sheath. The copulatory organ transmits both secretions (v. Graff, 'Monogr.,' p. 319).

#### 21. ACORRHYNCHUS CALEDONICUS (Claparède).

1861. *PROSTOMUM CALEDONICUM*, Claparède (35).

Length 1—2 mm. Body bluntly pointed in front, gradually widening behind, and rounded posteriorly. Colour, proboscis white, the rest of the body greyish brown with light areas, indicating the positions of the more bulky internal organs. Rhabdites very small, numerous, evenly distributed. Proboscis well developed (for an account of its structure see v. Graff, 'Monographie,' pp. 119—124). Two very long retractor muscles extend from its base to the posterior end of the body. Pharynx before the middle, with a marginal "seam." According to von Graff, the base of the extended proboscis is enclosed in a nervous commissure proceeding from the brain. Eyes two, provided with a lens. The genital pore is placed just behind the centre. Testes lie at the sides

of the pharynx. The vasa deferentia unite in a sperm-vesicle, close to which is the granule-vesicle. The long muscular cylindrical penis receives both secretions, and is enclosed in an inner chitinous sheath and an outer muscular one. The armature is in the form of hooks with rounded basal ends. The hooks vary in size and shape, and are disposed as in v. Graff's pl. x, fig. 17, of his 'Monographie.' The genital aperture is surrounded by numerous glands. The germaria lie at the sides of the penis. The reticular yolk-glands are of considerable extent.

HABITAT.—In tide-pools, and among *Fucus* and *Laminaria* below the surface of the sea. Kilmore, Skye (Claparède); Millport (v. Graff); Plymouth; Port Erin, Isle of Man (F. W. G.).

DISTRIBUTION.—Bergen (Jensen), Heligoland (Metschnikoff).

The well-developed musculature of these forms enables them to resist compression without rupture. If a mature individual be treated in this way the various parts of the genital apparatus stand out with diagrammatic clearness.

This species, closely similar to the next in external appearance, can be distinguished by the presence of the common muscular envelope round the vesiculæ seminales and granulorum.

### Genus 13.—MACRORHYNCHUS, v. Graff.

*Acrorhynchinæ* with a common genital aperture, two germaria, and paired elongate testes. Vesiculæ seminales and granulorum distinct, the duct of the latter with a special chitinous tube ('Monogr.,' p. 321).

Von Graff divides this genus into two subdivisions:—  
i. *Typici*.—Those in which a poison-dart (Gift-Stachel) is absent; duct of the vesicula seminalis without chitinous armature. ii. *Veneno si*.—Those provided with a poison-dart;

a chitinous investment for both the duct of the seminal and granule-vesicles.

i. TYPICI.

22. *MACRORHYNCHUS NAEGELII* (Kölliker, 17). Pl. XXXIX, fig. 5; Pl. XL, fig. 15.

Length 2.2 mm. in my largest specimens; v. Graff states that he has not seen larger ones at Millport, while Mediterranean examples range up to 4 mm. Body similar to *Acrorhynchus* in shape, cylindrical, bluntly pointed in front, broader behind. Colour variable. Proboscis usually white, the rest of the body dusky brown, through which the testes, ovaries, and penis can be indistinctly perceived with a hand-lens. Claparède (36) has described a variety from St. Vaastella-Hogue, which was white with a median dorsal yellow streak. A similar variety occurred at Plymouth (fig. 5). The colour was brown; at the base of the white proboscis and in the middle line was a yellow spot, visible in all positions of the animal; proceeding from this backwards along the mid-dorsal line was a bright yellow streak. These colours appear to be due to pigment in the parenchyma. Small rhabdites are plentifully developed in the epidermis, and the epithelium of the proboscis contains oval, highly refractive bodies, "Nematocysten entsprechenden Gebilde" (v. Graff, 'Monogr.,' p. 323). The histology and relations of the proboscis have been fully elucidated by v. Graff. The brain, bearing two eyes provided with lenses, is placed behind the proboscis, and behind this again is the spherical pharynx. The common genital pore lies behind the centre of the body. It leads into a very extensive atrium, the chitinous lining of which extends into the common passage receiving an anterior male subdivision and a posterior female portion. The testes occur at the sides of the body. The vasa deferentia unite with the contents of an accessory gland. The secretion of the granule-gland, however, is enclosed in a special sac, the lower part of which is chitinous. Its free edge is usually provided with a curved "spur," of variable form. This may

be absent. A remarkable variety is figured in Pl. XL, fig. 15. The ovaries, and between them the large spermatheca, lie posteriorly. One egg-capsule was present in many individuals at Plymouth in September. In November no adults could be found. They had probably died off.

**HABITAT.**—Similar to *Acrorhynchus caledonicus*. The two are, however, only occasionally found together. Plymouth Sound (F. W. G.); Millport (v. Graff, "Ich selbst habe in Millport niemals grössere Exemplare gesehen als Claparède's," p. 323, 'Monogr.').

**DISTRIBUTION.**—This is the commonest Rhabdocœle at Naples. Lesina, Messina, Trieste (v. Graff), Sebastopol (Uljanin), Black Sea (Czerniavsky), Madeira (Langerhans, MSS.).

### 23. *MACRORHYNCHUS CROCEUS* (Fabricius, 9).

Length 1.5 mm. Body reddish, swollen posteriorly, pointed in front, where it is nearly white. Proboscis very powerfully developed. Of the parts composing the genital apparatus, the most diagnostic is the copulatory organ. At its proximal cylindrical end it receives the secretions of the vesicula seminalis and granule-reservoir, which are contained in an elongate sac strengthened by spirally-arranged muscles. The distal portion is spirally twisted, and consists of two canals, each containing a part of the continuation of the proximal single cavity. The upper edge of this spiral is "toothed." The egg-capsule is stalked. Several points, such as the relations of the germ- and yolk-glands and the presence of a spermatheca, are not yet satisfactorily determined.

**HABITAT.**—Among *Fucus* and *Laminaria* below the surface of the sea. Millport (v. Graff); Plymouth (F. W. G.).

**DISTRIBUTION.**—Apparently abundant in the northern seas. West coast of Greenland (Levensen) and of Norway (Jensen), Faroe Islands (Schmidt), Denmark (Oersted), Wimmereux (Hallez).

Among the *Macrorhynchus* collected at Plymouth were two species apparently new. Since, however, my observations are incomplete, I will not further describe them than by saying that one species closely resembled *M. mamertinus*, v. Graff, in the form and position of its gonads. The pharynx was not so strongly developed.

## ii. VENENOSI.

### 24. *MACRORHYNCHUS HELIGOLANDICUS*, Metschnikoff (37).

Length .5—1.5 mm. Body rounded at both ends, cylindrical, white, sometimes with brown spots. The proboscis is typical but small. The bilobed brain bears lenticulate eyes. The pharynx is rather small, placed as far in front of the centre of the body as the genital pore is behind it. The reproductive organs were first described by Jensen. The great variability of certain (especially the chitinous) parts, their complexity, and the presence or absence of certain accessory organs (spermotheca, &c.) according to the particular stage of development, render this perhaps the most difficult of all Turbellaria to elucidate. Personally I have found young specimens (.5—1 mm. in length) fairly intelligible. In these the yolk-glands form finger-shaped masses extending from the base of the pharynx to the genital pore. In the adult they become reticular and very bulky. The elongate, narrow germaria consist of a single row of ova for the greater part of their length. Behind their point of union is the large spermotheca. All these organs, the yolk-germ-glands and spermotheca, open into a single female genital canal. This canal is chitinised internally, and leads to the genital atrium. For an account of the male gonads with figures see v. Graff, 'Monographie,' pp. 330-1, pl. ix; and Jensen, 'Turbellaria Norvegiæ,' pl. iv. The most important fact is that in addition to a chitinous sheath for the "granule-secretion," there is a common one for both this and the terminal vas deferens (see v. Graff, 'Monogr.,' p. 166, woodcut, fig. 9, G.). The poison-organ consists of a hollow chitinous stylet

enclosed at its proximal end by a muscular sheath containing the poison-glands. A strong retractor muscle passes from the blind end of this muscular sheath, and is inserted on the upper end of the granule-reservoir.

**HABITAT.**—At the commencement of the Laminarian zone, Millport (v. Graff); Plymouth; Port Erin, Isle of Man (F. W. G.). Young specimens abounded at the last locality in October, 1892.

**DISTRIBUTION.**—West Greenland (Levinsen), White Sea (Mereschkowsky, 48), Bergen (Jensen), Wimmereux (Hallez).

A most remarkable character of the Proboscidae, as a family, is the discontinuity of the gut caused by the development of the various genital organs, and in no form is this more conspicuous than in *Macrorhynchus heligolandicus*. In young specimens the gut is a closed sac surrounded by the body-cavity. As the gonads develop, becoming more and more bulky, the gut gets squeezed into any unoccupied spaces. Thus the gut-cells become scattered, and accumulate chiefly along the mid-dorsal surface. This fact accounts for the absence of a definite intestine in adult specimens.

#### Genus 14.—GYRATOR, Ehrbg., 1831.

*Acrorhynchinae* with two genital pores, of which the female is the anterior. Germarium single; testes elongate. Vesicula seminalis and granule-reservoir separate, the latter with a special chitinous duct (v. Graff, 'Monogr.,' p. 331).

#### 25. GYRATOR HERMAPHRODITUS, Ehrbg. (10).

1875. *PROSTOMA LINEARE*, McIntosh (45).

1879. " " Hallez (50).

Details of McIntosh's specimens are not given. I append the following observations which I have made on specimens taken in the neighbourhood of Manchester.

Length 1 mm. Body in the highest degree contractile, colourless, cylindrical, tapering anteriorly. Proboscis very mobile. Brain, eyes, and pharynx as in *Macrorhynchus*.

The genital organs are distinguished by the presence of a poison-dart appended to the copulatory organ. Hallez has given a full account of this with figures (see 43, pls. xx—xxii). The use of this stylet as an offensive weapon has been seen by Schmidt ('*Denkschr. math.-nat. Klasse,*' Wien, 1857) and Hallez ('*Arch. Zool. Expt.,*' 1873). The animal bends the hinder end of its body towards the ventral surface when close to its prey (small Entomostraca), which it stabs repeatedly with its poison-dart.

HABITAT.—In sea water this form is only known from St. Andrews under stones (McIntosh) and Madeira (Langerhans). It is widely spread over Europe in fresh water.

#### Subfamily HYPORHYNCHINÆ.

"Proboscis small, behind the anterior end, its sheath opening on the ventral surface. Muscular cone present. Numerous short muscular fibres constitute retractors. Spermatheca with chitinous appendage. Vesicula seminalis and granule-reservoir not distinct. Their contents, however, issue through special chitinous ducts" (v. Graff, '*Monogr.,*' p. 336).

#### Genus 15.—HYPORHYNCHUS, v. Graff.

##### 26. HYPORHYNCHUS ARMATUS (Jensen).

Length 1—1.5 mm. Body elongate, cylindrical, truncate at both ends, white. Hinder end provided with strong adhesive papillæ. The way in which these papillæ are used reminds one forcibly of a *Monotus* (see p. 487). The anterior end, beset with long flagella, is moved actively from side to side as it advances. Short rhabdites are present over the surface, modified on each side of the body behind the



middle into long vermiform bodies, in which Jensen perceived a central thread. The opening of the proboscis-sheath is ventral, and close to the anterior end. The proboscis itself is feebly muscular. The mouth is a transverse slit, surrounded by an arcuate transverse row of six adhesive papillæ. The eyes, two on each side, lie over the brain behind the proboscis. The genital pore is ventral, a short distance from the hinder end. The vasa deferentia are given off from the two rounded lateral testes. They unite along with the accessory secretion at the base of the spirally coiled ejaculatory duct. This consists usually of two coils and a terminal straight portion. The spermotheca is armed anteriorly with chitinous spines; posteriorly, according to Jensen, it communicates by a long narrow duct with the genital atrium. (For figures see Jensen's "Turbellaria Norvegiæ" [49], pl. iii, figs. 14—22.)

**HABITAT.**—Among *Zostera*, Plymouth Sound; tide-pools, Port Erin, Isle of Man (F. W. G.).

**DISTRIBUTION.**—Bergen (Jensen).

## 27. *HYPORHYNCHUS PENICILLATUS* (Schmidt, 32).

A young immature specimen that I refer rather doubtfully to this species measured .6 mm. in length. Body of a bright yellow colour, the pigment being deposited in fine granules at the base of the epidermal cells. Rhabdites small, occurring in numbers over the surface. The aperture of the proboscis-sheath is triangular, ventral, close to the anterior end. The eyes were fairly large, and provided with lenses. The genital organs were not developed, hence the doubt attaching to this example, which, however, in all remaining characters agrees with *H. penicillatus* as described by v. Graff.

**HABITAT.**—Among *Zostera*, Cawsand Bay, Plymouth (F. W. G.).

**DISTRIBUTION.**—Lesina (Schmidt, 32), Messina, and Naples (v. Graff).

## Family VORTICIDÆ.

Rhabdocœla with a common genital pore. Germaria and vitellaria united or distinct. Accessory female organs present. Uterus simple. Testes paired, compact. Mouth ventral, usually anterior. Pharynx dolioform.<sup>1</sup> Copulatory organ of various shapes (v. Graff, 'Monogr.,' p. 342).

## Subfamily EUVORTICINÆ.

Pharynx and brain well developed. Germaria small. Body-cavity extensive. Parenchyma small in amount. Free-living.

## Genus 16.—PROVORTEX, v. Graff.

Euvorticinæ with two germaria and two distinct, elongate, unbranched vitellaria. Testes rounded. Pharynx dolioform. Mouth in the anterior third. Vesicula seminalis enclosed by the penis. Copulatory organ traversed by the spermatozoa (v. Graff, *ibid.*, p. 344).

## 28. PROVORTEX BALTICUS (Schultze, 27).

Length .6—1 mm. Body cylindrical, truncate in front, the angles produced into blunt processes, widening towards the middle and tapering behind to a long "tail." Colour brown, due to scattered reticular pigment. Epidermis containing flagella interspersed between the cilia. Pharynx provided with a distinct seam, into which the pharyngeal retractor muscles are inserted. From the extended observations of von Graff and Jensen it appears that this species is divisible into macro- and micro-pharyngeal varieties. Eyes paired, reniform. The genital aperture is ventral, at the base of the "tail." The testes lie far forward at the sides of the pharynx, and lead into paired vasa deferentia. These unite along with the "granule-secretion" in the base of the copu-

<sup>1</sup> *I.e.* barrel-shaped. The term is, however, used in a technical sense, including certain structural peculiarities (see v. Graff, 'Monographie,' pp. 83-4).

latory organ. This organ is slightly variable in shape, and consists of a wide, cylindrical, tubular basal portion, opening through a narrow transverse slit, one edge of which is continued parallel to the axis of the cylinder, and then bends sharply at right angles. Germ- and yolk-glands lateral; near their point of union is a curved spermatheca.

**HABITAT.**—This very active tiny animal occurred abundantly among *Laminaria* and also in brackish water at Millport (v. Graff). Abundant in tide-pools, Port Erin, Isle of Man; less commonly at Plymouth (F. W. G.).

**DISTRIBUTION.**—West coast of Greenland (Levinsen), West Norway (Jensen), Copenhagen (Fabricius, 9).

### 29. *PROVORTEX AFFINIS* (Jensen).

Length .6 mm. Body stouter than in *Pr. balticus*, tapering posteriorly from the anterior third. Pharynx not so moveable as in the previous species. It is, however, in the form of the copulatory organ that these species are most easily and certainly distinguished. This is elongate, funnel-shaped, the terminal part of the duct bending at an obtuse angle with the proximal portion. Opposite this angle is a triangular plate projecting outwards from the surface of the duct.

**HABITAT.**—Along with *Pr. balticus*, Millport (v. Graff); Plymouth, along with *Monoporus rubropunctatus* (F. W. G.).

**DISTRIBUTION.**—Copenhagen (Fabricius), Bergen (Jensen).

### 30. *PROVORTEX RUBROBACILLUS*, n. sp. Pl. XXXIX, fig. 8; Pl. XL, fig. 12.

Length .75 mm. Body cylindrical, broadly rounded in front, tapering slightly posteriorly. Colour mottled brown to the naked eye. The effect is due to numerous rods of doubtful nature in the interior of the gut-cells. They were present in all individuals examined. Pharynx without a distinct "seam." The free margin is crenulate. Intestine extensive. The gut-cells contain 3—8 rods of reddish colour.

Whether they are zooxanthellæ (as described by v. Graff<sup>1</sup> in *Enterostoma zooxanthellæ*), or food-remains, is a moot point. Each eye possesses three lenses. The genital aperture is ventral, a short distance in front of the hinder end. A pair of testes lie at the sides of the pharynx; they lead by wide vasa deferentia into a vesicula seminalis. The penis contains proximally the separate granule-secretion and spermatozoa separated; distally it is converted into a chitinous copulatory organ, enclosing an inner muscular layer. The whole is bent into an S-shaped curve. As in *Pr. balticus*, one portion of the terminal margin is bent upon itself, and produced into an extremely fine, needle-like spine. Germaria and vitellaria as in *Pr. balticus*. A spermotheca is present near the genital pore.

HABITAT.—Dredged off the "New Grounds," Plymouth Sound (F. W. G.).

### C. *ALLÆOCÆLA*.

The following definitions are v. Graff's (53), as amended by Böhmig (57, pp. 464-5):

Alimentary canal and parenchyma generally sharply separated; a body-cavity absent in the adult. Nervous and excretory systems present. Testes follicular. Germ- and yolk-glands separate or united, paired; the latter irregularly lobed, rarely branched. Gonads contained in parenchymatous cavities without a membrana propria. Penis formed by folds of the genital atrium. No conspicuous chitinous copulatory organ.

### Family PLAGIOSTOMIDÆ.

Allæocœla with pharynx *variabilis* (except *Plag. bimaculatum*, where it is a pharynx *plicatus*), the size and position of which is subject to variation. Genital pore single or double; sometimes combined with the mouth. An otolith absent.

<sup>1</sup> 'Zool. Anzeiger,' 1886, p. 338.

## Sub-family PLAGIOSTOMINÆ.

Plagiostomidæ with a ventral and posterior genital aperture. Mouth anterior. Germaria and vitellaria distinct.

Genus 17.—PLAGIOSTOMA, O. Schmidt (28), 1852.

Without tentacles.

31. PLAGIOSTOMA DIOICUM (Metschnikoff, 37). Pl. XL, fig. 11.

Length .6—·7 mm. Body cylindrical, tapering very slightly in front of the posterior third. Colour yellow-brown, lighter anteriorly and at the sides; eye-pigment reddish-brown. The epidermis contains a few small rods and numerous highly refractive vesicles. Böhmig (57, p. 408) has seen these in sections; they are possibly excretory. Flagella are present anteriorly and posteriorly. Mouth anterior, subterminal. The pharynx is ellipsoidal, and lies altogether in front of the brain. The intestine is extensive, and corresponds generally to the form of the body. The brain is reniform, the slight concavity being directed anteriorly. A pair of nerves from the anterior and also from the hinder angles are conspicuous; three other pairs occur (Böhmig, 57, p. 410). Two eyes are present, provided with lenses. The genital aperture is ventral, and placed a short distance from the hinder end. The testes are scattered in the parenchyma. A muscular vesicula seminalis is placed close to the genital pore. The female organs are of considerable interest, as no one has yet found any trace of the yolk-glands. Since, however, it is known that these organs develop late, it is possible that specimens presenting them in a mature condition have not yet been seen. If, on the other hand, yolk-glands are really not present at any stage, their absence would constitute a feature in which this species resembles the genus *Acmostoma*. The ovaries consist of a lateral row of clear spherical cells extending from the brain to the hinder end, and surrounded by refractive granules. I have not noticed the

accumulation of ova behind the brain to which Böhmig refers (loc. cit., p. 316).

HABITAT.—Among littoral weeds, Plymouth (F. W. G.).

DISTRIBUTION. — Heligoland (Metschnikoff, 37), Trieste (Böhmig, 57).

The specimens that I have seen appear to bear a close resemblance to *Acmostoma Sarsii*, Jensen. The form, colour, eyes, relations of the pharynx, character of the ova, testes, position of the vesicula seminalis, and apparent absence of vitellaria are almost identical in the two species. The presence of a narrow "creeping sole" in *Acmostoma* is, however, a distinguishing feature.

32. *PLAGIOSTOMA SULPHUREUM*, v. Graff. Pl. XLI, fig. 20.

Length 2 mm. Body very elongate, cylindrical, parallel-sided for the greater portion of its length, somewhat conical in front, tapering posteriorly. Colour to the naked eye orange, the extreme anterior end paler; two large black eyes are conspicuous. Movements active, the front end being moved about as a flexible and highly sensitive "lip." The tail is provided with strong adhesive cells, by which the animal is securely fixed at will. The epidermis contains numerous rhabdites of a bright yellow colour, to which the tint of the animal is due. Mouth below, pharynx behind the brain. The pharynx is very small, the musculature being slightly developed. Numerous glands surround it. The intestine occupies the central part of the body, and is enclosed anteriorly by spherical glands. The genital aperture lies a short distance from the hinder end on the ventral surface. The small testes are placed behind the centre of the body in the middle line. The spermatozoa have a very characteristic form. They are divisible into a broad head, and a narrow pointed tail. A dark transverse band separates the head end off as a pointed lid. Down the centre runs a spiral thread. The ova develop from a median cellular mass which, according

to Böhmig (57, p. 365), lies close to the brain. In compression preparations it is driven posteriorly (Pl. XLI, fig. 30). The developing ova lie at the sides of the gut. The yolk-glands are paired, large, lobed organs, more or less enclosing the intestine and uniting behind the pharynx.

HABITAT.—In tide-pools among corallines, Port Erin, Isle of Man (F. W. G.).

DISTRIBUTION.—Trieste (v. Graff and Böhmig).

### 33. *PLAGIOSTOMA ELONGATUM*, n. sp.

Length 2 mm. Body cylindrical, stout, elongate, rounded in front, tapering rather suddenly posteriorly. Colour opaque white. Epidermis provided with cilia, which are longer anteriorly than elsewhere, and between which stiff flagella occur. Narrow oblong rhabdites are thickly scattered over the surface. They are homogeneous and highly refractive. The musculature is strongly developed, and this fact, combined with the opacity of the other organs, renders it a matter of difficulty to examine this species by compression. The mouth is subterminal. Pharynx large, barrel-shaped when at rest, situated behind the brain. It is very muscular, and can extend under and in front of the brain towards the mouth. The intestine is large, corresponding generally to the form of the body, slightly hollowed in front to receive the base of the pharynx. Two large irregular black eyes unite by strands of pigment across the brain. The genital pore is close to the hinder end. The male organs were not thoroughly developed in either of my two specimens, and the form of the mature spermatozoa remains unknown. The germaria lie at the sides of the posterior third of the body. The yolk-glands form narrow lobed masses at the sides of the gut, extending as far forward as the base of the pharynx.

HABITAT.—From coarse sand at the bases of *Corallina officinalis*, Plymouth (F. W. G.).

34. *PLAGIOSTOMA PSEUDOMACULATUM*, n. sp.

Length 2 mm. Body elongate, pointed behind, the anterior end not distinctly separated off from the rest of the body; hence it may be distinguished from *Pl. maculatum*, which this species closely resembles in form and in many points of structure. Colour white, a violet patch of reticular pigment between the eyes. Mouth lies beneath the brain. Pharynx very muscular. The genital aperture is ventral, at the base of the tail. The germaria lie right and left behind the pharynx; behind these again the testes. The vasa deferentia are distinctly swollen before entering the cylindrical muscular penis.

HABITAT.—This species, so far as my experience goes, belongs to a deep-channel fauna of Plymouth, characterised more especially by the presence of various Monotidæ, to be presently described. I have found it always associated with *Polydora ciliata* (Polychæta), which forms mud-tubes in hundreds on the muddy bottom of the Hamoaze.

This species differs from *Plagiostoma maculatum* in the absence of the red intestine and lateral head-grooves which characterise the latter.

35. *PLAGIOSTOMA SAGITTA* (Uljanin, 41).

Length 1 mm. Body elongate, conical in front, tapering gradually backwards from the middle. The tail not so long as in the preceding species. Colour opaque white with a slight yellowish tinge, due to the contents of the gut. Rhabdites, grouped in clumps, are present over the surface. Pharynx behind the brain, which is transversely elongate, deeply incised anteriorly. Two pairs of eyes are present, placed over the brain; the hinder pair is the larger, and is markedly reniform. Genital aperture at the base of the tail. The vesicula seminalis contains spermatozoa, which have a central rib, bearing broad triangular lateral membranes, exactly similar to the spermatozoa of *Plagiostoma maculatum*. Contrary to



Uljanin (41), I find two germaria present. They lie at the middle of the sides of the body.

HABITAT.—In 5 fms., among harbour débris, Plymouth (F. W. G.).

DISTRIBUTION.—Sebastopol (Uljanin).

36. *PLAGIOSTOMA CAUDATUM*, Levinsen (51).

Length 1.5 mm. Body when swimming cylindrical, tapering from the middle posteriorly, conical in front. Colour yellow, due to epidermal granules. Rhabdites few. Pharynx behind the brain. Eyes large, rhomboidal; between them a small mass of reticular pigment, with which, according to Levinsen, the pigment-cups of the eyes are sometimes connected. The genital aperture lies a short distance in front of the hinder end. The seminal vesicle leads by a narrow duct into the cylindrical muscular penis, surrounded by a double sheath, as in *Pl. reticulatum*.

HABITAT.—In 5½ fms., Plymouth Sound (F. W. G.).

DISTRIBUTION.—Egedesminde, west coast of Greenland (Levinsen).

37. *PLAGIOSTOMA VITTATUM* (Frey v. Leuckart, 23).

Length 1—2 mm. The latter size is that of individuals which have just laid their cocoons. v. Graff ('Monogr.,' p. 391) states that a length of 3 mm. is reached by specimens living on *Laminaria* below the surface. Jensen also (49, p. 58) finds larger specimens in such localities than at the surface. Tonnets taken near shore at Plymouth yielded small examples. Body convex above, broadly rounded in front, tapering to a finely pointed "tail" behind. It is well figured by van Beneden (33), pl. v, figs. 1 and 2. Colour more variable than in any other species of *Plagiostoma*. The typical coloration is three transverse bands of violet reticular pigment on a white ground; one central, one across the head,

and the third across the tail. v. Graff, in his Monograph, pl. xviii, fig. 6, has figured eight different varieties of the arrangement of these bands, which he observed in a single gathering among *Ulva* at Millport; and this does not exhaust the possible cases. Small specimens (.5—1 mm.) with a yellow ground-colour (due apparently to the contents of the gut-cells) are not uncommon. Since the "key" for the determination of species of this genus in v. Graff's Monograph is largely dependent on the arrangement of the pigment, these varieties are at first very troublesome. Moreover *Vorticeros auriculatum* (which frequently occurs among *Plagiostoma vittatum*) with retracted tentacles, can be in no way anatomically distinguished from a common variety of *Plag. vittatum*, in which the pigment is present over the greater part of the dorsal surface. With regard to the internal anatomy I can confirm the accounts of v. Graff and Jensen (49). Van Beneden (33), the first to discover the stalked yellow-brown egg-capsules, found them attached to the abdominal feet of the lobster. At Plymouth they were abundant in September on the sides of a vessel containing several individuals.

**HABITAT.**—Apparently more abundant on our northern than southern coasts. Millport, abundant (v. Graff); Plymouth; Port Erin, Isle of Man (F. W. G.).

**DISTRIBUTION.**—Faroe Islands (Schmidt), Bergen (Jensen), Heligoland (Leuckart, 23), Walcheren, on coast of Belgium (Slabber),<sup>1</sup> Ostende (van Beneden), Wimmereux (Hallez).

### 38. *PLAGIOSTOMA KORENI*, Jensen.

Length 1.4 mm. Body similar in shape to *Plag. vittatum*, but smaller, and rather narrower in front. The first half of the body is white, and behind this a broad transverse brown band (due to reticular pigment) over the dorsal surface and the sides. Behind this again are scattered brown spots. The brain, which bears two red eyes, is placed in front of

<sup>1</sup> 'Physikalische Belustigungen,' Nürnberg, 1775, pp. 31 and 36.

the spherical pharynx and mouth. The remaining anatomy has been investigated by Jensen (49), whose figures (pl. v, figs. 1—8) are highly characteristic.

HABITAT.—On the inner side of the Breakwater, and elsewhere among algæ between tide-marks, Plymouth Sound (F. W. G.); a specimen at Millport (v. Graff).

DISTRIBUTION.—Bergen (Jensen).

39. ? *PLAGIOSTOMA SIPHONOPHORUM* (O. Schmidt, 28).

Length .9 mm. Body elongate, truncate in front with rounded angles, tapering posteriorly. Along the mid-dorsal line is a narrow band of reticular black pigment, which expands laterally behind the eyes and extends between and beyond them anteriorly. Böhmig has shown (57, pp. 208—9) that this pigment is present in the gut-cells and not in the parenchyma. The mouth lies beneath the brain. The pharynx, when extended through the mouth, is narrow, cylindrical, expanded slightly at the distal end. My observations on the genital organs are incomplete. The penis is pyriform, armed at its base with small chitinous spines.

HABITAT.—In 15 to 18 fms., Plymouth Sound (F. W. G.).

DISTRIBUTION.—Lesina (Schmidt), Trieste (v. Graff, Böhmig).

As ripe sperm was not seen, this species remains doubtful. But other characters agree with *Pl. siphonophorum*, so I refer my specimen to this form.

40. *PLAGIOSTOMA GIRARDI* (Schmidt, 32).

Length 1.75—2 mm. Southern examples range up to 3 mm. Body slightly depressed, rounded in front, tapering behind, broadest in the middle. v. Graff's figure ('*Monogr.*' pl. xviii, fig. 12) does not represent the form well, whereas, as Böhmig has remarked, the figure of *Pl. ochroleucum* would

do so. Colour white. Movements sluggish. Rhabdites abundant over the surface. Pharynx small, opening through the mouth behind the brain. Eyes two, reniform, with lenses. According to Böhmig (57, p. 355), the "ciliated furrow" forms a transverse groove in front of the mouth, and does not correspond to a slight constriction which occurs behind the eyes. For the genital organs the accounts of v. Graff and Böhmig may be consulted. The spermatozoa consist of amidrib, bearing broad triangular hyaline membranes, and terminating in a short anterior and a longer posterior flagellum.

HABITAT.—Not uncommon 6—15 fms., Plymouth Sound (F. W. G.).

DISTRIBUTION.—Naples (v. Graff), where it is the most abundant Rhabdocœle; Trieste (v. Graff and Böhmig); Messina (v. Graff).

#### 41. PLAGIOSTOMA OCHROLEUCUM, v. Graff.

Length 5.5 mm. Colour whitish yellow. Mouth sub-terminal. Pharynx very small, beneath and in front of the brain. Remaining anatomy similar to Pl. Girardi.

HABITAT.—1½ fms. among Laminaria, Millport (v. Graff).

#### Genus 18.—VORTICEROS, O. Schmidt (28), 1852.

Plagiostominæ with two tentacles at the anterior end.

#### 42. VORTICEROS AURICULATUM (O. F. Müller, 4).

Length 1.5 mm. Body produced anteriorly into a pair of long tentacles. Behind the eyes it is slightly constricted, and then expands towards the middle, tapering behind to a fine point. The tentacles are not often seen fully extended. At the slightest alarm they can be completely withdrawn, and the

animal may continue to swim about in this condition. The colour is variable, but usually consists of a broad band of dark carmine reticular pigment on the upper surface, leaving the side margins free, and continued on to the tentacles. The anatomy differs in no important particulars from that of the genus *Plagiostoma*.

**HABITAT.**—Among *Ulva* and other littoral weeds, Plymouth; Port Erin, Isle of Man (F. W. G.); Millport (v. Graff).

**DISTRIBUTION.**—Naples, Trieste, Messina (v. Graff), Wimmereux (Hallez), Norwegian coast (Müller).

#### 43. *VORTICEROS LUTEUM*, v. Graff (53).

1852. *VORTICEROS PULCHELLUM*, O. Schmidt (28).

1879.        ,,                    ,,        var. *LUTEUM*, Hallez (50).

This species, established by v. Graff for the reception of a large specimen (8 mm. long), is distinguished from the preceding by its stouter appearance and uniform yellow colour. On two occasions at Plymouth an example measuring 2.5 mm. in length was taken. One was found among *Bugula turbinata* from 7 fms., the other among littoral weeds at a low spring-tide.

**DISTRIBUTION.**—Wimmereux (Hallez), Naples (v. Graff).

#### Subfamily ALLOSTOMINÆ.

*Plagiostomidæ* with one ventral and posterior genital aperture. Two germaria and two distinct vitellaria. Pharynx placed in the hinder half of the body, its mouth directed posteriorly.

This subfamily, as constituted by v. Graff, includes the genera *Enterostoma* and *Allostoma*. Concerning it our knowledge is in a most unsatisfactory condition. With regard to the former genus we do not possess a good description of any species, although these are abundant in northern and southern seas. Consequently the definition given above must

be considered provisional. Already *Enterostoma striatum*, v. Graff, has been investigated, with the result that Böhmig places it under the sub-family *Cylindrostominæ* (loc. cit., p. 469), and similar change in species hitherto considered as belonging to the *Allostominæ* may be expected to result from detailed investigations.

Genus 19.—*ENTEROSTOMA*, Claparède (35).

*Allostominæ* with uniformly ciliated body and without a circular "ciliated groove" on the head.

44. *ENTEROSTOMA AUSTRIACUM*, v. Graff. Pl. XXXIX, fig. 7.

Length .75 mm. Body rounded anteriorly, tapering to a blunt "tail" behind. Colour usually yellow, with a black spot (due to the intestine) in the centre; occasionally the general colour is white, the gut being yellow. The colour of the surface is due to the presence of yellow granules in the epidermis; that of the gut to its contents. The yellow epidermal granules are massed together in small heaps, which are not so conspicuous or large as figured by v. Graff (pl. xix, fig. 9, Monograph). Exceedingly small, slender rhabdites are present in groups in the epidermis. The pharynx is cylindrical, very muscular, and is inserted at the hinder edge of the extensive gut, which, following the outline of the body, reaches as far forward as the brain. The eyes are arranged in two pairs, an anterior and a posterior pair. The former are slightly the smaller, and their lenses are directed outwards and backwards; the lenses of the posterior pair face forwards and outwards. The genital aperture is a short distance from the hinder extremity. Round the brain are the developing testes. The pyriform muscular penis lies behind the pharynx.

HABITAT.—In 4—18 fms., Plymouth and Port Erin (F. W. G.).

DISTRIBUTION.—Trieste (v. Graff).

45. *ENTEROSTOMA FINGALIANUM*, Claparède (35).

Length 1 mm. Body elongate, cylindrical, rounded at both ends. Colour white; the short, almost central gut reddish. The epidermis contains small fusiform rhabdites, figured by Hallez (50, pl. ii, fig. 25). Mouth at the commencement of the posterior third. Pharynx cylindrical, at the hinder margin of the intestine. Brain bilobed. Eyes fairly large, arranged as in *Ent. austriacum*. Genital pore between the mouth and the hinder end. Testes numerous, surrounding the brain. Vasa deferentia exhibit dilatations along their course. Penis pyriform, containing masses of accessory secretion in its basal portion; provided at its tip with small papillæ. Claparède's original description and figures are not sufficiently distinctive to enable us to determine whether the germ- and yolk-glands are distinct or not. In my specimen the yolk-glands form lateral masses uniting behind the brain, and again posteriorly behind the genital aperture. The germ-glands lie at the sides of the pharynx, and appear to be separate from the yolk-glands. As, however, only a single specimen was available, further observations are greatly needed on this and other points, such as the presence of a ciliated "head-furrow" (which Böhmig has demonstrated in other forms by the use of methylene-blue in cases where superficial observation had previously failed) and the possible connection of genital and oral apertures.

HABITAT.—Skye (Claparède); among *Balanus*, 10 fms., Plymouth Sound (F. W. G.).

DISTRIBUTION.—Wimmereux (Hallez).

46. *ENTEROSTOMA CÆCUM*, v. Graff.

Length 1·7 mm. Body gradually tapering forwards from the hinder end. Beneath the epidermis are yellowish-green granules, especially abundant at the sides. The pharynx is cylindrical, muscular, placed far posteriorly. The spermatozoa consist of a central rib bearing lateral membranes, and

produced into a fine flagellum in front and behind. Eyes absent. For further details and figures see v. Graff, 'Monogr.,' p. 404, and pl. xix, figs. 15—17.

HABITAT.—A specimen at Millport in a tide-pool (v. Graff).

v. Graff described this form as the only blind Plagiostomid. I have, however, found a probably new species of Plagiostoma in which the eyes were wanting.

Genus 20.—ALLOSTOMA, van Beneden (33).

Allostominæ in which the "circular furrow" at the level of the brain is provided with long cilia.

47. ALLOSTOMA PALLIDUM, van Beneden (33).

Length 2 mm. Body cylindrical, tapering slightly towards each extremity. The anterior sixth is sharply separated from the rest of the body by a transverse marking, the nature of which is not quite clear. It is probably due to the ciliated "circular furrow." Colour yellowish white. The epidermis contains numerous pseudo-rhabdites. Considering rhabdites as a condensed glandular secretion, pseudo-rhabdites are intermediate between the amorphous secretion and rhabdites. The mouth is posterior; the pharynx short, leading into an extensive gut. v. Graff has described the genital organs fully. Testes surround the brain. Vasa deferentia convey the sperm in balls to the base of a pyriform penis, in front of which lie the ovaries. The oviducts unite and open through the subterminal genital pore. Yolk-glands lateral, lobed. (See v. Graff, 'Monogr.,' pl. xix, figs. 12—14.)

HABITAT.—Millport (v. Graff).

DISTRIBUTION.—Ostende (van Beneden, v. Graff).

Van Beneden (33) has described the oval egg-capsules, which are very small, and extruded one at a time. The young when



hatched are without a definitive pharynx, gut, eyes, or brain. They become sexually mature in three weeks.

Subfamily CYLINDROSTOMINÆ.

v. Graff's definition of this sub-family ('Monogr.,' p. 409) has been materially altered, owing to Böhmig's researches. It now reads thus (Böhmig, 57, p. 469):

Plagiostomidæ with a ciliated "circular groove."

The oral and genital apertures combined. A germ-yolk-gland present. Spermotheca present, connected with the ovigerous cell-mass ("Keimlager").

Genus 21.—CYLINDROSTOMA, Oersted (21).

The limits of this genus are not yet satisfactorily defined. v. Graff divided it into prosoporous and opisthoporous forms, according as the mouth was anterior or posterior. The latter have been excluded by Böhmig in his definition of the genus. v. Graff's original extension of the genus is, however, here adopted, pending a thorough examination of the Opisthopera.

48. CYLINDROSTOMA QUADRIOCULATUM (Leuckart, 23).

Length .5—·9 mm. Body colourless, somewhat depressed, rounded in front, tapering posteriorly to a long "tail" beset with adhesive cells. Mucus-rods ("Schleim-stäbschen"), of an irregular granular character, occur in the epidermis. Flagella are interspersed among the cilia in front and behind. At the level of the brain a pair of well-marked ciliated furrows are present. Mouth ventral, in front of the brain. Pharynx elongate, cylindrical, extending from the brain to the centre of the body; its anterior margin is crenulate, and provided with stout flagella. Brain almost cubical. The genital aperture is combined with the mouth. This remarkable discovery, made by Böhmig, corrects former mistakes due to misleading compression preparations. The testes form large follicular masses surrounding the brain. The different stages in the develop-

ment of the spermatozoa can be well observed. Behind the penis are a pair of short, wide vasa deferentia, which open into a highly glandular vesicula seminalis. The penis is a muscular, cup-shaped organ receiving both spermatozoa and granule-secretions from the vesicula, which it transmits through the genital atrium (underneath the pharynx), and so to the exterior. The spermatozoa are elongate, wider in front than behind. The central axis of the tail is markedly granular, and is continued forwards as a spiral thread, wound three times round the surface of the "head." The posterior end of the body is occupied by the large spermotheca. The germ-yolk-gland is composed of an anterior vitelline, and a posterior germinal portion.

HABITAT.—Kilmore, Skye (Claparède); abundant in tide-pools, Millport (v. Graff); among *Ptilota*, *Ceramium*, and other algæ, Plymouth (F. W. G.).

DISTRIBUTION.—Faroe, west coast of Norway (Claparède and Jensen), Heligoland (Leuckart), Ostende (van Beneden), Sebastopol (Uljanin).

49. *CYLINDROSTOMA INERME* (Hallez, 50). Pl. XXXIX, fig. 4.

Length 1 mm. Body oval, broadly rounded in front, tapering behind, of a bright yellow colour. Opposite the level of the brain, right and left, are a pair of lateral grooves, bordered by long cilia. The epidermis contains masses of granular yellow pigment and rhomboidal rhabdites. Mouth ventral, behind the brain. The pharynx is cylindrical, with a crenulate anterior margin. The genital organs resemble those of *Cyl. quadrioculatum* very closely; a spermotheca, however, is absent.

HABITAT.—Among fine red seaweeds, Plymouth (F. W. G.).

DISTRIBUTION.—Wimmereux (Hallez).

This species exhibits very great similarity to *Cyl. Klostermanni*, Jensen, especially in form, colour, and general anatomy.

The chief points of distinction are the absence of calcareous bodies in the epidermis, and of a spermatheca.

50. *CYLINDROSTOMA ELONGATUM*, Levinsen. Pl. XLI, fig. 19.

Length .6—8 mm. Body very elongate, narrow, cylindrical, slightly tapering and rounded in front, pointed behind. An apparent groove was seen just above the level of the brain, separating off the portion of the conical head in front of it. Colour yellowish to the naked eye; a black spot (the intestine) lies in the centre. The epidermis bears specially long cilia at the extremities. Small mucus-rods are present in large numbers. Glands open at the anterior end in front of the brain. Mouth ventral, posterior. Pharynx attached to the hinder end of the gut, barrel-shaped, its free margin crenulate. The intestine has a very small longitudinal extent, not greatly exceeding the transverse diameter of the body. It contains yellow-green and reddish-brown remains (chiefly diatoms). Brain cuboidal, the angles rounded off, without fissures. Four eyes, the posterior pair being distinctly the larger. Genital aperture almost terminal, just under the anterior end. Testes eight to nine in number, in front and at the sides of the brain. Vasa deferentia lead to the base of the posteriorly-directed, pyriform penis. Numerous glands open at this point, and their secretions are arranged in a radiate way. The germ-yolk-glands are bulky, and lie at the sides of the gut; they unite behind the brain. Behind and at the sides of the pharynx is the ovarian portion of the gland.

HABITAT.—Among tide-pools, Wembury Bay, near Plymouth (F. W. G.).

DISTRIBUTION.—Egedesminde, Greenland (Levinsen).

Genus 22.—*MONOPHORUM*, Böhmig, 1891.

*Cylindrostominae* with united mouth and genital apertures. Pharynx directed backwards, the penis forwards. The spermatheca opens into the genital

atrium. The germinal portions of both germ-yolk-glands are fused together in the middle line dorsally.

51. *MONOOPHORUM STRIATUM* (v. Graff).

Length 1 mm. Body cylindrical, rounded in front, pointed behind. Colour carmine to the naked eye. Under the microscope, however, it is seen that the reticular pigment is well developed, leaving the margins of the body and the outer sides of the eyes almost free. The surface of the body has a characteristic "streaked" appearance, caused by the grouping of the longitudinal muscles into bundles of four to six. In the intervals small rhabdites are plentiful. The cilia are very strongly developed. Böhmig has discovered that the oral and genital apertures unite. The pharynx is very contractile. The spermatozoa are collected in a pair of vasa deferentia and transferred to the globular base of the penis, the terminal part of which is narrow and cylindrical. For a more detailed account see Böhmig (57), pp. 435—447.

**HABITAT.**—Dredged in 4 fms. off the Duke Rock, Plymouth Sound (F. W. G.).

**DISTRIBUTION.**—Trieste, among *Ulva* (v. Graff, Böhmig).

Family *MONOTIDÆ*.

Allœocœla with two genital apertures. A spermatheca present. Two germaria and two distinct vitellaria. Testes follicular, closely aggregated between the pharynx and the brain. Pharynx directed posteriorly. An otolith present. Elongate flat forms, with a narrow anterior end, and a broad posterior extremity furnished with "adhesive cells."

Genus 23.—*MONOTUS*, Diesing.<sup>1</sup>

*Monotidæ* in which the female genital pore lies in front of the male.

52. *MONOTUS LINEATUS* (O. F. Müller, 2).

1773. *FASCIOLA LINEATA*, O. F. Müller (2).  
 1853. *PLANARIA FLUSTRÆ*, Dalyell (29).  
 1861. *MONOCELIS LINEATA*, Claparède (35).  
 1861. *MONOCELIS AGILIS*, Claparède (35).  
 1865. *TYPHLOPLANA FLUSTRÆ*, Johnston (38).  
 1875. *MONOCELIS RUTILANS*, McIntosh (45).  
 1882. *MONOTUS LINEATUS*, v. Graff (53).

This synonymy refers merely to the works of authors who have described British examples of this species.<sup>2</sup> For a fuller list see v. Graff (53), p. 418.

Length 2—2·5 mm. Body very elongate, appearing to the naked eye as a fine white thread. The hinder end assumes the form of a disc when the animal contracts. By means of adhesive papillæ present on the surface of this "Haftscheibe" it clings very tenaciously to the substratum. Colour variable, sometimes absent, more frequently present in the form of brown or grey reticular pigment. The epidermis of the anterior end is markedly thicker than elsewhere, and bears numbers of well-developed sensitive flagella. This part of the body is constantly employed during life in active movements in all directions. Should it meet with an obstacle it retracts with amazing rapidity. The rhabdites are only feebly developed. Owing to the great contractility of the body the positions of the organs are difficult to define. Considering, however, the animal to be in a fully extended state, the mouth is a short distance behind the centre of the body. The pharynx is cylindrical, very muscular, its proximal end being almost central. The gut is extensive; when contracted it becomes distinctly sacculated. In the middle line anteriorly

<sup>1</sup> Diesing, K. M., "Revision d. Turbellaria, Rhabdocœlen," 'Sitzungb. d. Akad. Wien,' Bd. xlv, 1862, p. 211.

<sup>2</sup> A method adopted throughout this memoir.

is the otolith, composed of a vesicle containing a central concretion bearing two double lateral ones. Immediately in front of this is the single transverse brown "eye," and behind it the brain. The male genital pore lies at the commencement of the adhesive "tail;" the female pore between this and the pharynx. The testes are numerous. The vasa deferentia run back to a muscular vesicula which opens into a papilla surrounded by accessory glands. This soft papilla is the copulatory organ. The single pair of germaria lie at the base of the pharynx. The vitellaria occupy the sides of the body.

**HABITAT.**—Hebrides (Claparède, 35); Firth of Forth, "on *Flustra hispida*" (Dalyell, 29); Millport (v. Graff); St. Andrews (McIntosh, 45); Port Erin, Isle of Man; Plymouth (F. W. G.).

**DISTRIBUTION.**—Very wide. West coast of Greenland (Levinsen), south and west coast of Norway (Claparède), Baltic (Müller, Schultze), North Sea (van Beneden), Madeira (Langerhans), Naples, Messina, Trieste (v. Graff), Black Sea (Uljanin, Czerniavsky).

This species is readily distinguished from *M. fuscus* by its unarmed penis.

### 53. *MONOTUS FUSCUS* (Oersted, 16).

Length 1.5—3 mm. Form similar to *M. lineatus*. Colour very variable, usually brown, but white, purple, and even dark blue varieties have been recorded by Jensen and v. Graff. Examples 1 mm. in length are usually white and colourless. Larger specimens (2 mm.) are frequently carmine, gradually becoming brown as they grow older. The meaning of this change<sup>1</sup> in the reticular pigment is not understood. Similar changes in some Opisthobranchiate Molluscs are known (*Aplysia*, see Garstang, 'Journal Marine Biol. Assoc.,' N.S., vol. i. No. 4, p. 411); and in this case the change in colour appears to go hand in hand with a change of surround-

<sup>1</sup> Already remarked by v. Graff (53), p. 422.

ings. Pharynx, brain, otolith, and eye as in *M. lineatus*. The male pore is placed further forward than in the latter species. The vasa deferentia open into the neck of the very muscular vesicula seminalis. The copulatory organ is a hollow chitinous spine of variable shape, connected at its base by muscles to the wall of the seminal vesicle. Numerous accessory glands open at this level. The spermatozoa are whip-shaped, the handle being stout, the lash a very fine thread. Opening to the exterior through the female genital pore is the spermotheca, provided, according to v. Graff and Jensen, with secondary lobes. The remaining parts of the female genital apparatus do not materially differ from those of *M. lineatus*.

HABITAT.—This species extends its range to the higher parts of the littoral zone. In consequence it is liable to be exposed to the air for some hours. Many of its devices for obtaining a moist position during ebb-tide have been described by Hallez and v. Graff. Thus the former observer collected *Balani*, the latter *Chitons* and *Patellæ* at low tide. After placing these in sea water, *Monotus fuscus* crept out of gills or thoracic limbs as the case might be. In the Isle of Man I have found them nestling among the appendages of *Balani*. Millport (v. Graff); Port Erin, and Plymouth (F. W. G.).

DISTRIBUTION.—Faroe Islands (Schmidt, 24), Bergen (Jensen, 49), Dröback and Denmark (Oersted, 16), Heligoland (v. Graff), Cuxhaven in the Baltic (Schultze), Ostende (van Beneden [33] and v. Graff), Wimmereux (Hallez, 50).

#### 54. *MONOTUS ALBUS*, Levinsen (51).

Length 1.3 mm. (i. e. half that of Levinsen's specimen). Body elongate, narrow, the hinder end not expanded into a disc, colourless; the contents of the gut reddish. Ocular pigment absent. Pharynx posterior. A large spermotheca containing a refractive secretion opens to the exterior in front of the penis, which is armed with a shoe-shaped chitinous copulatory organ, bearing a couple of lateral teeth on the free margins.

HABITAT.—One specimen in a tide-pool, Plymouth (F. W. G.).

DISTRIBUTION.—Jacobshavn, West Greenland (Levinsen).

Genus 24.—AUTOMOLOS, v. Graff (53).

Monotidæ in which the female pore lies behind the male.

55. AUTOMOLOS UNIPUNCTATUS (Oersted, 16).

- |       |   |
|-------|---|
| 1826. | PLANARIA UNIPUNCTATA, Fabricius (9).        |
| 1844. | MONOCELIS UNIPUNCTATA, Oersted (16).        |
| 1851. | „ „ Schultze (27).                          |
| 1861. | „ SP. (? UNIPUNCTATA, Oe.), Claparède (35). |
| 1875. | „ UNIPUNCTATA, McIntosh (45).               |
| 1878. | „ SPINOSA, Jensen (49).                     |

Length 1—1.5 mm. Body resembling *Monotus fuscus* in form, the hinder end, however, not expanded into an adhesive disc. Usually colourless. Ocular pigment is absent. Otolith with a pair of simple accessory concretions. The mouth, pharynx, and intestine resemble those of the preceding species. My specimens, as might be concluded from their small size (Jensen's were 3 mm., Schultze's measured as much as 6.6 mm.), were immature, and in consequence the genital ducts were not fully developed. According to the naturalists just named, the penis lies behind the male genital pore. It consists of a vesicula seminalis which conveys both spermatozoa and accessory secretions into the coiled ductus ejaculatorius, the terminal portion of which when extended is finger-like, and provided with small spines of variable shapes on its exterior. (See Schultze [27], pl. ii, and Jensen [49], pl. vi, fig. 9.) The two oviducts unite in the anterior region of the body, and the common duct runs back to the female genital pore, which also receives the duct of a vesicle—apparently spermotheca and uterus combined, since Jensen found sperm and ova in it.

HABITAT.—Skye (Claparède); St. Andrews, under stones



between tide-marks (McIntosh) ; among littoral algæ, Plymouth (F. W. G.).

DISTRIBUTION. — Bergen (Jensen), coast of Denmark (Fabricius, Oersted), Greifswald (Schultze), Madeira (Langerhans), Black Sea (Uljanin, Czerniavsky).

56. *AUTOMOLOS HORRIDUS*, n. sp. Pl. XLI, fig. 21.

Length 1.5 mm. Body somewhat flattened. A slight constriction occurs at the level of the otolith, separating off an anterior conical portion. Behind this "neck" the body gradually increases in width, to the posterior third of its length which ends in a sharply pointed "tail." Pigment is absent, the gut alone giving a grey tinge to the otherwise white body. Flagella are present at each extremity, and also occur at intervals for a short distance behind the anterior end. Packets of rhabdites occur in large numbers on the surface of the body (fig. 21). Adhesive cells are present, although feebly developed, on the tail. The musculature is strong, enabling the animal to execute very active movements, and to flex the sides of the body ventrally towards the middle line. The mouth lies at the commencement of the posterior third. The pharynx, inserted into the gut at the centre of the body, is cylindrical and very muscular. The intestine lies chiefly in front of the pharynx. Its cavity is produced into about twelve cæca on each side, placed fairly symmetrically. The specimen under examination was starved, and in this condition the limits of the gut branches can be clearly defined. Brain placed behind the otolith, oval, the long axis coinciding with that of the body. An eye is absent. Testes in this specimen not well developed. They occur behind and at the sides of the brain. Vasa deferentia open behind the pharynx into a vesicula seminalis, surrounded by accessory glands. The penis is pyriform and muscular. The single pair of germaria lie opposite the base of the pharynx. Elongate yolk-glands are placed at the sides of the gut. An accident prevented the determination of the oviducts.

HABITAT.—One specimen dredged in 12 fms., Plymouth Sound (F. W. G.).

57. ? *AUTOMOLOS OPHIOCEPHALUS* (O. Schmidt). Pl. XL, fig. 18.

1861. *MONOCELIS OPHIOCEPHALA*, Schmidt (34).

1882. *AUTOMOLOS OPHIOCEPHALUS*, v. Graff (53).

Length 1.5 mm. Body of a pink colour, very slender, elongate, the anterior end broader than the rest of the body, and separated off by a slight constriction. The hinder end when freely moving tapers gradually to a point. During contraction it becomes thickened and widened. Flagellæ appear to be absent. The rods are accumulated in packets chiefly at the two extremities. Individual rhabdites are longer at the anterior, shorter at the posterior end—exactly the reverse of the case in *A. hamatus*, Jensen. Strong adhesive cells occur on the “tail.” The pharynx is placed about the commencement of the posterior third. When extended the free end expands, the base becoming constricted. The intestine, which contains pinkish granules, is markedly sacculated. The pouches numbered about twenty on each side, and in compression-preparations appeared to be fairly definitely paired. Between successive gut-sacs were muscular dissepiments. Ocular pigment is absent. Testes occupy spaces in front and at the sides of the pharynx. The vasa deferentia lead to a vesicula seminalis, and this opens, along with the accessory glands, into the penis, a pyriform muscular organ, similar in position and form to that of *A. hamatus*. The pair of germaria lie at the base of the pharynx, the yolk-glands accompanying the gut-pouches and lying between them. The oviducts were not observed.

HABITAT.—Dredged in twenty fms., Plymouth Sound (F. W. G.).

DISTRIBUTION.—Corfu (O. Schmidt).

Schmidt's description of this species does not agree in all points with the diagnosis just given of my own specimen. The differences consist in the following details: the presence of

ocular pigment in front of the otolith, and the relations of the pharynx and ovaries. The latter, in his specimen, occupied a position behind and not in front of, the pharynx. The extreme contractility of the pharynx itself, and also of the body-wall, cause, especially during compression, marked changes in the position of the various organs. It is therefore possible that Schmidt's figure (34, pl. iv, fig. 3) may not represent the natural relations. v. Graff (53) does not mention the position of the ovaries, upon which Schmidt laid stress. For the present, therefore, and until more specimens are available, I place the Plymouth specimen under Schmidt's species, with which in almost all other points it appears to be identical.

### Sub-order 2.—TRICLADIDA.<sup>1</sup>

#### Family PLANARIIDÆ.

#### Genus 25.—GUNDA, O. Schmidt (1860).

#### 58. GUNDA ULVÆ (Oersted).

- ? 1768. *HIRUDO LITTORALIS*, Ström (1).  
 ? 1776. *PLANARIA LITTORALIS*, Müller (3).  
 1844. „ *ULVÆ*, Oersted (16).  
 1857-8. *PROCERODES ULVÆ*, Stimpson (32a).  
 ? 1860. *PLANARIA LITTORALIS*, van Beneden (33).  
 1861. *FOVIA LITTORALIS*, Diesing, S. B., 'Akad. wiss. Wien,'  
 Bd. xlv.  
 1861. *PROCERODES ULVÆ*, Diesing, loc. cit.  
 1865. *PLANARIA ULVÆ*, Johnston (38).  
 1870. „ „ Uljanin (41).  
 1878. *PROCERODES ULVÆ*, Jensen (49).  
 1880. *PLANARIA ULVÆ*, Czerniavsky (52).  
 ? 1880. *SYNHAGA AURICULATA*, Czerniavsky (52).  
 1881. *GUNDA ULVÆ*, Lang, 'Naples Mittheil.,' ii.  
 1887. „ „ Iijima, 'Journ. Coll. Sci. Imp. Univ. Japan,'  
 vol. i, part 4.  
 1889. „ „ Wendt, 'Archiv f. Naturgeschichte,' Bd. i,  
 Heft 1.

Length 3—7 mm. Breadth .4—1 mm. Body of uniform

<sup>1</sup> This sketch of the two marine Triclad of our shores will at least serve to show how much still remains to be done in the group. The synonymy is very difficult, and requires a thorough revision.

breadth. Anterior margin truncate, produced at the angles into a pair of distinct forwardly-directed auricles. Behind these a slight "neck" occurs. Posterior end broadly rounded or bifid. Colour variable. Young specimens are pale grey. In older examples the pigment is darker, and has a streaky appearance. On the dorsal surface just behind the eyes the pigment is arranged as a median and two lateral bands. The two latter cease behind the "neck." The median one runs forward between the eyes, and then dividing into 3—4 bands, it disappears. The modified strip of integument ('Tast-Organ,' which occurs among all groups of Turbellaria) is present. Pharynx inserted at the centre of the body. Two eyes are present anteriorly. They are placed in the white areas bounded by the pigment stripes. The genital pore lies slightly behind the commencement of the posterior third. Testes occur between the intestinal branches throughout the length of the body. The single pair of germaria are placed just behind the eyes and outside the lateral nerves. Vasa deferentia run at the sides of the pharynx and open into the peg-like penis, which is directed obliquely dorso-ventrally. The yolk-glands lie in the septa under the alimentary canal. The oviducts unite, and the common duct thus formed opens into the neck of the uterus, which is placed behind the genital atrium. The movements of this animal closely resemble the leech-like progression of fresh-water Planarians.<sup>1</sup>

HABITAT.—Among roots of Laminaria, Berwick Bay (Johnston, 49); in brackish water on west coast of Scotland (McIntosh, 45).

DISTRIBUTION.—Coast of Denmark, Holland, Belgium, Norway, Sweden, Black Sea, Baltic.

Genus 26.—FOVIA, Stimpson (32A).

59. FOVIA AFFINIS, Stimpson. Pl. XXXIX, fig. 9.

1844. PLANARIA AFFINIS, Oersted (16).  
1853. ,, HEBES, Dalyell (29).

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<sup>1</sup> This account is chiefly taken from Iijima, loc. cit.

1857-8. *FOVIA AFFINIS*, Stimpson (32a).

1865. *PLANARIA AFFINIS*, Johnston (38).

1878. *FOVIA AFFINIS*, Jensen (49).

Length 4—6·5 mm. Body linear-oblong, convex above, flat beneath. The form of the anterior end is described by Johnston and figured by Dalyell as slightly enlarged and rounded. Oersted's (16) pl. i, fig. 6, probably represents this species. The explanation of the plate states it to be *Planaria littoralis*, which, however, is not the case, since the latter is synonymous with *Planaria ulvæ*. A specimen taken at Plymouth is figured on Pl. XXXIX, fig. 9. The anterior end tapers slightly, and when viewed "end on" presents two slight lobes, which are used in a vigorous sensitive way, as in the case of *Convoluta paradoxa*.

The colour varies from greenish-brown to wood-brown. An oval white spot in the hinder half of the body marks the pharynx. The two eyes lie each at the inner side of a white area, and from them a pair of dark parallel streaks of pigment run to the anterior margin.

The movements of the animal are very striking. The most usual method of locomotion is by arching the body and drawing the hinder end up to the anterior one. These "geometer" or leech-like movements are repeated with great rapidity. This kind of motion is chiefly effected on moist surfaces. When, however, the water is deeper, the usual gliding ciliary movement is adopted. The hinder part of the body is kept on the substratum, while the anterior extremity is raised up and constantly extended and retracted, the body as a whole partaking of the steady forward movement.<sup>1</sup>

**HABITAT.**—Among algæ, Firth of Forth (Dalyell); Plymouth (F. W. G.).

**DISTRIBUTION.**—Coasts of Denmark, Norway, and Sweden.

<sup>1</sup> Bergendal ("Studien ü. nordischen Turbellarien," 'Ofvers af Kongl. Vetensk-Akad. Förhandlingar,' 1890, No. 6) has described a species apparently synonymous with the present one, in which the uterus has a separate external opening. He defines a new genus, *Uteriporus*, containing the single species *U. vulgaris*, Berg. An accident prevented a re-examination of my specimen.

**Sub-order 3.—POLYCLADIDA.****A. ACOTYLEA.****Family PLANOCERIDÆ.**

<sup>1</sup> Mouth and pharynx subcentral. Main-gut rarely extends in front of or behind the pharyngeal sheath. Dorsal tentacles present. Eyes occur (1) on or round the bases of the tentacles; (2) as a double cephalic group; (3) on the body margin. Development usually direct.

Genus 27.—*PLANOCERA*, de Blainville,<sup>2</sup> 1826.

Body broad, leaf-like. Tentacles tapering, contracting into temporary pits. Brain and tentacles lie at the beginning of the second fourth of the body. Marginal eyes absent. Pharynx at rest lies completely folded in its sheath. Two genital apertures some distance from the hinder end.

**60. PLANOCERA FOLIUM (Grube).**

1840. *STYLOCHUS FOLIUM*, Grube (14).

1844. *PLANOCERA FOLIUM*, Oersted (16).

1856. " " Johnston (38).

1884. " " Lang (54).

Length 1.4 mm. Body extremely contractile, so that a definite shape cannot be stated. The ground-colour is pale yellow; the main-gut and its branches are brown, ending in marginal black spots. Small white spots (due to the underlying ovaries) are dotted over the dorsal surface. On this surface, nearly one fourth the length of the body from the anterior end, are the cylindrical tentacles, which are during life capable of being suddenly extended and as quickly retracted into pits. Round the bases of these tentacles are

<sup>1</sup> The definitions of families and genera of Polyclads are taken from Lang (54).

<sup>2</sup> de Blainville, 'Dictionnaire des Sciences naturelles,' art. "Planaire," t. xli, 1826.

clusters of eyes. The two genital apertures lie behind the mouth, the male pore in front of the female.

HABITAT.—The coralline region, Berwick Bay (Johnston).

DISTRIBUTION.—Palermo (Grube).

Genus 28.—*STYLOCHOPLANA*, Stimpson (32A).

Planoceridæ with a delicate body expanded anteriorly. Marginal eyes absent. Pharynx only slightly folded at rest. 6—7 pairs of secondary gut-branches. Genital apertures separate or united. Penis unarmed. Penial sheath serves as genital atrium. Vesicula seminalis opens into the vesicula granulorum, and this direct into the ductus ejaculatorius. Bursa copulatrix and accessory vesicle present.

61. *STYLOCHOPLANA MACULATA*, Quatrefages (18).

- ? 1836. *PLANARIA SUBAURICULATA*, Johnston (12).  
 1845. *STYLOCHUS MACULATUS*, Quatrefages (18).  
 ? 1853. *PLANARIA CORNICULATA*, Dalyell (29).  
 1863. *STYLOCHUS MACULATUS*, Claparède (36).  
 ? 1865. *LEPTOPLANA SUBAURICULATA*, Johnston (38).  
 1866.       "               "               Ray Lankester (39).  
 1874.       "               "               McIntosh (45).  
 1884. *STYLOCHOPLANA MACULATA*, Lang (54).

Length 12—16 mm. Body flat, elongate, increasing in width from the hinder end forwards, the anterior fourth expanded laterally. The general colour is warm brown, due to the underlying gut-branches. Along the mid-dorsal surface, pale areas indicate the position of the pharynx and the genital pores. A pair of dorsal tentacles are present. Mouth mid-ventral, leading into the pharynx, the walls of which are plaited. 5—6 eyes are borne by each tentacle, and 7—8 occur round their bases. The male genital pore lies at the commencement of the hinder fourth of the length of the body;

the female pore a short distance behind this. The penis is pyriform, and receives the contents of a vesicula seminalis and granule-gland. The uterus lies in front and at the sides of the pharynx; it opens to the exterior along with the spermotheca through the vagina.

HABITAT.—Berwick Bay (Johnston); Firth of Forth (Dal-yell); Firman Bay, Guernsey (Lankester); St. Andrews (McIntosh); Jersey (Koehler).

DISTRIBUTION.—St. Malo (Quatrefages), St. Vaaste-la-Hogue (Claparède).

#### Family LEPTOPLANIDÆ.

Mouth and pharynx subcentral. Main-gut usually extends in front of, rarely behind, the pharyngeal sheath. Branches numerous. Male copulatory organ directed posteriorly. Tentacles absent. Eyes—(1) two lateral groups on the areas representing the tentacles of Planoceridæ; (2) double cephalic group; (3) marginal; (4) irregularly disposed over the head. Direct development.

#### Genus 29.—LEPTOPLANA, Ehrenberg (10).

Leptoplanidæ with elongate, delicate body. Pharyngeal sheath long. Lateral pouches numerous. Pharynx not completely folded. Genital apertures distinct. Granule-gland and vesicula seminalis separate. Marginal eyes absent. Eyes of group (1) larger than those of (2).

#### 62. LEPTOPLANA TREMELLARIS (O. F. Müller).

- 1774. FASCIOLA TREMELLARIS, O. F. Müller (2).
- 1776. PLANARIA TREMELLARIS, O. F. Müller (4).
- 1814. „ FLEXILIS, Dal-yell (6).
- 1840. „ TREMELLARIS, W. Thompson (15).
- 1844. LEPTOPLANA TREMELLARIS, Oersted (16).
- 1845. PLANARIA FLEXILIS, Johnston (20).



1845. *POLYCELIS LÆVIGATUS*, Quatrefages (18).  
 1849. *PLANARIA FLEXILIS*, Thompson (25).  
 1853.     "          "          Dalyell (29).  
 1865. *LEFTOPLANA TREMELLARIS*, Johnston (38).  
 1866.     "          *FLEXILIS*, Ray Lankester (39).  
 1874.     "          "          McIntosh (45).  
 1886.     "          *TREMELLARIS*, Koehler (55).  
 1886. *POLYCELIS LÆVIGATUS*, Koehler (55).

Length 12—25 mm. Body delicate, of variable shape, more or less elongate, broader in front than behind, the anterior margin semicircular; young specimens, as Dalyell has remarked, have the outline of a spherical triangle. The colour, if present, is brown; it is, however, extremely variable in amount and intensity: it is due partly to parenchymatous pigment, partly to the gut branches. In the middle line, not far from the hinder end, are two white areas; the foremost represents the male copulatory organ, the one behind it the "shell-gland." Between these and the brain a brown median area, surrounded by a clear whitish space, represents the main-gut and the uterus outside it. A V-shaped spot leading to the male pore is due to the underlying vasa deferentia. The ovaries appear (especially on a black ground) as white dots. From the white ventral surface the plaited pharynx and genital organs may be seen. Active swimming movements are produced by the expanded edges of the anterior end of the body. Between the male and female genital apertures is a depression, the lips of which are strongly muscular, and constitute a "sucker." The mouth is in front of the centre. It leads into the strongly puckered pharynx, lying in its sheath. From this the main-gut arises, and runs forwards towards the brain, and backwards to the commencement of the posterior third, giving off as it does so the numerous lateral branches, which in turn subdivide and end in fine cæca along the margin. The brain is distinctly bilobed. The lobes are oval, their long axes parallel to one another and to that of the body. Five anterior pairs of nerves supply the region in front and at the sides of the brain, and two lateral ones the rest of the body. The eyes

vary in number and arrangement. In front of the brain are usually two distinct patches of loosely arranged eyes at the bases of the nerves (corresponding to the eyes at the bases of the tentacles in Planoceridæ). Opposite the bases of the fifth pair of nerves is a compact group of larger, chiefly reniform eyes. In some specimens, however, the tentacular and cephalic groups of each side are continuous with one another. The genital apertures have already been noticed. From the numerous scattered testes, vasa efferentia arise. These gradually unite to form the pair of vasa deferentia which run at the sides of the pharynx, and before uniting at the base of the penis give off a posterior branch, which joins the one of the other side behind the female genital pore. The male copulatory organ consists of a ductus ejaculatorius, and the strongly muscular vesiculæ seminales and granulorum. The ova scattered throughout the body accumulate after fertilisation in the long uterus, which completely (in adult specimens) surrounds the pharynx and genital-apparatus. The uterus communicates with the exterior by a median duct, which in its lower portion is surrounded by the voluminous "shell-gland."

HABITAT.—Firth of Forth (Dalyell); Cultra, Belfast Bay (W. Thompson); Rothesay (Johnston); Firman Bay, Guernsey (Ray Lankester); St. Andrews (McIntosh); Jersey, Guernsey, Herm (Koehler); Plymouth Sound and neighbourhood, from littoral zone to 20 fms. (W. Garstang, F. W. G.); Hilbre Island, mouth of the Dee, Port Erin, Isle of Man (F. W. G.); Aberystwyth (J. H. Salter).

DISTRIBUTION.—Black Sea, Mediterranean, west coast of France, coast of Holland, Denmark, Baltic, North Sea, Red Sea.

The distinctive peculiarities of this species are the possession of a "sucker" and the simplicity of the female copulatory organ. Thus the "antrum femininum," or cavity into which the female genital pore leads directly, remains simple, while in

*Leptoplana alcinoi* and *vitrea* its walls are very muscular, and the organ becomes a bursa copulatrix. External form and colour, as Lang has forcibly stated (54, p. 482), afford no secure basis for the foundation of characters by which the species of *Leptoplana* may be distinguished.

### 63. *LEPTOPLANA MERTENSII* (Claparède).

1861. *CENTROSTOMUM MERTENSII*, Claparède (35).

Length 18 mm. Body oval, white or yellowish. Two groups of eyes on the dorsal surface.

As no details as to the structure of the genital organs are given, it is impossible to satisfactorily assign a position to this species.

HABITAT.—On *Laminaria*, Lamdash Bay, Arran (Claparède).

## APPENDIX TO LEPTOPLANIDÆ.

### 64. *PLANARIA ATOMATA*, O. F. Müller.

1777. *PLANARIA ATOMATA*, O. F. Müller (4).  
 1823. " " Fleming (8).  
 1839. " " Forbes and Goodsir (13).  
 1844. *LEPTOPLANA ATOMATA*, Oersted (16).  
 ? 1845. " *DRÆBACHENSIS*, Oersted (21).  
 ? 1853. *PLANARIA MACULATA*, Dalyell (29).  
 1865. *LEPTOPLANA ATOMATA*, Johnston (38).  
 1874. " " McIntosh (45).

Length 10—12 mm. Body oval, slightly wider in front than behind, rounded at both extremities. Colour variable, the ground-tint white or brown, spotted with reddish-brown, white beneath. Ova are seen as white dots over the upper surface. Two "tentacular" and two cephalic groups of eyes are present. The only known fact about the genital organs is that the penis has a bulbous base, and a transparent terminal duct which contains a hard stylet.

HABITAT.—Coast of Scotland (Fleming); Orkneys and

Shetlands (Forbes and Goodsir); Firth of Forth (Dalyell); St. Andrews (McIntosh).

DISTRIBUTION.—Naples (Delle Chiaje), coast of Holland, Germany, Denmark, Baltic (Dröback).

*Planaria atomata* has never been described in a sufficiently diagnostic way to render possible the identification of specimens with it. Consequently the above synonymy is very probably incorrect, but it is in no one's power to tell what the authors quoted did mean by their *Planaria atomata*. Thus Forbes and Goodsir, Fleming, Johnston, and McIntosh merely give the name and the record. Even those (as Müller and Oersted) who vouchsafe anatomical facts state the size, the form of the body, the position and arrangement of the eyes, and the form of the penis, and these do not by themselves, signalise a species of *Leptoplana*. Evidently a fresh and full description of a form is needed, which, if it differs from other existing species, may be called *atomata*, although its unity with the species of that name can only extend to the points mentioned. Comparisons with the new fully described *atomata* would henceforth be possible. Such a full account of a species agreeing in the form of the body, the position of the eyes, and the composition of the penis is to be found in Jensen's description of *Leptoplana Dræbachensis*.

The small differences that justified Oersted in separating these two species were the following :

	<i>Leptoplana Dræbachensis</i> , Oe.	<i>Leptoplana atomata</i> , O. F. Müller.
Oersted (21)	Length 4 lines. Body "antice obtuso, dein sensim angustiore." Eyes arranged in an anterior linear clump, and a posterior triangular one of 7.	Length 3—4 lines. Body "subovali, postice angustiore." Eyes arranged in four clumps. Those of the posterior ones are the larger.

With regard to the arrangement of the eyes, Jensen's specimens of *L. Dræbachensis* differ from Oersted's just as much or as little as does *L. atomata*. Oersted does not mention a hard penis in *Dræbachensis*, although he describes it in

*L. atomata*. Taking these facts into account, it may, perhaps, be said that Oersted's and Jensen's specimens have as much right to be classed in the same species as has Oersted's *L. atomata*.

For the future recognition of *L. Drøbachensis* I quote Jensen's diagnosis.

Length 10 mm. Breadth 4—5 mm. Body slightly narrowed posteriorly, rounded at both ends. Dorsal surface red with scattered darker spots, and with a longitudinal area, down the centre of which runs a broken white line. Ventral surface white. Four paired groups of eyes. Anterior groups placed longitudinally, hinder group directed outwards and backwards, composed of larger eye-specks. Mouth subcentral. Penis styliiform, hardened at its apex or for its whole length. Vagina connected with the spermotheca by a long duct provided with a moniliform series of dilatations (Jensen [49], pl. vii, figs. 10—14).

## B. *COTYLEA*.

### Family EURYLEPTIDÆ.

*Cotylea* usually provided with marginal tentacles. Brain anterior, behind the tentacles. Mouth just behind, rarely in front of the brain. Pharynx directed forwards, cylindrical. Main-gut behind the pharyngeal sheath. Male copulatory organ simple, directed forwards, placed just behind or beneath the sheath of the pharynx. A hard stylet in the penis. Female genital pore between the penis and the sucker. Eyes (1) in or round the tentacles; (2) double cephalic group, sometimes greatly elongated.

#### Genus 30.—*PROSTHECERÆUS*, Schmarda.<sup>1</sup>

Body smooth, delicate. Pharynx bell-shaped. Main-

<sup>1</sup> Schmarda, L. K., 'Neue wirbellose Thiere, beobachtet und gesammelt auf einer Reise um die Erde, 1853—1858,' Bd. i, 1859.

gut extending to posterior extremity. Body around the pharynx and main-gut frequently thickened. Uterine glands corresponding to the number of the secondary gut-branches. Tentacles well developed, pointed, moveable. Two small cephalic groups of eyes. Brightly coloured forms.

65. *PROSTHECERÆUS VITTATUS* (Montagu).

1815.	<i>PLANARIA VITTATA</i> ,	Montagu (7).
1823.	" "	Fleming (8).
1840.	" "	Thompson (15).
1845.	" "	Johnston (20).
1846.	" "	Thompson (22).
1857.	" "	Harvey (31).
1865.	<i>EUBYLEPTA VITTATA</i> ,	Johnston (38).
1884.	<i>PROSTHECERÆUS VITTATUS</i> ,	Lang (54).
1886.	" "	Koehler (55).

Length 3·7—5 cm. Body elliptical, tapering towards both extremities. The tentacles are lamellar, broad at their bases, which enclose between them the extreme anterior tip of the body in such a way as to separate it off slightly from the margin. The general colour is yellow, the margins white. The median ridge is distinguished by a black line. Right and left of this a number of black lines (increasing in number and distinctness with the age of the individual) run from the brain towards the hinder end. Those near the median plane are almost straight; the peripheral run parallel with the body margin. The mouth lies behind the brain. The main-gut is long, and gives off large numbers of secondary gut branches, which anastomose freely. Eyes occur over the brain as a pair of small, clearly defined cephalic groups, on the anterior margin and in the tentacles. The sucker is subcentral. Halfway between it and the mouth is the male aperture, and behind this the female genital pore. The vesicula seminalis and granule-gland open independently into the ductus ejaculatorius.

HABITAT.—Estuary of Kingsbridge, S. Devon (Montagu); coast of Scotland (Fleming); Strangford Lough (W. Thompson); between tide-marks at Roundstone, Connemara (W. Thompson); British coast (Harvey); Falmouth (J. Cranch, vide Johnston, 38); Jersey, Guernsey, Herm (Koehler); two specimens off Stoke Point, near Plymouth, 15 fms., on *Diazona* (J. T. Cunningham, MSS.); Plymouth Sound (W. Garstang).

DISTRIBUTION.—Mediterranean, west coast of France, Scandinavia, Denmark.

66. *PROSTHECERÆUS ARGUS* (Quatrefages).

1845. *PROCEROS ARGUS*, Quatrefages (18).

1859. *PROSTHECERÆUS ARGUS*, Schmarda, loc. cit.

1868. *EURYLEPTA ARGUS*, Keferstein (40).

1884. *PROSTHECERÆUS ARGUS*, Lang (54).

1886. *PROCEROS ARGUS*, Koehler (55).

Length 6—10 mm. Body oval, bearing two short marginal tentacles separated by the anterior extremity. Dorsal surface somewhat convex, orange with white spots. The eyes are numerous: on each side of the middle line extending behind the brain, and continued forwards to the ventral faces of the tentacles. Thus the marginal, tentacular, and cephalic groups are continuous.

HABITAT.—Between tide-marks at Grand Havre, Guernsey (Koehler).

DISTRIBUTION.—St. Malo (Quatrefages, Keferstein).

Genus 31.—*CYCLOPORUS*, Lang (1884).

Dorsal surface papillose. Pharynx short. Cells of main-gut almost filiform. About seven pairs of secondary branches. Uterine glands correspond to the number of the latter. The peripheral gut-branches open to the exterior through epithelial pores. Male pore close behind the mouth. Copulatory organ beneath and behind the pharyngeal sheath. Cephalic group of eyes not sharply defined. Tentacles small, sometimes rudimentary.

67. *CYCLOPORUS PAPILLOSUS*, Lang (54). Pl. XXXIX, fig. 2.

1880. *PROCEROS TUBERCULATUS*, Schmidtlein, 'Mittheil. Zool. Stat. Neapel,' Bd. ii.

1881. „ „ Lang, *ibid.*, Bd. iii.

Length 10—14 mm. Body elliptical with blunt extremities. In front the antero-lateral margins are produced to a variable extent as a pair of small, pointed tentacles. The dorsal surface is typically covered with small coloured papillæ—absent, however, in the variety *lævigatus*. Excepting the margins, the body is opaque. The ground-colour is yellowish-white. The main-gut and its six pairs of branches are brown, red, yellow, &c. In adult specimens they are largely concealed by the genital organs, but reappear on the margin, where their terminations are usually brightly coloured. The colour of the dorsal tubercles is variable and due to pigment in the epidermis. When the tubercles are absent their position is indicated by pigment-spots. Thus the colour is due partly to the contents of the gut, to pigment, and to the genital organs. Combinations of these three sources of colour account for the diversity between individuals of the same and of different ages, and appear to be correlated with the substratum (generally species of *Leptoclinum* and other Ascidians). Three to four black spots are present in specimens of the *lævigatus* variety, round the first pair of secondary gut-branches. (For good descriptions of the appearance of this animal at different stages of growth see Lang, 54, pp. 568—571.)

The mouth, just behind the brain, leads into a conical pharynx, the apex of which is directed backwards and is continued into the long main-gut. From this six lateral pairs of branches arise at right angles, which, after branching and anastomosing freely, end in terminal vesicles opening to the exterior through temporary epidermal pores at the moment of the expulsion of fæcal matter. The elongate cephalic group of eyes borders the white area produced by the pharynx, and extends forward beyond the brain. There is also a distinct group at the base and on the ventral surface of the tentacles.



The male genital pore lies close behind the mouth, the female aperture halfway between the anterior end and the subcentral sucker. The vesicula seminalis is very large. The uterus is a large lobed sac surrounding the main gut; the uterine glands are numerous (10—11 on each side). Surrounding the female pore is the very large radiate "shell-gland."

**HABITAT.**—On compound Ascidians and the sponge *Hymeniacidon sanguinea*, 5—15 fms., Plymouth (W. Garstang, F. W. G.); Port Erin, Isle of Man, 18 fms. (H. C. Chadwick). *Var. lævigatus* between tide-marks, Port Erin, and neighbourhood (W. J. Beaumont, F. W. G.).

**DISTRIBUTION.**—Naples (Lang).

This variable species may be easily mistaken for *Stylostomum variabile*. It is, however, recognisable by the presence of a continuous median gut-branch over the pharynx, whereas in *Stylostomum* the pharyngeal region appears as an uninterrupted white area, bordered laterally by the gut-diverticula.

**Genus 32.**—*EURYLEPTA*, Ehrenberg, 1831 (10).

Body smooth. Tentacles long, tapering. Usually five pairs of secondary gut-diverticula. The intestine is brightly coloured. Male genital pore beneath the hinder end of the pharyngeal sheath. One pair of uterine glands is present. Cephalic group of eyes extending posteriorly far beyond the brain.

**68. EURYLEPTA CORNUTA (O. F. Müller).**

1776. *PLANARIA CORNUTA*, O. F. Müller (3).  
 1831. *EURYLEPTA CORNUTA*, Ehrenberg (10).  
 1832. *PLANARIA CORNUTA*, Johnston (11).  
 1845.     "     "     Thompson (19).  
 1845.     "     "     Johnston (20).  
 1853.     "     "     Dalyell (29).  
 1865. *EURYLEPTA CORNUTA*, Johnston (38).  
 1865.     "     DALYELLI, Johnston (38).  
 1866.     "     *CORNUTA*, Ray Lankester (39).

Length 1·5—3·75 cm. Breadth about half the length. Body elliptical during motion, almost circular at rest, broadly rounded behind. In front are two elongate tentacles. The somewhat convex dorsal surface is, with the exception of the margins, opaque, of a bright orange-red colour dotted with white, due to parenchymatous pigment, and to a greater extent to the contents of the alimentary canal. In front an elongated, oval, raised, white ridge represents the underlying pharynx. The ventral surface is of a pale reddish colour, and upon it the gut, male and female apertures, and sucker are visible. The mouth is one-third of the distance from the anterior end to the sucker, i. e. close behind the brain. The pharynx is well developed, cylindrical, extending almost as far back as the centre, in front of which it opens into the extensive main-gut. From this a median and 5—6 lateral pairs of branches arise, which after branching slightly end in marginal forked cæca. The minutely moniliform appearance of these is due to the presence of sphincter-muscles at the points of constriction. Each tentacle receives a branch of the intestine. Extending from the brain towards the hinder margin of the pharynx are two groups of eyes, which stand out very clearly against the white underlying pharyngeal region. Posteriorly they are divergent, and consist of small, loosely aggregated eye-specks, which become larger and crowded in front, the two groups converging towards the brain. Eyes are also present in the tentacles and around their bases. The sucker is well developed, and serves to attach the animal very firmly to the substratum. The male genital aperture lies under the hinder end of the pharynx. The vasa efferentia unite in a large expanded duct on each side, from which the two vasa deferentia arise. The ductus ejaculatorius receives the contents of the granule-gland and the large vesicula seminalis. Just in front of the sucker lies the female pore, surrounded by the extensive radiating shell-gland. The uterus lies at the sides of the main-gut. A single pair of uterine glands are present.

HABITAT.—“ On the coast of Berwickshire, in deep water on

corallines and shells" (Johnston, 11); on *Laminaria*, 6—10 fms., Belfast Bay (W. Thompson); Firth of Forth (Dalyell); Firman Bay, Guernsey (Ray Lankester); Bordeaux (Koehler); Plymouth, in 2—6 fms., and between tide-marks (W. Garstang, F. W. G.).

DISTRIBUTION.—Naples (var. *Melobesiarum*, Lang), St. Malo (Keferstein), Dröback (Müller).

Genus 33.—*OLIGOCLADUS*, Lang (1884).

Body smooth. Tentacles long, capable of movement. Mouth in front of the brain. Pharyngeal sheath produced posteriorly into a closed diverticulum, which extends beyond the sucker. Pharynx cylindrical. Three to four pairs of secondary gut-branches. The main-gut apparently opens to the exterior at its hinder end. Male and female genital apertures lie under the pharyngeal sheath. Four pairs of uterine glands are present. The double cephalic eye-group sharply defined, not elongated behind.

69. *OLIGOCLADUS SANGUINOLENTUS* (Quatrefages). Pl. XXXIX, fig. 3.

1845. *PROCEROS SANGUINOLENTUS*, Quatrefages (18).

? 1864. " " Grube.<sup>1</sup>

1884. *OLIGOCLADUS SANGUINOLENTUS*, Lang (54).

1886. " " Koehler (55).

Length 8—11 mm. Breadth 3—4 mm. Body delicate, fairly transparent. Form elongate, parallel-sided, broadly rounded behind, produced in front into a pair of long, pointed, contractile tentacles, between which the extreme anterior end projects slightly. Colour white, especially marked along the margins. The mid-dorsal line is brownish or carmine, owing to the underlying main-gut and its median branch. The latter exhibits two conspicuous swellings, one at the point of origin, the other behind the brain. Three to four lateral diverticula

<sup>1</sup> 'Die Insel Lussin v. ihre Meeresfauna,' 1864.

arise on each side of the main-gut, and are of a brilliant carmine colour at first, becoming much less conspicuous towards the periphery. The pharynx and genital organs appear as white patches round the main-gut. The mouth is placed in front of the brain. The gut-branches do not anastomose. Eyes are present at the bases of the tentacles, and two sharply defined cephalic groups converge at the anterior end of the brain. The position of the genital apertures has already been mentioned. The male pore lies in front of the female.

**HABITAT.**—Between tide-marks, Grève d'Azette, Jersey (Köhler); Plymouth Sound, 5—20 fms. (F. W. G.); Port Erin, Isle of Man, 12—15 fms. (W. J. Beaumont and F. W. G.).

**DISTRIBUTION.**—Island of Lussin, Adriatic (Grube), Naples (Lang).

After much consideration I have referred several specimens dredged at Plymouth and elsewhere to this species. The distinguishing points are the position of the mouth in front of the brain; the male genital aperture underneath the anterior end of the pharyngeal sheath; and the short, sharply defined group of eyes over the brain.

#### 70. OLIGOCLADUS AURITUS (Claparède).

1861. EURYLEPTA AURITA, Claparède (35).

1884. OLIGOCLADUS AURITUS, Lang (54).

Length 18.5 mm. Body oval, transparent, white, the intestine bright reddish-brown. Mouth in front of the brain. Pharynx cylindrical. Main-gut gives rise to three pairs of secondary branches, which do not anastomose. Eyes are present in and round the bases of the tentacles, but, according to Claparède, are absent over the brain. The male genital pore occurs just behind the mouth; the female aperture is described by Claparède as almost central. Lang suggests that this author probably mistook the sucker for the pore. The vasa deferentia are scarcely so swollen as in *O. sanguinolentus*, and the vesicula seminalis rather larger than

in the latter. The granule-gland and copulatory organ agree exactly in both species. Claparède figures large rounded bodies which may possibly prove to be the accessory uterine glands (Lang).

HABITAT.—On *Laminaria*, Lamlash Bay, Arran (Claparède).

A more exact description of this species is necessary before the specific identity or difference of *Oligocladus sanguinolentus* and *auritus* can be regarded as proved. It appears fairly clear that they both possess the same generic characters—the subterminal mouth, position of the genital pores, and multiple uterine glands. No satisfactory points of difference can at present be determined. On the contrary, it is noticeable that it is just those organs which Claparède describes accurately—the mouth, pharynx, and intestine, and the male copulatory organ—which agree exactly with the corresponding structures in *O. sanguinolentus*.

Genus 34.—*STYLOSTOMUM*, Lang (1884).

Body smooth. Tentacles rudimentary. Oral and genital apertures open on a common depression immediately behind the brain. Main-gut with 5—6 pairs of secondary non-anastomosing branches. The median anterior branch is absent over the pharyngeal region. Male copulatory organ lies under the anterior part, the female organ under and behind the hinder part of the pharyngeal sheath. Two uterine glands. Cephalic eyes few in number.

71. *STYLOSTOMUM VARIABILE*, Lang. Pl. XXXIX, fig. 1.

- ? 1853. *PLANARIA ELLIPSIS*, Dalyell (29).
- ? 1865. *LEPTOPLANA ELLIPSIS*, Johnston (38).
- ? 1875.        "        "        McIntosh (45).
- 1884. *STYLOSTOMUM VARIABILE*, Lang (54).
- 1884. *STYLOSTOMUM ? ELLIPSIS*, Lang (54).

Length 5—9 mm. Body elliptical, broadly rounded

behind, tapering slightly in front. The extreme anterior margin truncate. Tentacles more conspicuous in adults than in young specimens, where they form mere blunt marginal projections. Immature specimens derive their coloration from the white or yellowish-white ground-tint and from the branches of the intestine, which, owing to the transparency of the body, are clearly visible. The colour of the gut-branches is scarcely the same in any two specimens, and may be red, orange, brown, black, &c. In mature examples the genital organs conceal the greater part of the alimentary canal. The mouth lies immediately behind the brain. It leads into a cylindrical pharynx, which, lying in its sheath, appears from the dorsal surface as a white oval area. Bounding the sides of this are the first pair of gut-branches, a median branch being absent. In front of the pharynx these two branches unite and from this point a very short median branch runs to the anterior end. Eyes are present below and above the tentacle bases, and also as two divergent series over and slightly beyond the brain. Very characteristic are two pairs of eyes close to the hinder margin of the brain, and a pair on its outer and anterior angles. The relation of these eyes to those of the larva may be gathered from Pl. XXXIX, fig. 1, which represents a young specimen of the present species. The male genital pore is combined with the mouth behind the brain; the female pore lies in front of the centre, the sucker just behind it. Granule-gland and vesicula seminalis open into the penis. The vesicula receives the separate vasa deferentia. The uterus encloses the main-gut. A very extensive shell-gland surrounds the female genital pore.

**HABITAT.**—Firth of Forth (Dalyell, 29); not uncommon between tide-marks (McIntosh 45); Falmouth, at low water (W. Garstang); Plymouth, in  $4\frac{1}{2}$  fms., along with young specimens; Port Erin, Isle of Man, in 12 fms. (F. W. G.).

**DISTRIBUTION.**—Naples (Lang).

This species, closely similar to young smooth specimens of

*Cycloporus papillosus*, may be distinguished by the absence of a median gut-branch over the white pharyngeal region, by the presence of only 5—6 pairs of secondary branches (*Cycloporus* possesses 8—9) to the intestine, and by their non-anastomosing character.

I have included *Planaria ellipsis* of Dalyell and others under this species, since his figures agree exactly in the points just mentioned.

### III. SUMMARY.

1. British marine Turbellaria, as at present known, include about fifty-seven species of Rhabdocœlida, twelve of Polycladida, and two Tricladida, making a total of seventy-one species. The numbers represent the examination of a limited extent of our coast (Millport, St. Andrews, Skye, the Isle of Man, Plymouth, and Channel Islands) during about three months of the year (July to September).

2. The following twenty-eight species are added to the British fauna in the present paper.

#### POLYCLADIDA :

*Cycloporus papillosus*, Lang.

#### ACÆLA :

*Proporus venenosus* (O. Sch.).

*Monoporus rubropunctatus* (O. Sch.).

*Aphanostoma elegans*, Jensen.

#### RHABDOCÆLA :

*Promesostoma ovoideum* (O. Sch.).

„ *solea* (O. Sch.).

„ *agile* (Lev.).

„ *lenticulatum* (O. Sch.).

*Byrsophlebs Graffi*, Jensen.

*Mesostoma neapolitanum*, v. Graff.

*Hyporhynchus armatus* (Jensen).

? „ *penicillatus*, (O. Sch.).

*Provortex rubrobacillus*, n. sp.

## ALLOECÆLA :

- Plagiostoma dioicum*, Metschnff.  
 „ *sulphureum*, v. Graff.  
 „ *Girardi* (O. Sch.).  
 „ *pseudomaculatum*, n. sp.  
 „ *sagitta* (Vlj.).  
 „ *elongatum*, n. sp.  
 „ *caudatum*, Lev.  
 „ (?) *siphonophorum* (O. Sch.).  
*Vorticeros luteum*, v. Graff.  
*Cylindrostoma inerme*, Halley.  
 „ *elongatum*, Lev.  
*Monoophorum striatum* (v. Graff).  
*Monotus albus*, Lev.  
*Automolus horridus*, n. sp.  
 „ ? *ophiocephalus* (O. Sch.).

3. The relations of the Turbellarian fauna of our coasts with that of neighbouring seas cannot be determined with certainty until more extended observations are recorded than we possess at present. Mediterranean and Adriatic forms occur on our south-western stations (Plymouth, &c.). Thus seven Polyclads and sixteen Rhabdocœles (33 per cent. of our fauna) are common to Naples, Trieste, and Plymouth. A large proportion (about 70 per cent.) of Scandinavian forms occur on our coast.

## IV. APPENDIX.

## SYNOPSIS OF THE FAMILIES, SUB-FAMILIES, GENERA, AND SPECIES OF BRITISH MARINE TURBELLARIA.

## I. RHABDOCÆLIDA.

Section A.—ACÆLA.<sup>1</sup>

1. With a single genital pore . . . Family *Proporidæ*.  
   *a.* Without spermotheca . . . Genus *PROPORUS*.  
 Species:—*P. venenosus* (elongate, yellow, two eyes present, provided each with a large lens).

<sup>1</sup> For the definition accidentally omitted see p. 440.



- b. With spermotheca . . . . . Genus **MONOPORUS**.  
 Species:—*M. rubropunctatus* (eyes without lenses, composed of red pigment-masses placed in the epidermis).

2. With two genital pores, the female pore in front of the male . . . . . Family **APHANOSTOMIDÆ**.

- a. Spermotheca with soft, non-chitinous mouth-piece . . . . . Genus **APHANOSTOMA**.

Species:—*A. diversicolor* (central part of the anterior end violet, extremities yellow). *A. elegans* (centre of the body with a lobate green spot).

- b. Spermotheca with chitinous mouth-piece

Genus **CONVOLUTA**.

Species:—*C. saliens* (with alternate longitudinal rows of cilia and rhabdites). *C. paradoxa* (with two eyes and "yellow cells" in the parenchyma). *C. flavibacillum* (dorsal surface very convex, no "yellow cells," sides of the body only slightly flexed ventrally).

#### Section B.—RHABDOCÆLA.<sup>1</sup>

3. With sexual and asexual reproduction. Female accessory organs absent . . . . . Family **MICROSTOMIDÆ**.

- a. Sexes separate. Head with a pair of lateral grooves. A pre-œsophageal cæcum present

Genus **MICROSTOMA**.

Species:—*M. grænlandicum* (eyes absent, a red spot usually present anteriorly).

- b. Hermaphrodite. Proboscis present. A posterior and sometimes lateral bundles of setæ

Genus **ALAURINA**.

Species:—*A. Claparedii* (proboscis with numerous papillæ, and a pair of ciliary tufts at its base; posterior bundle of setæ only).

4. With one or two genital apertures. Male accessory

<sup>1</sup> See p. 448.

organs present. Pharynx usually mid-ventral, rosulate (i. e. rosette-like) . . . . . Family **Mesostomidæ**.

I. A single genital aperture, two germaria, and two vitellaria. Accessory reproductive organs absent

Sub-family **Promesostominæ**.

a. Characters of sub-family . Genus **PROMESOSTOMA**.

Species:—*P. marmoratum* (copulatory organ coiled, crosier-like). *P. ovoideum* (penis pyriform, pigment-cup of eye simple). *P. solea* (pigment-cup of eye with hook-like process over outer surface of lens). *P. lenticulatum* (copulatory organ provided distally with radial triangular ridges). *P. agile* (copulatory organ curved, simple).

II. Two genital apertures. The male pore in front of the female. Germarium single. Sub-family **Byrsophlebinæ**.

a. Characters of sub-family . Genus **BYRSOPHLEBS**.

Species:—*B. Graffi* (vitellaria unbranched; copulatory organ widely funnel-shaped, the terminal margin with a triangular projection). *B. intermedia* (vitellaria branched, copulatory organ elongate, the terminal margin entire, and with a curved chitinous spur).

III. A common genital aperture. Germ-yolk-glands present. Testes rounded. Spermotheca with chitinous appendages . . . . . Sub-family **Proxenetinæ**.

a. Characters of sub-family . Genus **PROXENETES**.

Species:—*P. flabellifer* (copulatory organ retort-shaped, complex; duct of the spermotheca with chitinous teeth). *P. cochlear* (copulatory organ composed of three spoon-shaped pieces).

IV. A common genital pore. One germarium. Female accessory organs present. Testes elongate

Sub-family **Eumesostominæ**.

a. Copulatory organ traversed throughout its length by the ducts of male secretions . Genus **MESOSTOMA**.

Species:—*M. neapolitanum* (copulatory organ funnel-shaped, the margin with a spur; atrium very large).

5. The anterior extremity converted into a tactile proboscis, provided with a (usually complex) musculature

Family **Proboscidæ.**

I. Proboscis simple, with a sheath or muscle-cone. Short muscle-bundles serve as retractors

Sub-family **Pseudorhynchinæ.**

*a.* Characters of sub-family Genus **PSEUDORHYNCHUS.**

Species:—*P. bifidus* (hinder extremity bifid; copulatory organ conical, with a screw-like ridge on its outer surface).

II. Proboscis provided with a sheath opening in front, a muscle-cone, and four long retractors.

Sub-family **Acrorhynchinæ.**

*a.* Distinct seminal and granule vesicles, enclosed, however, in a common muscular sheath.

Genus **ACRORHYNCHUS.**

Species:—*A. caledonicus* (copulatory organ composed of small chitinous spines).

*b.* Duct of granule-vesicle with special chitinous investment . . . . Genus **MACRORHYNCHUS.**

Species:—*M. Naegelii* (copulatory organ tubular, with a curved spur longer than the tube). *M. croceus* (chitinous tube long, continued directly into the "spur"). *M. helgolandicus* (a chitinous investment enveloping granule-vesicle and vas deferens; a poison-dart present).

*c.* Two genital pores, the female in front of the male pore. Granule-vesicle with chitinous investment

Genus **GYRATOR.**

Species:—*G. hermaphroditus* (colourless; copulatory organ with a straight poison-dart).

III. Proboscis small, behind the anterior end, its sheath opening on the ventral surface. Granule- and seminal

vesicles not separate. Their contents, however, issue by distinct ducts . . . Sub-family **Hyporhynchinæ**.

*a.* Characters of the sub-family

Genus **HYPORHYNCHUS**.

Species:—*H. armatus* (copulatory organ composed of two fused chitinous, spiral tubes; pigment not reticular; six papillæ round the mouth. *H. penicillatus* (copulatory organ composed of two spoon-shaped pieces).

6. A single genital aperture. Pharynx large, dolioform. A uterus and paired testes present . . . Family **Vorticidæ**.

I. Germaria small, body-cavity capacious, free-living

Sub-family **Euvorticinæ**.

*a.* Two germaria and two unbranched vitellaria

Genus **PROVORTEX**.

Species:—*P. balticus* (copulatory organ with a spirally-curved spur on the margin). *P. affinis* (copulatory organ slightly bent distally). *P. rubrobacillus* (with red rods in the gut-cells; copulatory organ with a finely pointed straight spur to the margin).

Section C.—**ALLÆOCÆLA**.

Gut and parenchyma, with one exception (*Plagiostoma bi-maculatum*), distinct. Body-cavity absent in the adult. Testes follicular. Penis formed by a fold of the wall of the genital atrium. A conspicuous chitinous copulatory organ absent.

7. An otolith absent . . . Family **Plagiostomidæ**.

I. Genital aperture single, ventral, posterior. Mouth anterior. Germaria present. Sub-family **Plagiostominæ**.

*a.* Without tentacles . . . Genus **PLAGIOSTOMA**.

Species:—A. With four distinct eyes: *Pl. sagitta*.

B. With two eyes.

AA. Mouth terminal or subterminal: *Pl. dioicum* (1—5 mm. long, yellow, pharynx in front of

brain). *Pl. elongatum* (white, pharynx large, when retracted it lies behind the brain). *Pl. ochroleucum* (5.5 mm., pharynx subterminal).

BB. Pharynx and mouth behind brain.

a. Epidermis without pigment: *Pl. Girardi* (colourless, 2 reniform eyes). *Pl. siphonophorum* (with median longitudinal band of black reticular pigment). *Pl. pseudomaculatum* (violet pigment between the eyes, without distinct lateral grooves). *Pl. vittatum* (pigment variable, usually in the form of three transverse bands).

β. Epidermis pigmented: *Pl. sulphureum* (epidermis with yellow rods). *Pl. Koreni* (transverse band of parenchymatous pigment). *Pl. caudatum* (rhabdites few, head marked off by lateral grooves).

b. With two tentacles at the anterior end

#### Genus VORTICEROS.

Species:—*V. auriculatum* (violet reticular pigment over the greater part of dorsal surface). *V. luteum* (pigment uniformly yellow).

II. A single posteriorly-placed genital aperture. Two germaria and two distinct vitellaria. Pharynx directed backwards . . . . Sub-family Allostominæ.

a. Without a circular ciliated groove on the head

#### Genus ENTEROSTOMA.

Species:—*E. austriacum* (four eyes; pigment in rounded yellow masses). *E. fmgalianum* (pigment absent, colour due to food). *E. cæcum* (eyes absent).

b. With a circular ciliated groove at the level of the brain . . . . Genus ALLOSTOMA.

Species:—*A. pallidum* (adults 2—3 mm. long; granular mucus-rods [pseudo-rhabdites] in the epidermis).

III. Circular ciliated groove on the head. Oral and genital apertures combined. A pair of germ-yolk-glands present . . . Sub-family *Cylindrostominæ*.

*a.* With characters of sub-family

Genus *CYLINDROSTOMA*.

Species:—*Cyl. quadrioculatum* (pharynx directed forwards; body colourless). *Cyl. inerme* (epidermis yellow, containing rhabdites but no "calcareous bodies;" spermotheca absent). *Cyl. elongatum* (pharynx directed backwards; four eyes present).

*b.* Pharynx directed backwards, the penis forwards. Spermotheca opens into genital atrium.

Genus *MONOPHORUM*.

Species:—*M. striatum* (pigment carmine, reticular; muscles grouped in longitudinal bundles).

8. With two genital apertures, two germaria, and two vitellaria. An otolith present . . . Family *Monotidæ*.

*a.* Female genital pore in front of the male

Genus *MONOTUS*.

Species:—*M. lineatus* (an eye present in front of the otolith; copulatory organ a soft papilla). *M. fuscus* (copulatory organ a chitinous tube). *M. albus* (penis, a boat-shaped, chitinous copulatory organ with a pair of lateral teeth near the "bows").

*b.* Female genital pore behind the male aperture

Genus *AUTOMOLOS*.

Species:—*A. ophiocephalus* (an eye usually present in front of the otolith; head expanded). *A. unipunctatus* (an eye absent; penis a spinous tube). *A. horridus* (head slightly marked off from the body; rhabdites giving a spinous appearance to the animal; penis soft, muscular).

## II. TRICLADIDA.

A single (rarely double) genital aperture behind the mouth.  
Pharynx central or post-central . . . . . Family Planariidæ.

- a.* Penis directed dorso-ventrally. Uterus opens into genital atrium. Head truncate. Eyes wide apart  
Genus GUNDA.

Species:—*G. ulvæ* (the angles of the anterior margin produced into “lappets”).

- b.* Head produced in the centre. Eyes approximated  
Genus FOVIA.

Species:—*F. affinis* (pharynx behind the middle).

## III. POLYCLADIDA.

## Section A.—ACOTYLEA.

1. Dorsal contractile tentacles present. Tentacular, cephalic, and marginal groups of eyes . . . . . Family Planoceridæ.

- a.* Body leaf-like. Marginal eyes absent  
Genus PLANOCERA.

Species:—*Pl. folium* (tentacles placed behind commencement of second quarter of length; body yellow-brown).

- b.* Body distinctly enlarged in front. Tentacles placed well apart at end of first fifth of the body.

Genus STYLOCHOPLANA.

Species:—*St. maculata* (two genital apertures).

2. Mouth subcentral. Main-gut extending in front of (rarely behind) the pharyngeal region. Tentacles absent

Family Leptoplanidæ.

- a.* Body slightly enlarged in front. Marginal eyes absent . . . . . Genus LEPTOPLANA.

Species:—*L. tremellaris* (a “sucker” present between the male and female genital pores). *L. Mertensii* and *L. atomata* (doubtful species, see pp. 501–2).

## Section B.—COTYLEA.

3. Anteriorly-placed marginal tentacles usually present. Mouth just behind (rarely in front of) the brain. Penis with a hard stylet . . . . . Family EURYLEPTIDÆ.

*a.* Brightly coloured. Body thickened over the main gut. Tentacles large, moveable. Two small cephalic eye-groups . . . . . Genus PROSTHECERÆUS.

Species:—*Pr. vittatus* (body yellow, with longitudinal thin black lines). *Pr. argus* (dorsal surface orange-coloured; length up to 10 mm.).

*b.* Dorsal surface usually papillose. Tentacles small. Peripheral gut-pores to the exterior

Genus CYCLOPORUS.

Species:—*C. papillosus* (a median gut-branch over pharyngeal region).

*c.* Intestine brightly coloured. Tentacles long. Mouth behind brain. Cephalic eye-groups extending far behind brain . . . . . Genus EURYLEPTA.

Species:—*E. cornuta* (eyes not quite extending back to hinder edge of white pharyngeal region; body bright red).

*d.* Tentacles long. Mouth in front of brain. Pharyngeal sheath with a posterior cæcum

Genus OLIGOCLADUS.

Species:—*O. sanguinolentus* (body whitish, intestine usually carmine; a short cephalic eye-group).

*O. auritus* (eyes absent over the brain [Claparède]).

*e.* Tentacles rudimentary. Oral and male genital apertures united behind brain. A median gut-branch absent over the pharyngeal region

Genus STYLOSTOMUM.

Species:—*S. variable* (intestinal branches brightly coloured).



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## DESCRIPTION OF THE FIGURES ON PLATES XXXIX, XL, & XLI,

Illustrating Mr. F. W. Gamble's paper on "Contributions to a Knowledge of British Marine Turbellaria."

Pl. I represents the living animals, Pls. II and III compression- and other preparations.

*Alphabetical List of Reference Letters for all the Figures.*

*B. C.* Bursa copulatrix. *BR.* Brain. *BS.* Spermotheca. *CH.* Chitinous portion of copulatory organ. *CI.* Cilia. *COP.* Copulatory organ. *D.* Intestine. *DO.* Vitellarium. *E.* Eye. *EI.* Ovum. *FL.* Flagella. *GER.* Germarium. *GO.* External genital aperture. *KD.* Granule-gland. *L.* Lens

of eye. *M.* Mouth. *ME.* Muscular envelope. *MR.* Mucous-rods. *N.* Nucleus of epidermal cells. *OT.* Otolith. *PA.* Packets of rhabdites. *PE.* Penis. *PH.* Pharynx. *RH.* Rhabdites. *RS.* Receptaculum seminis. *SE.* Spermatozoa. *SP.* Pharyngeal glands. *TE.* Testis. *V. D.* Vasa deferentia. *VG.* Vesicula granulorum. *VS.* Vesicula seminalis. *W.* Ciliated groove.

## PLATE XXXIX.

FIG. 1.—Young *Stylostomum variabile*, Lang. Natural length 9 mm. The three pairs of eyes placed over the brain are very conspicuous, and persist in the adult (see p. 512).  $\times 65$ .

FIG. 2.—*Cycloporus papillosus*, var. *lævigatus*, Lang. Natural size. This form exhibits almost complete similarity in colour, form, and consistency with the Ascidians on which it is usually found.

FIG. 3.—*Oligocladus sanguinolentus*, Quatref. Length 1.1 cm.  $\times 6$ .

FIG. 4.—*Cylindrostoma inerme* (Hallez). Length 1 mm. The drawing is made from a specimen slightly compressed. Zeiss obj. C, oc. 4, cam. luc.  $\times 55$ .

FIG. 5.—*Macrorhynchus Naegelii*, Köll. Length 2.2 mm. This is a colour variety similar to what Claparède observed at St. Vaaste (see p. 462).  $\times 30$ .

FIG. 6.—*Promesostoma lenticulatum* (O. Sch.). Natural length .5 mm. The carmine-coloured gut is visible.  $\times 100$ .

FIG. 7.—*Enterostoma austriacum*, Grff. Natural length .75 mm. The yellow colour is due to groups of pigment-granules, the black spot to the contents of the intestine.  $\times 40$ .

FIG. 8.—*Provortex rubrobacillus*, n. sp. Natural length .6 mm. The brown spots are due to the contents of the gut-cells.  $\times 70$ .

FIG. 9.—*Fovia affinis* (Oe.) (probably *Uteriporus vulgaris*, Bergental). Natural length .4.5 mm. The figure is carefully drawn from a freely-moving specimen. The slight lobes of the anterior margin are seen when the animal is viewed from below and in front; this view also shows a slight median projection—similar, in fact, to what occurs in *Convoluta paradoxa*.  $\times 8$ .

FIG. 10.—*Promesostoma marmoratum* (Schultze). Natural length 1.5 mm.  $\times 20$ .

## PLATE XL.

FIG. 11.—*Plagiostoma dioicum*, Metschff. Natural length .6 mm. Compression-preparation.  $\times 200$ .

FIG. 12.—*Provortex rubrobacillus*, n. sp. Natural length .6 mm. Compression-preparation.  $\times 150$ .

FIG. 13.—*Promesostoma lenticulatum* (O. Sch.). Compression-preparation.  $\times 150$ . Concerning the organs marked R. S. and B. C. see p. 454.

FIG. 14.—*Promesostoma agile* (Lev.). Natural length .5 mm. Compression-preparation.  $\times 220$ .

FIG. 15.—*Vesicula granulorum* and its chitinous investment taken from *Macrorhynchus Naegelii*, Köll. The thickened margin is produced into two curved "spurs." As a rule only one is present.  $\times 220$ .

FIG. 16.—Copulatory organ of *Promesostoma marmoratum* (Schultze) (partly after v. Graff).  $\times 200$ .

FIG. 17.—Copulatory organ of *Promesostoma lenticulatum*.  $\times 600$ .

FIG. 18.—*Automolos* (?) *ophiocephalus* (O. Sch.). The living animal fully extended.  $\times 40$ .

## PLATE XLI.

FIG. 19.—Hinder portion of *Cylindrostoma elongatum*, Lev., to show the relations of the genital apparatus.  $\times 500$ .

FIG. 20.—*Plagiostoma sulphureum*, Grff. Natural length 2 mm. Compression-preparation.  $\times 70$ .

FIG. 21.—*Automolos horridus*, n. sp. Natural length 1.5 mm. Compression-preparation.  $\times 100$ .

## Peculiarities in the Segmentation of certain Polychætes.

By

**Florence Buchanan, B.Sc.,**

From the Zoological Laboratory of University College, London.

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With Plate XLII.

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IN the last volume of the 'Zeitschr. f. wiss. Zool.' (vol. liv, 1892, p. 569) a paper appeared entitled "Ueber Anomalien der Segmentierung bei Anneliden und deren Bedeutung für die Theorie der Metamerie," by C. J. Cori, dealing chiefly with the intercalation of half-segments, and with cases in which the furrows dividing successive segments externally have become continuous, thus forming a spiral going once, or more than once, round the body of the animal. Cori found seventeen out of about two hundred common earthworms (*Lumbricus terrestris*) abnormal in one of these two ways. He also found one specimen of a *Lumbriconereis*, one of *Halla parthenopeia*, one of *Diopatra neapolitana*, and one of *Hermodice carunculata* with intercalated parts of segments. He does not mention, however, how many specimens of each of these species he examined; and from his account one is naturally inclined to look upon such occurrences as rare, and to call them, with him, abnormalities. It may, therefore, be worth while to point out that there is at least one family of Polychætes, judging from over eighty specimens coming from different parts of the world, in which cases of intercalation and of spiral segmentation are so common as to be regarded rather as normal individual variations than as abnormalities. This family, from which Cori gives but one

example, is the Amphinomidæ, and the genus in which such variations particularly occur is the genus *Amphinome* (Blv.), Brüg, in its widest sense,—including, therefore, the genera *Eurythoë* and *Hermodice* of Kinberg and the genus *Linopherus* of Quatrefages, as well as *Amphinome* s. str. Kub.

Amongst the Polychætes collected by Professor Haddon in the Torres Straits, which have been for some time, and still are, in my hands for the purpose of identification, there are sixteen specimens of the genus *Amphinome* sufficiently well preserved and complete for examination with regard to the point at issue. Of these fourteen belong to the sub-genus *Eurythoë*, and six of these have each a half-segment completely or incompletely intercalated. The position of the intercalated segments will be seen from the following table :

	Total Number of Segments.		Intercalated Half-segment.	Description of Half-segment.
1	107½	. On the right side between Segments 20 and 21		Complete.
2	98½	. „ left	23 „ 24	„
3	72½	. „ right	19 „ 20	Incomplete, fused with 19th.
4	34½	. „ „	14 „ 15	
5	34½	. „ „	11 „ 12	„
6	88	. (23rd and 24th parapodia on the right side almost fused, which amounts to incomplete intercalation of a segment on the left side).		

The other two members of the genus in the collection belong to the sub-genus *Linopherus*, and of these one is regularly segmented, while the other has two and a half of its segments arranged as a spiral, beginning on the ventral and ending on the dorsal surface.

	Total Number of Segments. <sup>1</sup>	Begins.	Spiral	Ends.	Number of Rounds.
7	135½	. On ventral surface of 75th half-segment, left side	. On dorsal surface of 77th half-segment, left side		2½

<sup>1</sup> In all cases where spiral segmentation is involved the total number of segments means the total number of pairs of parapodia + the segments (if any) at the anterior end without parapodia. In the same way when a spiral is said to begin (or end) on a segment *x*, it means that it begins (or ends) opposite



The spiral is therefore a right-handed one as viewed from the dorsal surface. This will be understood by reference to fig. 1 (Pl. XLII), although in the specimen there represented the spiral is half a turn longer.

In another collection of Polychætes from shallow water off Ramesvaram Island in the Gulf of Manaar, sent to me for identification by Mr. Thurston, of the Madras Central Museum, there are seventeen specimens of *Amphinome* (all belonging to the sub-genus *Eurythoë*), of which two have intercalated half-segments, and six (one of them the same as one of the two with intercalated half-segments) have spirals of varying lengths. The position of both these variations with regard to the whole animal in the different specimens will be seen from the following table :

Total Number of Segments.	Intercalated Half-segment.		Description.	
1 . 97½ .	On the right side between Segments 21. and 22—		Complete.	
2 . 63½ .	“	“	“ 12 “ 13 “	
Total Number of Segments.	Begins.	Spiral Ends.	Number of Rounds.	De- scription. <sup>1</sup>
3 . 127 .	On dorsal surface of 116th half-segment, left	On dorsal surface of 116th half-segment, right	1 .	Left-handed.
4 . 110 .	Ditto 16th, right	Ditto 17th, left	2 .	Right-handed.
5 <sup>2</sup> . 86 .	Ditto 32nd, right	Ditto 34th, left	3 .	Right-handed.
6 <sup>3</sup> . 76½ .	Ditto 18th, left	On ventral surface of 21st half-segment, left	3½ .	Left-handed.
7 . 75½ .	On ventral surface of 14th half-segment, left	On dorsal surface of 25th half-segment, left	11½ .	Right-handed.
2 . 63½ .	Ditto 17th, left	Ditto 17th, right	1 .	Right-handed.

the  $x$ th parapodium on the side of the body mentioned (or the  $x$ th parap.—2 in the case of the *Eunicidæ*).

<sup>1</sup> The description of the spiral given in this column applies when the animal is viewed from the dorsal surface with its anterior end in front.

<sup>2</sup> Pl. XLII, fig. 1.

<sup>3</sup> Pl. XLII, fig. 2.

In the spirit collections of the British Museum there are fifty specimens belonging to the genus *Amphinome* well enough preserved for one to be certain whether or not the segmentation is regular and bilaterally symmetrical. Of these, twenty-seven present variations in symmetry of one kind or another. It is the presence of another species of *Amphinome* (*A.* [s. str.] *rostrata*, Pall.), of which there are no specimens in the other two collections, which raises the proportion so greatly. Of this species there are seventeen specimens, of which only one is regularly segmented throughout. The other sixteen all have their segmentation irregular towards the posterior extremity of the body, and the irregularity may take the form either of a spiral or of intercalation of half-segments, but more frequently a condition obtains which would seem to be intermediate between regular and spiral segmentation,—that is to say, the furrows which separate the segments form short spirals instead of circles; but, as they are not continuous with one another, the segments themselves do not take the form of a spiral. The arrangement will be best understood by a glance at fig. 4, where I have represented five successive segments whose intervening furrows do not meet on the dorsal surface. Sometimes it is on the ventral surface that they do not meet, and sometimes they do not meet on either in which case the furrows form a number of half-rounds of spirals. Very frequently there are one or more complete segments in the midst of a succession of incomplete ones. These and other details are shown in the following table :

Locality.	Total Number of Segments.	Segments whose two Halves are not opposite each other.	
1. (Not given) . . .	65	54—56 inclusive 58—65	} On the dorsal surface.
2. Bermudas . . .	56	38—48 42—44	} On the ventral surface.
3. " . . .	55	40—44 46—50 42—45	} On the dorsal surface. } On the ventral surface.
4. " . . .	52	39—41 47—49	} On the dorsal surface.
5. Australian seas . . .	60 $\frac{1}{2}$	41—45	" " "
6. " " . . .	55	41—43 47—50	} " "
7. " " . . .	55	44—49	" " "
8. " " . . .	54	39—54	" " "
9. " " . . .	54	44—48	" " "
10. Madras . . .	59	32—40 47—52	} " "
11. Porto Rico . . .	52	37—41 43—46	} " "
12. (Not given, but from the Museum Leach) }	65	54—56 58—65	} " "
13. " " . . .	56	35—41	" " "

Locality.	Total Number of Segments.	Begins.	Spiral Ends.	Number of Rounds.	Description.
14. (Not given, but from the Museum Leach)	56 $\frac{1}{2}$	47th dorsal, left	50th ventral, left	3 $\frac{1}{2}$	Left- handed.
15. <sup>1</sup> Australian seas . . .	60 $\frac{1}{2}$	30th vent., right 44th vent., left	30th ventral, left 49th dorsal, left	1 5 $\frac{1}{2}$	Left- handed. Right- handed.
5. <sup>2</sup> " " . . .	60 $\frac{1}{2}$	45th dorsal, right	50th ventral, right	5 $\frac{1}{2}$	Right- handed.
13. <sup>3</sup> (Museum Leach) . . .	56	34th dorsal, right	48th ventral, right	—	Right- handed.

<sup>1</sup> Segments 38—41 are also irregular on the dorsal surface in this specimen.

<sup>2</sup> When the same specimen has more than one kind of irregularity it occurs more than once in the list, but is referred to by the same number.

<sup>3</sup> The spiral in this specimen is interrupted in the middle by the irregularity in Segments 35—41.

Locality.	Total Number of Segments.	Intercalated Half-segments.
16. Australian seas	. 50 $\frac{3}{2}$ .	3 on right side between 49 and 50. (but incomplete)

No. 16 of the above list deserves especial mention. Unfortunately it is broken posteriorly, and so near to the critical point that it is difficult to be quite certain of what one sees. I have, however, represented what I saw, to the best of my ability, in fig. 5. It will be seen, by reference thereto, that the forty-ninth and fiftieth segments on the left side have no dorsal setæ nor branchiæ, and that on the right side between those two segments there are three other segments (*a*, *b*, and *c*) intercalated. I think there is a fourth segment intercalated on the right side, but of this I cannot be quite certain, as I could only see it on the dorsal surface. At any rate, the result is to make the posterior extremity of the body, as much as there is of it, coil bodily to the left.

Of the other thirty-three Amphinomes in the British Museum collection, twenty-six belong to the sub-genus *Eurythoë*, seven to the sub-genus *Hermodice*. Of these ten (? eleven), nine *Eurythoës* and one (? two) *Hermodices* present irregularities in segmentation, the nature of which will be seen from the following table :

Species.	Locality.	Total Number of Segments.	Intercalated Half-segment.	Description.
17 . <i>A. (E.) com- planata</i>	. St. Vin- cent's	. 117 $\frac{1}{2}$ .	On the right side between Seg- ments 59 and 60	. Incomplete (fused with 60).
18 . " "	. " "	. 140 $\frac{1}{2}$ .	On the right side between Seg- ments 4 and 5	. Incomplete (fused with 5).
19 . " "	. Zanzibar	. 136 $\frac{1}{2}$ .	On the right side between Seg- ments 19 and 20	. Complete.
20 . " "	. (Not given)	. 47 $\frac{1}{2}$ .	On the right side between Seg- ments 10 and 11	. "
21 . " "	. (Not given)	. (Incom- plete ante- riorly)	On the left side between Seg- ments 10 and 11 from the pos- terior end.	. "

Species.	Locality.	Total Number of Segments.	Spiral		Intercalated Half-segment.	Description.
			Begins.	Ends.		
22 . A. (E.) alcyonia	G. of Suez .	68 .			A piece intercalated on the middle of the dorsal surface between Segments 17 and 18, and between Segments 54 and 55.	
23 . A. "complanata"	Sir C. Hardy's Island	. 130 .	121st dors., right	. 127th dors., left	. 7 .	Right-handed.
24 . (Notgiven)	Roderiguez	. 114 .	14th dors., right	20th dors., left	. 6 .	Right-handed.
			19th dors., right	21st dors., left	. 2 .	Right-handed.
25 . (Notgiven)	Ramesvaram	. 105 .	62nd dors., right	68th dors., left	. 7 .	Right-handed.
			85th dors., right	86th dors., left	. 2 .	Right-handed.
26 . A. (H.) nigrolineata	(Notgiven)	43 .	28th dors., left	29th dors., right	. 2 .	Left-handed.
27 . A. (H.) runculata	St. Vincent	. Incomplete,	only one end of the spiral seen.			

Of these, No. 24 is the most remarkable. The irregularly segmented part is represented in fig. 3. From this figure and the key attached (3 B) it will be seen that there is one spiral of two coils beginning in the middle of and intertwined with another of seven.

With regard to the internal organs: wishing to preserve one intact specimen of each kind of spiral, I have only been able to cut sections of two of the specimens at my disposal (namely, Nos. 5 and 6 from the Madras collection). The condition in which the specimens were was not such as to guarantee any results from dissection, and horizontal sections seemed, therefore, the best method of examination. The sections of one of these specimens, No. 6, were worth very little, as the animal was rather broken in the twenty-first segment, and consequently only the anterior part of the spiral could be cut. From the other specimen, of which I cut sections, No. 5, all

I have been able to make out is that the nephridia, or at least renal organs of some sort (for, in the state of preservation the specimen was in, all one could see of a renal organ was a solid mass of tissue containing yellowish concretions, and a short duct leading to the exterior), occur regularly one in each half-segment; that the blood-vessels spring very irregularly from the dorsal vessel and form plexuses in the segments on each side of the alimentary canal, and a sinus round the alimentary canal itself. They seem to be equally irregular in segments which are regular externally, but in both cases injury to the tissues generally, owing to the state of preservation,<sup>1</sup> may have caused the blood-vessels to break, and thus assume an irregularity when put together from sections. The nerves go out in this specimen quite regularly in pairs; one pair to both the thirty-second parapodia, one to both the thirty-third, and one to both the thirty-fourth. The septa are throughout the body incomplete, but as far as they do project into the body-cavity they seem to follow the external boundaries of the segments. I hope, in the course of time, to obtain specimens which will enable me to come to more definite conclusions with regard to the internal organs in the different varieties of spirals. It would also be very interesting to examine specimens of *A. rostrata* internally, and so get different intermediate conditions.

There are but few other genera in the family Amphinomidæ, and there are none of them very common. There is, however, one other genus at least in which irregularity in segmentation occurs, though I have only noticed it at present in one specimen. This is the genus *Chloeia*, of which I suppose I have seen about twelve specimens altogether, and the one specimen I refer to is in the possession of the Royal College of Surgeons' Museum. It has thirty-five segments, and of these the halves of each of the last eight are not opposite one

<sup>1</sup> I should mention that the specimens were not intended for histological work, but only for museum specimens, and as such all the Amphinomes in the Madras collection are very well preserved considering how difficult Polychætæ are to preserve well.

another on the ventral surface, so that a condition somewhat similar to that in most specimens of *Amphinome rostrata* obtains.

I had not noticed spiral segmentation in any other family of Chætopods before the publication of Cori's paper (except for a doubtful case of it in a Sabellid, which I shall have to refer to later on). Seeing that he found it in such a different group as the earthworms (and apparently it was only in earthworms that he found the spirals), I thought it would be worth while to look through the specimens I had of other families, and those in the Zoological Museum of this College, paying especial attention to the segmentation. Although I did not look through by any means all the specimens in my charge, I looked through a fairly large number, and I looked through almost all the specimens in the Zoological Museum here. The result was curious: only in two species out of the many examined did I find spiral segmentation again, but in these two species it was more common even than in the genus *Amphinome* (taking it as a whole); and not only was the proportion of individuals that had this kind of segmentation very great, but also the number of spirals in each individual was most striking.

There are six specimens of *Lumbriconereis impatiens*, sent from Naples, in the Zoological Museum here. Of these, two (young ones) seem to be regularly segmented throughout; the other four (one young one) have spirals of different lengths, as seen in the following table:

Total Number of Segments.	Begins.	Spiral Ends.	Number of Rounds.	Description.
1. 462	In 186th half-segment, ventral, right	. 186½th dors., right <sup>1</sup>	. ½ <sup>1</sup>	Left-handed.
	In 445th half-segment, ventral, left	. 446th dors., left	. 1½	Right-handed.
	In 450th half-segment, dorsal, right	. 451st dors., left	. 2	Right-handed.

<sup>1</sup> This is a true spiral, though a short one, and not an intercalated half-segment, for the furrow has a spiral course (see fig. 7). The same holds for the three quarters of a round in spec. 4.

Total Number of Segments.	Begins.	Spiral	Ends.	Number of Rounds.	Description.
2. 442½	In 203rd half-segment,		206th dors.,	4	Left-handed.
	dorsal, left		right		
	In 304th half-segment,		306th dors.,	2½	Right-handed.
	ventral, left		left		
3. 407	In 182nd half-segment,		185th dors.,	3½	Left-handed.
	ventral, right		right		
	In 245th half-segment,		247th dors.,	3	Left-handed.
	dorsal, left		right		
4. 200 (about)	In 108th half-segment,		108th vent.,	¾	Left-handed.
	dorsal, left		left		

Also a segment incompletely intercalated on the left side between the 125th and 126th segments.

The other species in which the spiral arrangement is so common is one of which Cori also examined a specimen, and he remarks on the large number of so-called abnormalities in it, though he only describes two cases of intercalation. This species is *Halla Parthenopeia*. Of the two specimens of it in the Zoological Museum here (both of them from Naples), one has eleven and the other twelve distinct asymmetrical parts, the nature of which and their relation to the whole length of the animal will be seen in the following table:

Total Number of Segments.	Begins.	Spiral	Ends.	Number of Rounds.	Description.
1. 567½	219 ventral, left		221 dorsal, left	2½	Right-handed.
	225 ,, right		226 ,, right	1½	Left-handed.
	227 dorsal, left		228 ,, ,,	2	„
	336 ,, ,,		337 ,, ,,	2	„
	345 ventral ,,		345 ,, ,,	½ <sup>1</sup>	Right-handed.
	383 ,, ,,		385 ,, left	3	„
	487 dorsal ,,		491 ,, right	5	Left-handed.
	517 ,, ,,		518 ,, ,,	2	„
	536 ,, right		537 ,, left	2	Right-handed.

The same specimen has a half-segment intercalated between 234th and 235th segments on left side.

„ „ „ piece intercalated on the dorsal surface on right side of the 383rd segment.

„ „ „ half-segment on the right side and two pieces in the mid-dorsal line intercalated between 501st and 502nd segments.

<sup>1</sup> See foot-note, p. 537.



Total Number of Segments.	Begins.	Spiral	Ends.	Number of Rounds.	Description.
2. 489 .	104 dorsal, right	.	105 dorsal, left	. 2	Right-handed (but not well marked).
115	„ left	.	? <sup>1</sup>	. ?	Left-handed.
146	„ „	.	148 dorsal, right	. 3	„
153	„ „	.	154 „ „	. 2	„
169	„ right	.	170 „ left	. 2	Right-handed.
178 ventral	„ „	.	179 „ right	. 1½	Left-handed.
187	„ left	.	191 „ left	. 4½	Right-handed.
365 dorsal	„ „	.	366 „ right	. 2	Left-handed.
{	389 „ right	.	392 „ left	. 2	Right-handed.
	390 „ „	.	390 „ „	. 1	„
	391 „ „	.	391 „ „	. 1	„
451	„ „	.	451 „ „	. 1	„
455	„ „	.	459 „ „	. 5	„

The occurrence of right-handed and left-handed spirals not only in the same individual, but very close together in the same individual, is well shown. The three spirals bracketed in the second specimen deserve special mention, as we have here a second case of spiral within spiral. The arrangement is shown in fig. 6, and can easily be understood by reference to its key (fig. 6 B). It will be seen that there are two short spirals of one coil each, both inside a larger one of two coils. I hope in a short time to have specimens of *Halla* at my disposal for dissection, and feel sure they will yield interesting results.

With regard to other Eunicidæ, I have looked through a fairly large number of specimens belonging to the genus *Eunice* and to the genus *Marphysa*, a few *Diopatras*, one very long *Arabella* (with over nine hundred segments), and two or three other species of the genus *Lumbriconereis*, but without finding any irregularities in the segmentation.

The only other Polychætes in which I have, so far, noticed what appears to be spiral segmentation is a *Sabella*. There are in the Madras collection four specimens of what I believe

<sup>1</sup> The parapodia on the right side of Segments 115—118 had been previously removed in this specimen, evidently by some one who had noticed the peculiarity. I cannot, therefore, be certain where the spiral ends.

to be a new species of *Sabella*. The change of setæ in three of them takes place between the eighth and ninth segments. In one specimen, however, there are nine pairs instead of eight thoracic parapodia, and the change on the left side takes place distinctly in front of the ninth ventral shield, whereas that on the right takes place distinctly behind it (fig. 8). This is accounted for by the fact that the second ventral shield is divided on the left side, and there is a separate parapodium to each half. Thus in taking a ventral view of the animal we see what appears to be a spiral beginning in the third half-segment on the ventral surface, left side, and going on into the abdomen to end (?) in the hundred and second segment on the ventral surface, right side, about twelve segments before the end of the body. The reason why one cannot say with absolute certainty that this is a case of spiral segmentation is that the segments are not marked off from one another on the dorsal surface, and one cannot therefore trace them right round the body. But the ventral view of the animal shows exactly the condition which obtains throughout the length of any spiral beginning and ending on the same surface in the other *Chætopods*. If it is a spiral it is a right-handed one, and remarkable for its length. I cannot be quite certain of its ending in the hundred and second segment, as the segments at the posterior end of the body are extremely narrow and very difficult to follow; but it certainly does not end before, at least not on the ventral surface.

Before leaving the subject I should like to draw attention to the existence of spirals similar to those we have been considering in another group of animals altogether. In a recent number of the 'Quarterly Journal of Microscopical Science' (vol. xxxiv, 1892) Baldwin Spencer, in describing the female of *Pentastomum teretiusculum*, Baird, says that there are occasionally incomplete segments wedged in on one side or the other between the complete ones. He figures one specimen with two of these so-called wedges, but to me it looks very much as though there were a spiral going four times round the body (i. e. between his two

“wedges”). I was confirmed in this opinion by the examination of a specimen of *Pentastomum* which I happened to have by me (from Professor Haddon's collection), and which is apparently a female of the same species. In this one specimen there are three spirals to be traced :

Total Number of Segments.	Begins.	Spiral	Ends.	Number of Rounds.	Description.
67	In 8th half-segment, ventral, left	.	In 16th ventral, right	9	Right-handed.
	In 17th half-segment, ventral, right	.	In 19th ventral, left	3	Left-handed.
	In 33rd half-segment, ventral, right	.	In 43rd ventral, left	11	„

Baldwin Spencer's casual mention of variation in symmetry, and the fact of my finding three spirals at once in the only specimen of *Pentastomum* available, lead me to infer that spirals and wedges are probably as common, at any rate in this one species of *Pentastomum*, as in the special *Polychætes* we have been considering. And it seems to me interesting for the whole theory of segmentation to find such asymmetrical variations occurring almost normally in two very different groups of segmented animals. Cori has already drawn attention to the intercalation of half-segments in the *Cestodes* (and it would seem that it is especially in *Bothriocephalus latus* that such variations occur). So that we have here a third group of segmented animals in which variations in symmetry may be common.

With regard to Cori's suggestions as to the origin of these variations, we have as yet too few data to say anything either for or against them. His statement that the irregularities occur more frequently in the middle of the body than at either end is not confirmed by the specimens I have examined, as reference to the above tables will show. As far as Ehlers' suggestion is concerned, that such irregularities are the result of regeneration of lost parts, I will mention that I have frequently seen *Polychætes* regenerating heads or tails (and amongst others four or five *Amphinomes*, one *Halla*, and one *Lumbriconereis impatiens*), but in all cases except

one the regenerated part was attached quite regularly to the rest of the animal. This of course shows very little, as it may have been that in all these cases the body of the animal had been broken off symmetrically previous to regeneration, and one could only expect to get asymmetry where the body had been broken in a plane not at right angles to the long axis of the body. The one specimen that I have seen asymmetrical at the point of juncture of the regenerated and main portion of the body is the No. 5 of the Australian Amphinomes, where the anterior eleven and a half segments have been regenerated, and the half-segment on the right side is apparently the first of the new segments. It would be interesting to know whether the species or genera in which asymmetrical variation particularly occurs are especially remarkable for their power of regeneration. Even if the intercalation of half-segments were shown to be due to regeneration, it would still remain to be shown that the spiral arrangement is likewise due to it. The fact of spirals occurring in *Pentastomum*, where, as far as we know, regeneration does not take place, seems to me against this hypothesis. It would be very interesting to make experiments on the living animals of those species in which irregular segmentation is common with regard to regeneration of lost parts, and also to watch their development.

In conclusion, I should like to thank Professor Weldon, in whose laboratory I am working, for his kindness in giving advice with regard to this and other work. My thanks are also due to the authorities of the British Museum for kindly giving me access to their collections during the last few years; and to Mr. Stewart, of the Royal College of Surgeons' Museum, for letting me examine the *Polychætes* which are in the possession of the Museum.<sup>1</sup>

<sup>1</sup> An interesting paper by T. H. Morgan on the same subject as the above, but dealing chiefly with *Oligochætes*, has recently appeared in the 'Journal of Morphology,' vol. vii, Nov., 1892, pp. 245—251. As that number of the journal had not arrived here when my paper was sent to press, I have been unable to introduce the results contained in it; but the editor of this journal kindly called my attention to it on receiving my manuscript, and I give the reference for the convenience of those interested in the subject.

## EXPLANATION OF PLATE XLII,

Illustrating Miss Florence Buchanan's paper on "Peculiarities in the Segmentation of certain Polychætes."

FIG. 1.—Six segments of an Amphinome (Madras Collection, No. 5), of which three form a simple right-handed spiral, beginning and ending on the dorsal surface. Dorsal view. Enlarged.

FIG. 1 A.—Ventral view of the same segments.

FIG. 1 B.—Diagrammatic representation of the spiral.

FIG. 2.—Six and a half segments of an Amphinome (Madras Collection, No. 6), of which three and a half form a left-handed spiral, beginning on the dorsal and ending on the ventral surface. Dorsal view. Enlarged.

FIG. 2 A.—Ventral view of the same segments.

FIG. 2 B.—Diagrammatic representation of the spiral.

FIG. 3.—Ten segments of an Amphinome (British Museum Collection, No. 24) in which there are two right-handed spirals, one inside the other. Dorsal view. Enlarged.

FIG. 3 A.—Ventral view of the same segments.

FIG. 3 B.—Diagrammatic representation of the spirals. The longer one is represented as though lined with black, the smaller one as though with a shaded lining.

FIG. 4.—Five segments of an Amphinome rostrata (British Museum Collection, No. 3), showing a condition intermediate between normal and spiral segmentation. Dorsal view. Enlarged.

FIG. 4 B.—Diagrammatic representation of the same.

FIG. 5.—Incomplete posterior end of an Amphinome rostrata (British Museum Collection, No. 16), showing segments intercalated on the right side causing the body to coil to the left. Dorsal view. Enlarged.

FIG. 5 A.—Ventral view of the same.

FIG. 6.—Six segments of a Halla Parthenopeia (in U. C. L. Museum, No. 2), showing two small spirals inside one larger one. Enlarged.

FIG. 6 A.—Ventral surface of same.

FIG. 6 B.—Diagrammatic representation of the spirals.

FIG. 7.—Two and a half segments of a *Lumbriconereis impatiens* (in U. C. L. Museum, No. 1), showing a spiral of half a round. Dorsal and ventral view.  $a-a_4$  marks the course of the groove. Enlarged.

FIG. 8.—Ventral view of the anterior region (without the branchiæ) of a *Sabella* (probably a new species) from Ramesvaram Island, showing a spiral beginning on the left side in the third half-segment and continued into the abdominal region. Slightly enlarged.

## REVIEW.

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### The Nephridia of Leeches.

1. "Recherches sur la structure des organes segmentaires des Hirudinées," par H. Bolsius, S.J., de Bois-le-Duc, 'La Cellule,' t. v, 1890, pp. 369—436, 3 pls.
2. "Intrazelluläre Gänge. Erwiederung auf einige Anklagen des Herren F. Leydig," von H. Bolsius, S.J., 'Biologischen Centralblatt,' Bd. x, 1890, pp. 654—656.
3. "Nouvelles recherches sur la structure des organes segmentaires des Hirudinées," par H. Bolsius, S.J., Professeur au Collège des Pères Jésuites à Louvain, 'La Cellule,' t. vii, fasc. 1, 1891, pp. 1—77, 3 pls.
4. "Anatomie des organes segmentaires des Hirudinées d'eau douce, d'après les recherches cytologiques," par H. Bolsius, S.J., Professeur au Collège de la Compagnie de Jésus à Louvain, 'Annales de la Société Scientifique de Bruxelles,' t. xvi, 1892, pp. 1—69, 2 pls.
5. "Les organes ciliés des Hirudinées: 1. L'organe cilié du genre Nephelis," par H. Bolsius, S.J., Professeur au Collège des Pères Jésuites à Louvain, 'La Cellule,' t. vii, fasc. 2, 1891, pp. 1—31, 2 pls.

"LA structure des organes segmentaires, prise dans son ensemble, d'après les données de nos savants devanciers, n'est admise par nous pour aucun genre, pour aucune espèce, de toutes celles que nous avons examinées."

This is indeed true, and were M. Bolsius' view correct my own results, for instance, must have been very largely the outcome of imagination.

M. Bolsius has devoted several years to the subject, and has had all the modern methods at his disposal. He has endeavoured to work out the structure of these organs in much

greater detail than I attempted to do ; and had he been able to correct here and there errors in my results I should not have been surprised, or should at any rate have been content to leave future observers to judge between us.

It is, however, not a question of occasional errors ; M. Bolsius has entirely misinterpreted his sections, or else I, to say nothing of my predecessors, evolved a conception of these organs out of my inner consciousness.

I am induced to review the matter in some detail, in order not merely to defend my views in all important particulars, but to point out that what I believe to be M. Bolsius' errors in fact are due to errors in method ; that they are owing, in short, to his abuse of the very methods which should have (which have in many respects) helped him.

It is quite clear that whatever value attaches to M. Bolsius' voluminous productions depends upon the new facts therein set forth. Phylogenetic or homogenetic considerations, or, indeed, generalisations of any sort, M. Bolsius studiously avoids. He naïvely remarks, it is true, in the introduction to his first paper, that "segmental organs" are not confined to the leeches, but are found in all Annelids ; and, further, that certain organs, which are described as their homologues, are found in animals occupying various positions in the animal scale up to the Vertebrates themselves ("jusqu'aux Vertébrés eux-mêmes"). If I appreciate the exact force of these last words they display a curious conception of the animal genealogical tree.

Now M. Bolsius' facts fall under two headings, cytological facts and anatomical facts. With the former I here concern myself little, but I have not the slightest hesitation in saying that all his most important anatomical results are absolutely erroneous.

I attribute M. Bolsius' errors to the abuse of a method. M. Bolsius, however, takes great credit to himself over his choice of methods ; his latest publication (4) commences thus :—  
"Pour arriver à un but sans trop s'exposer à faire fausse route, il faut prendre les moyens les plus propres à cette fin.



C'est là une vérité reconnue à tel point par tout le monde, qu'il semble presque ridicule de la mentionner.

“ Et cependant, lorsqu'il s'agit de l'application, cette vérité est trop souvent méconnue.

“ La matière que nous allons traiter après tant d'autres savants en donne une preuve palpable. L'anatomie des organes segmentaires des Hirudinées d'eau douce a été le sujet de bien de recherches. Néanmoins la structure exacte de ces merveilleux organes n'a pas été mise en lumière par nos savants devanciers.

“ La seule raison en est que les moyens dont ils se sont servis n'étaient point en proportion avec le but qu'ils se proposaient d'atteindre.”

It is very sad and serious that so many pages of a journal like that of the Société Scientifique de Bruxelles should be taken up by anatomical results which can easily be shown to be erroneous; but there is a humorous side to the fact that M. Bolsius should blame his predecessors for not using methods which were at the time when they wrote not invented, or in their infancy, while his own errors are due to neglect of the simple methods used by those whom he blames.

Direct observation of hundreds of fresh nephridia and of teased macerated preparations, aided by a comparatively rude series of sections, enabled me to give twelve years ago an account of the nephridium of the medicinal leech, erroneous in many particulars as I afterwards discovered, but which I now maintain was much nearer the truth in its general plan than M. Bolsius' recent account.

M. Bolsius has had enormous advantages in the methods at his disposal,<sup>1</sup> with this result,—led away by the fascinating methods of serial section-cutting, he has almost entirely neglected simple dissections. Dissection appears, indeed, to

<sup>1</sup> I note that the staining fluid stated by M. Bolsius to give the best results is one of which the formula has not yet, he says, been published, but one which is very much used in the laboratory at Louvain. This surely savours somewhat of quackery. But M. Bolsius is probably not the person to blame in the matter.

be for him a lost art. He declares himself unable to mount a fresh nephridium entire. This may be so, but he goes further, and says, "Il n'est pas possible d'extirper l'organe segmentaire en entier, sans tirailler ou comprimer ses éléments constituants en quelque manière. Après une assez longue série de tentatives inutiles, nous en sommes tenu exclusivement à la méthode des coupes." Of course there is a reservation in the words "sans tirailler ou comprimer," but if M. Bolsius had persevered in examining the fresh nephridia, in spite of a little injury in preparation, he would never have committed himself to the diagram which can hardly be said to adorn the first plate of his first paper (1,<sup>1</sup> fig. 1). Any good student, dissecting the leech for the first time, could make a drawing more nearly resembling the object itself. I may point out, by-the-by, that the way in which the lateral blood-vessel is shown in this drawing indicates the utter want of attention paid by our author to matters of gross anatomy.

It is desirable to say a word with regard to M. Bolsius' method of stating his discoveries before we pass to the facts themselves.

There is a style about M. Bolsius' writing, the introduction of which into papers setting forth the results of original research is much to be regretted. Every one who works at a subject which has been already worked at by several investigators is pretty certain to find much to contradict; but M. Bolsius is for ever faintly praising the work of his predecessors, whose results he then proceeds to denounce as totally erroneous—results which, if M. Bolsius' statement were correct, must have been in many cases not the outcome of observation, but of pure imagination. The whole style, if I read correctly between the lines, indicates rather an attempt to secure the glorification of M. Bolsius than a desire to add to our knowledge of the truth. There is, moreover, in places a vindictiveness which is fortunately more often met with in religious controversy than in the records of scientific research. The sixteen pages of what

<sup>1</sup> These figures in thick type refer to the list of papers given above.

appears to be little short of quibble, which M. Bolsius devotes to an endeavour to convince Leydig, and all who take the trouble to read them, that that histologist does not now know what meaning he attached to certain words written many years ago, show an utter want of that feeling of regard which younger histologists should entertain towards that famous pioneer in our science.

M. Bolsius prefers to use Williams' term "segmental organs" for the nephridia, because this "dénomination, qui a pour elle l'ancienneté, nous rappelle que cet organe se présente dans une classe d'animaux dont le corps est composé d'une manière spéciale, c'est-à-dire dans les vers." This is quite in accordance with the way in which he persistently shuts his eyes to all questions of homogeny: it is superfluous to discuss the question at a time when so many of the best Continental authors have adopted Lankester's term "nephridia" (Lang, Eisig, and others).

M. Bolsius' conception of the nephridium in the large leeches simplifies enormously the idea of its structure, and, as he says, renders it much easier to explain; though why this should be an advantage if the conception is incorrect is not obvious.

M. Bolsius says of the nephridium of the medicinal leech that it is a compact organ, the two extremities of which are slender, and ordinarily approach one another. Three regions may be distinguished:

(a) The superior region with anastomosing canals.

(b) The median region with anastomosing canals surrounding a collecting or central canal.

(c) The inferior region with a collecting canal, without anastomosing canals.

M. Bolsius then describes the cells occurring in these three regions, and his figures show that, so far as the median region is concerned, he recognises that the calibre of the ductules increases "à mesure qu'on descend vers l'orifice inférieur de l'organe." If this is the general view he takes of the structure of the organ, no wonder that he considers that my own and Schultze's figures and description show a "compli-

cation étonnante." The difference is so great that I hardly know how to criticise M. Bolsius' description. I assume that we are dealing with the same leech, though I certainly took no pains to verify the species with which I worked. My specimens were purchased as medicinal leeches from Messrs. Henry Potter and Sons, of London, who import large numbers of leeches for the London market. I distinguished between at least two varieties, but noted only the differences in the matter of coloration.<sup>1</sup>

Since receiving M. Bolsius' most recent memoir I have examined a number of fresh nephridia from the medicinal leech in use here, and a number of Clepsine, embryonic and adult; and have worked over all my old preparations, including a series of sections through the region of a nephridium in *H. medicinalis*, which I had not previously used for this purpose. The greater number of these sections (sixty-nine) I have drawn with a camera, and have reconstructed the nephridium from the drawings. The other sections of the series (thirty-nine in number) pass only through portions of the vesicle, testis, lobe, and funnel. I have also treated in the same way a series of fifty-one sections through a *Nephelis* in the region of a nephridium.

To speak for the present of *Hirudo* only, I am convinced that the results given in my last paper were, except in a few matters of detail, correct. I am not now concerned with the question as to how far those results were based upon my own researches, and how much I owed to Leydig, Lankester, Schultze, Lang, and others. I merely refer to my own paper, since I was the author who immediately preceded M. Bolsius in dealing with this subject. I will, however, point out in this connection that I have laid no claim to be the dis-

<sup>1</sup> I do not suppose that there is any doubt whatever about our having used the same leech. I just refer to the matter because the leech in use in the hospital here (Madras) is undoubtedly a different leech. It is much larger, there are considerable differences in the structure of the genital organs, and the nephridia are different, and in a most interesting condition: the funnel, and indeed the whole of the "testis lobe," is absent. The latter is represented by a small piece which curls round on the edge of the "apical lobe."

coverer of the intra-cellular nature of any of the lumina of the gland. That some of the cells had within their substance an arborescent extension of a system of ducts was pointed out to me by Lankester in 1879; and that the lumen of what I had called the "central duct," and which I imagined to be intercellular when I published my first paper, was also intra-cellular was demonstrated to me by Lang, at Naples, in 1882.

I maintain that M. Bolsius' diagrams of the nephridium of *Hirudo* (1, fig. 1; and 4, fig. 17) are fundamentally wrong, and that my diagram, which is here reproduced, together with the original description, is in the main correct.<sup>1</sup>

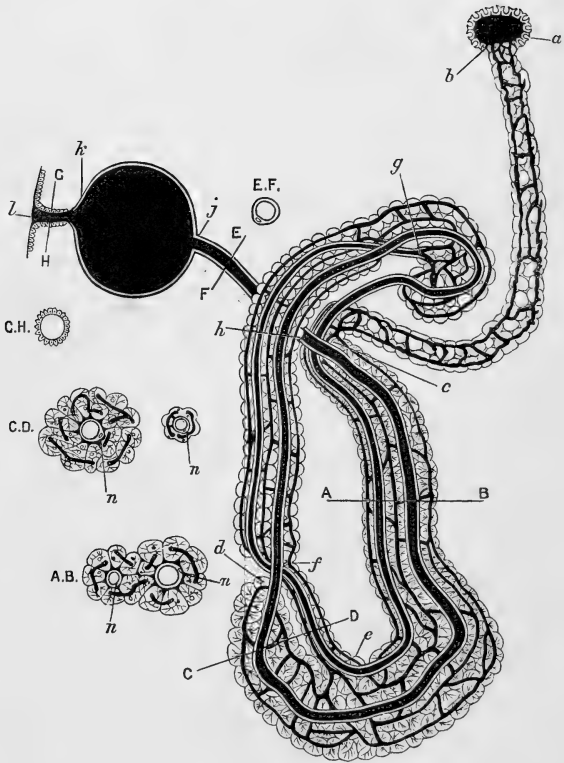
In the first place, has the duct ("canal collecteur"—Bolsius) a complicated course such as I ascribe to it, or is M. Bolsius right when he says—

"Le cours du canal collecteur, selon nous, est tout ce qu'il y a de plus simple. Le canal, tortueux il est vrai, s'avance toujours vers l'orifice inférieur. Durant ce trajet, il est accompagné extérieurement d'une ou de plusieurs assises de cellules à canaux latéraux. Jamais le canal ne revient sur ses pas à travers un mem'e massif de ces cellules"?

This question of the course of the duct is more or less intimately bound up with that as to the division of the gland into lobes.

I continue to use here the terms "duct" and "ductule," as they are convenient terms which fall in with my theory of the structure of the gland. I use "duct" for the lumen and its walls when those walls are simple drain-pipe cells, and "ductules" for lumina which branch in a cell: in this latter case it is obviously inappropriate, especially when the branching is extensive, to include the walls of the lumen—i. e. the substance of the cell—under the term. This distinction between the terms is convenient and intelligible, but not, perhaps, strictly accurate, as I now find lumina in some of these

<sup>1</sup> It will be noted that in Planche I of M. Bolsius' memoir (4), figs. 1—4 are Schultze's, and figs. 5—16 my own; figs. 17—23 only are by M. Bolsius. M. Bolsius invites comparison between our diagrams and his own.



*Hirudo*.—Diagram of a nephridium. *a*. Funnel. *b—c*. Testis lobe. *c—d*. Main lobe. *e—d*. That portion of the main lobe not represented in *Clepsine*. *e*. Point where the recurrent ductules leave the main lobe on their way to the apex *g*, and where the recurrent duct re-enters the main lobe when returning from the apex *g*. *e—f*. Recurrent lobe; for the remainder of their course the recurrent ductules and duct traverse the apical lobe, *f—g*. *g*. Apex and point where the recurrent ductules collect to form the recurrent duct; this latter, as in *Clepsine*, returns to *e*, re-enters there the main lobe, emerges thence at *h* to pass across to the apex, and traversing the apical lobe returns to *f*, where it passes across into the free end of the main lobe *d*; it emerges from the main lobe at *h*. *h—j*. The vesical duct (efferent duct). *j—k*. The vesicle. *l*. The aperture to the exterior.

A B, C D, E F, G H. Sections through the regions so marked. *n, n*. Nuclei.

Section A B shows the cells of the main lobe, with their branching ductules; the nuclei of these cells are drawn but not lettered. The cells are grouped around two perforated cells, which contain the "recurrent" and "main" portions of the duct. *n, n*. Nuclei in the walls of these perforated cells.

Section C D passes through the cæcal end of the main lobe, and also through the recurrent lobe. The main lobe section shows similar arrangements to those shown in the section A B. The section through the recurrent lobe shows the recurrent ductules branching in the cells, which are grouped around the perforated cell containing the recurrent duct.

Section E F passes through one of the perforated cells containing the vesical duct.

Section G H passes through the numerous cells bounding the duct in the last portion of its course, and lined internally by a prolongation of the cuticle from the body surface.

drain-pipe cells other than the central lumen. These may be vacuoles (M. Bolsius figures what he calls vacuoles in his 1, fig. 23); but I think that it is more likely that they are ramifications of the central lumen in the cell substance, just as the lumen in, for instance, a cell of the main lobe consists of a branching tube running into the neighbouring cells with ramifications in the substance of the cell itself.

I propose to speak of the course of the duct and the arrangement of the lobes in one or two particular spots as a test of M. Bolsius's views.

It can very easily be proved, for instance, by dissection that the testis lobe is distinct from the apical lobe, and that it joins the anterior limb of the main lobe at the point where the latter is joined by the vesical duct; in other words, that the vesical duct, coming from the vesical, first plunges into a mass of glandular cells, near what most of my readers will doubtless allow me to call the "funnel" end of the organ. A study of a few nephridia mounted fresh under the microscope, or stained and mounted whole in Canada balsam, must, I think, convince even M. Bolsius that this is so, and that his diagrams (1, fig. 1; and 4, fig. 17) are therefore fundamentally wrong. If he is really unable, as he says, to make satisfactory preparations of this kind he should find it perfectly easy to trace in a series of sections the testis lobe passing round the edge of the apical lobe to the point where its cells join those of the anterior limb of the brain lobe, and to trace the vesical duct from the vesicle until it plunges into a mass of glandular cells at this point; into the mass of cells, in fact, which constitute the anterior limb of the main lobe. If the nephridium is built upon the plan suggested by M. Bolsius the term used by him, "l'extrémité de l'organe," obviously refers to the "funnel" end of the testis lobe, since this is the only region where the cells with ductules do not envelop a duct. One may speak of the course of the organ from this point to the vesicle (*a* to *b* to *c* to *d* to *e* in 4, fig. 17). According to M. Bolsius, the collecting canal always advances along this course towards the vesicle. Now once it is established—and there is,



I assert, no shadow of doubt but that it is so—that the duct which is about to run to the vesicle runs along in the anterior limb of the main lobe towards the vesicle in a direction opposite to the course of the organ itself as defined above, all doubt that a portion of the duct may be recurrent disappears.

To return to the lobes. I have re-examined their arrangement, both by means of sections and whole nephridia, both fresh and after maceration for twenty-four hours in 10 per cent. nitric acid, and have not the slightest doubt but that my previous account was correct. I cannot understand how M. Bolsius can have failed to notice that in the posterior limb of the horseshoe the main lobe, with its cells perforated by fine arborescent ductules, comes suddenly to an end. In specimens macerated in nitric acid it is easy to separate the recurrent lobe from the main lobe, and to see that it, and not the end of the main lobe, is continuous with the apical lobe.

Then, so far as the duct is concerned, that there are two ducts running through the anterior limb of the main lobe I have often seen in fresh nephridia; and in three separate series of sections I have traced to my entire satisfaction the vesical duct entering and running through the main lobe, leaving it to enter the apical lobe near *d* (woodcut, *Hirudo*), passing along the apical lobe round the apex and then coming out from the lobe and running for some distance as a separate duct, then plunging once more into the main lobe near where it first entered that lobe, passing along the anterior limb and along the recurrent lobe to the apical lobe. Of so much of its course I am quite convinced; that it passes as a duct along the apical lobe again to the point *g* I am nearly sure, but its walls become here so excessively thin that it is difficult to trace it with absolute certainty. I shall, however, assume that my impression is correct, and that it passes as a duct to *g*. There it certainly communicates with the ductules.

The ductules present more difficulty. They possess well-marked characters in different parts of the organ. The ductules in the testis lobe, those in the greater portion of the main lobe, and those in the apical lobe are all very different

from one another. I am still in doubt as to whether the ductules in the cells of the main lobe enveloping the duct near A (woodcut, *Hirudo*) are in direct communication with those of the cells enveloping the other duct running parallel to it, viz. the duct near B; the former are larger and less branched than the latter, still I believe that communications exist. It is not, however, my intention to review my own work in detail here; I am dealing with M. Bolsius. He considers it impossible for the duct to enter twice the same mass of cells. I can only say that I am satisfied that a continuous duct in its windings does pass twice through the anterior limb of the main lobe, and must add that preconceived notions of possibilities must give place to facts. I confess that I do not see much difficulty about it. The arrangement is not very different from that which obtains in the nephridium of *Lumbricus*, where different limbs of a continuous intra-cellular duct get bound together into one mass. It is still more like what I hope shortly to show to be the structure of the nephridium of *Moniligaster*, where the duct passes two or three times through a mass of cells, themselves penetrated by arborescent ductules.

M. Bolsius confirms Lang's opinion that the ductules open into the ducts at various places: Schultze and I deny the existence of these communications. It is a mere matter of observation, and it is difficult to argue the point. M. Bolsius and Lang both express surprise at the rarity of these communications, but neither of them states how often he thinks he has observed them; certainly, if such communications occur, one would expect them to be very frequent. I have seen several places in sections where one might imagine such a communication to exist, but a moment's reflection will show how easily such an appearance might be produced in sections. In fresh specimens, where the duct and ductules have both been very clear, I have never seen any appearance whatever of a communication. The most difficult portion of the organ to observe in regard to this matter is the apical lobe, where the duct which comes from the recurrent lobe has very thin walls,

and the ductules are very big. Wherever I have seen in this region an appearance of a communication it has been between the ductules and the duct, and that in very thin sections and where the duct is obliquely cut. Sections and fortunate fresh preparations show the ductules passing from cell to cell so very clearly that if the alleged communications exist it would probably be perfectly easy to see them. I still believe that the system of ductules communicates with the duct at one point only, the point marked *g* in my diagram.

Since I join issue so completely with M. Bolsius in my general conception of the organ, it is hardly worth while to enter further into details; I have no doubt but that in some minute points M. Bolsius has added to our knowledge of the structure of the constituent cells of these organs, and it is a pity in my opinion that he did not confine himself to such matters.

The funnel deserves a word or two, although M. Bolsius has only given us as yet a detailed account of what he calls "l'organe cilié" in *Nephelis*. M. Bolsius's attitude with regard to the funnel may be gathered from the following quotations:

"Pour nous, ces 'entonnoirs' à l'extrémité de l'organe font défaut" (*Hirudo*, *Aulastoma*).

"Nous nions l'existence d'un entonnoir à l'endroit indiqué" (*Clepsine*, *Nephelis*).

"La plupart de nos savants devanciers—Leydig, Lang, Gegenbaur, Bourne—ont considéré les organes ciliés de la *Nephelis* et d'autres *Hirudiées* comme des entonnoirs terminant leurs organes segmentaires du côté du cœlom, et, par suite, comme les homologues des entonnoirs bien connus des Chétopodes.

"En effet, l'analogie de ces diverses productions est frappante et leur homologie morphologique ne paraît pas douteuse."

"Mais si ces organes (les organes ciliés) possèdent chez les *Nephelis* la même signification morphologique que chez les Chétopodes, ils présentent certainement chez ces êtres

des rapports anatomiques très différents, et une fonction physiologique tout autre.”

“Nos recherches établissent que les organes ciliés ne méritent pas le nom d’entonnoirs terminaux des organes segmentaires.

“1°. On ne peut les appeler entonnoirs, pour la bonne raison qu’ils ont la forme de cupules pourvues d’un plancher, ou fond imperforé.

“2°. Ils ne terminent pas les organes segmentaires.”

“Tout en conservant la même signification morphologique que les entonnoirs des Chétopodes, ils perdent chez la *Nepheleis* la valeur réelle, anatomique et fonctionnelle d’entonnoirs terminaux des glandes segmentaires.”

“Ils fonctionnent comme moteurs du sang dans la partie non contractile, ou cœlomique, de la canalisation sanguine.

“Ils sont des lieux de prolifération des hématoctes.”

My own views were expressed as follows:

“The lumen of the funnel often appears, however, to be occluded, its place being occupied by a mass of vacuolated protoplasm; the funnel does not probably possess much functional activity. This occluding of the lumen is, as we shall see, carried to a much greater extent in *Hirudo*” (*Pontobdella*).

“The ciliary current carries corpuscles down the funnel from time to time. These cannot apparently pass further, and lodge in the dilatation.”

“The contents seem to consist mainly of degenerating or macerating corpuscles” (*Pontobdella*).

“I have found it perfectly easy to trace the funnels in my sections; these open into the ventral sinus; following upon the neck of the funnel is a dilatation corresponding to that described above in *Pontobdella*, and as in the latter genus it becomes packed with corpuscles” (*Clepsine*).

“The arrangement and the character of the funnel about to be described seems to me to be explicable by a theory of degeneration following upon loss of function” (*Hirudo*).

“Although it is a point exceedingly difficult of determina-

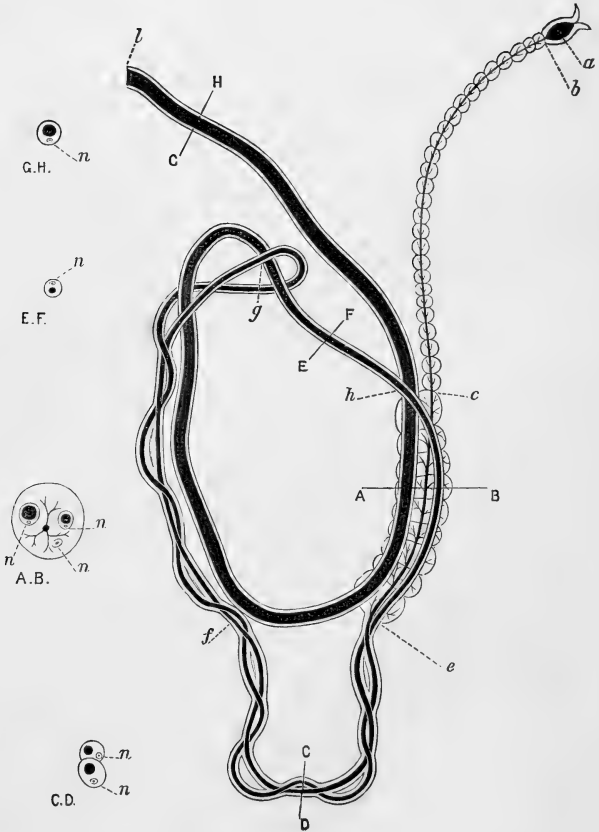
tion, the communication between the lumen of the tubules and the cœlomic sinus seems to have been obliterated" (Hirudo).

"The nephridium, then, in all cases opens into cœlomic space on the one hand, and to the exterior on the other."

These extracts speak for themselves; the last of my statements above quoted presupposes a little imaginative power in the reader. The funnel is for me a part of the nephridium, and it does open into the cœlomic space; but the communication between its lumen and that of the nephridial tubules is, generally at any rate, obliterated. That this structure may be called a funnel will, I think, be admitted by every one who knows that we use the word "funnel" in English in a morphological sense; and the desirability of calling it a funnel if one thinks as I do, and as M. Bolsius does, that it is the morphological homologue of the Chætopod funnel, must be obvious to all who wish to make their researches upon a special subject of use to zoologists generally. M. Bolsius in his account of the anatomy of the nephridia flatly denies the existence of a funnel to these organs, and then proceeds to write a special paper (5) upon it, only under a different name. This is an example of M. Bolsius' method of writing; it is a misleading method.

The funnel is always (in the genera with a compact nephridium) placed close to the "extremity" of the nephridium, though not always perhaps in actual anatomical connection with it; and the striking point, the point which it is desirable to emphasise, is that this funnel, always in relation with the "extremity" of the nephridium, occupies such a different position in the various Hirudinean genera; it lies in the ventral sinus in *Clepsine*, in a special sinus in *Pontobdella*, in a special sinus of a different nature in *Nephelis*, and in a (potential) peritesticular sinus in *Hirudo*.

The funnel has in most genera, at any rate, lost its original function, and M. Bolsius puts forward two hypotheses with regard to its new functions. I can express no opinion with regard to the second of these without further research; but if



Clepsine.—Diagram of a nephridium. *a*. Funnel. *b—c*. Testis lobe. *c—e*. Main lobe. From *e*, through *f*, to the apex *g*, and back through *f* to *e*, runs the recurrent duct; this then passes through the main lobe to *h*, where it runs across to the apex *g*. *g—f* corresponds to the apical lobe of *Hirudo*: from *f* the duct runs across to *e*, where it re-enters the main lobe; at *h* it emerges and passes as efferent duct to *l*, the external aperture.

*A B, C D, E F, and G H*. Sections through the regions so marked. *n, n*. Nuclei. The section *C D* is taken a little to the right hand of the line *C D*.

Section *A B* is a cell of the main lobe with its nucleus *n*, and contains branching ductules; and in addition to these it surrounds in two places perforated cells containing the duct in two subsequent portions of its course, also showing nuclei, *n, n*, in their walls.

Section *C D* shows two perforated cells in juxtaposition, each containing a portion of the recurrent duct; the one as it goes to, the other as it comes from, the apex.

Section *E F* shows the single perforated cell which contains the duct in that portion of its course.

Section *G H* shows the similar but larger cell containing the efferent duct.

M. Bolsius were in the habit of examining organisms whole, and living under the microscope, instead of at once plunging them into Gilson's fluid and cutting sections of them, he would, I think, never have committed himself to the theory that the funnel assists the circulation in any appreciable degree. In the first place the ciliary currents tend to drive particles into the funnel, and in the second place every contraction of the body-wall in these and such like animals causes more commotion in the cœlomic fluid than fifty of such funnels in a row would do.

I now turn to M. Bolsius' account of the anatomy of the nephridia in *Clepsine* and *Nephelis*, but I do not propose to deal with these genera at length. My own observations upon these organs in these genera were comparatively scanty, but they were sufficient; and I have recently fully confirmed them, so as to convince me that M. Bolsius' account is absolutely incorrect. According to M. Bolsius the organ has the form of a ribbon composed of a single chain of cells. This chain is perforated by three canals of unequal length. These canals take their origin in the cytoplasm itself of certain cells. The three canals unite in the inferior portion of the organ, which contains a single lumen only. There is a much reduced urinary vesicle.

An examination of a small living *Clepsine* shows at once the long loop with two ducts (*e* to *f* of my diagram; woodcut, *Clepsine*), joining at either end a region with three ducts; and if a small *Clepsine* be macerated for twenty-four hours in 10 per cent. nitric acid, and then washed and stained and carefully teased, large pieces of nephridium may be easily isolated. I have just got out, for instance, the region where the chain of cells coming from the funnel joins (at *c*) the heap of cells through which the vesical duct runs, and the duct from which my transverse section (*E—F*) is taken is clearly seen leaving the same mass of cells at the same point. Neither of these regions—which may be perfectly easily seen by the methods I have mentioned—could find a place in M. Bolsius' scheme. I have never worked out the whole course of the duct in *Clep-*



sine as carefully as Schultze has done, but all my observations tend to confirm those of that author. M. Bolsius finds the recurrence of the duct a "genetic" impossibility. I did not overlook the difficulty, which is more real here than in *Hirudo*, as will be seen from the following paragraph.

"Except, perhaps, in the region of the funnel, and from the vesicle to the exterior (the latter portion possibly an epiblastic invagination), the lumen is contained in a perforated cell, and is continuous throughout. In some regions the cell so perforated contains a network of finer ductules, which open within the cell into the duct, e. g. in *Clepsine* (fig. 6 of B<sup>1</sup>) and in *Hirudo* (fig. 7 of B, C, D). In other regions the cell resembles a drain-pipe. At certain spots the duct in this latter condition re-enters a mass of cells, as in *Hirudo* (fig. 7, d), or even appears to re-enter a single cell, as in *Clepsine* (fig. 6, e). With regard to this latter condition, I may point out that numerous nuclei have been described in cells so re-entered, and they may represent groups of cells fused together. It is a point needing further investigation."

M. Bolsius has observed, at any rate, two nuclei in a "cell;" and I am surprised that, as a professed cytologist, he has not paid more attention to the matter (especially when none of the cells in *Hirudo* possess more than one nucleus), and has not tested my suggestion, before flatly denying the assertions of Leydig, Gegenbauer, Whitman, Lang, Schultze, Vejdovsky, myself, and others, as to the presence of a single continuous duct. My hypothesis as to cell fusions must be tested by careful embryological work; but I may add that in all the teased preparations I have recently examined I have found one nucleus in all cells perforated by one duct, two nuclei in all "cells" perforated by two ducts, and three nuclei in all "cells" perforated by three ducts. My observations have, however, not been sufficiently numerous to enable me to lay down a law in this matter. My diagram (woodcut, *Clepsine*, A, B) and its description and the reference to it in the text are, I admit, bad; the three ducts, one branched and the other two

<sup>1</sup> These references refer to the woodcuts here reproduced.

unbranched, and the three nuclei should have been shown as they are represented in the diagram, but not the outlines of the smaller cells: nor should I have spoken of two cells as lying within the third. I still believe that we have three cells fused together, but we have as yet no evidence as to their relation to one another.

M. Bolsius makes a great deal of his discovery of the fact that many of the "cells" in *Clepsine* are joined to one another by three prolongations, each of which gives passage to a duct. I have never seen (nor apparently has Schultze) in teased preparations anything like M. Bolsius' fig. 8 (3), although I have had eight or ten of the "cells" in question in contact with one another. I have less hesitation in denying the correctness of M. Bolsius' view since he has given drawings (fig. 7, A—M, 3) of the successive sections from which he has constructed his diagram and his theory. I maintain that the reconstruction of the sections figured does not give the diagram obtained by M. Bolsius, and I imagine that he has overlooked the further course of the ductules figured as separate in c and d. Nor is M. Bolsius any nearer the truth with regard to the organ in *Nephelis*, as he could, I think, easily convince himself if he would examine the whole organ dissected out fresh or in young living specimens, or in teased preparations.

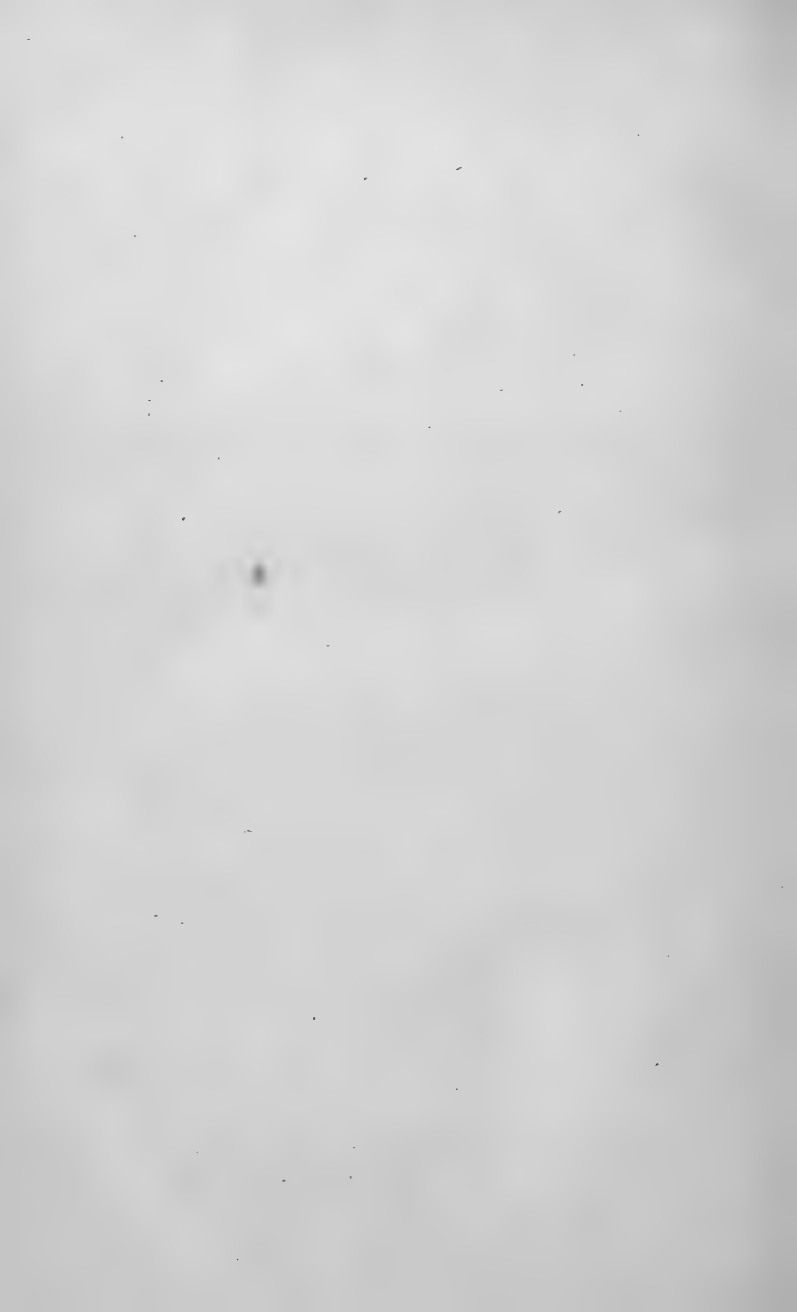
It is unnecessary for me to enter into further detail. I may, however, remark again, in conclusion, that M. Bolsius' astounding misconception of the anatomy of these organs is due to his abuse of a method. Every one who has studied such organs, both by means of serial sections and whole or teased preparations of fresh or preserved material, must have come to the conclusion that there are many cases where the sections admit of various interpretations, or are even, taken by themselves, positively misleading. M. Bolsius states, it is true, that he has used other methods to control the interpretation of his sections, but from his statements quoted above, and from the anatomical results that he has obtained, I feel sure that his

use of other methods has been absurdly inadequate to the problem he set himself to solve.

A comparative study of the nephridia of leeches and of M. Bolsius's views anent them may well serve as a startling warning of the danger incurred in zoological research by paying too great attention to serial sections while neglecting the older and all-important methods. My desire to formulate this warning and to emphasise it by reference to a very striking example is my excuse for having given so much attention to M. Bolsius.

A. G. BOURNE.

THE PRESIDENCY COLLEGE, MADRAS ;  
September 12th, 1892.



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