On Phoronis ovalis, Strethill Wright.

By

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With Plates 7, 8, and 9.

Introduction.

In 1913 Miss R. E. Roper, who was working with Professor A. Meek at the Polyzoa of the Northumberland coast, was kind enough to send to the British Museum an empty shell of Neptunea antiqua bearing specimens of Alcyonidium mammillatum, Alder. On examining the surface of the shell on which this Polyzoon was growing, a curiously eroded appearance was noticed. In order to ascertain the meaning of this appearance, a fragment of the shell was decalcified; and it was at once obvious that the substance of the shell was traversed by the burrows of numerous boring animals. A few of these belonged either to the Sponge, Cliona, or to a small Polychæte, probably Polydora ciliata. The great majority of them belonged, however, to a minute species of Phoronis, which has proved to correspond closely with the description of P. ovalis given by Strethill Wright (1856[1], 1856[2]) in the papers in which the genus Phoronis was established. The Neptunea which is here considered was obtained to the south-east of St. Mary's Island, off the Northumberland coast, in 16 fathoms; and it has been registered in the British Museum collection as 13. 7. 10. 1–2.

Since the publication of the original description, P. ovalis appears never to have been rediscovered (cf. Selys-Longchamps, 1907, p. 188); and it has been supposed that the species had been founded on the immature condition of some other species. I am happy to be able to confirm the accuracy of Strethill Wright's account; and to show, by the occurrence of well-developed ovaries and testes, that it must be regarded as an adult form, in spite of its minute size and the small number of its tentacles. The examination of the Northumberland material has furnished some explanation of the fact that this interesting species has so long escaped notice. Although present in very large numbers in the material under consideration, it is so completely concealed in the substance of the shell that its presence would not have been suspected unless the shell had been decalcified. Although I have not obtained other specimens, there seems every reason to think that the species will be discovered in equal abundance when shells of Neptunea or other Molluscs from the north-east coast of England and the east coast of Scotland are examined by the method of decalcification.

A further result of the present investigation has been to demonstrate the occurrence of a remarkably active process of reproduction by fission, in confirmation of the results of certain other observers, for other species; though taking place with far greater frequency than is indicated by anything that has previously been published.

The genus Phoronis was established by T. Strethill Wright in a paper communicated to the Royal Physical Society of Edinburgh on April 23rd, 1856, and published in two Edinburgh journals (1856[1], 1856[2]). Two species were distinguished—P. hippocrepia, the tubes of which were embedded in a stone obtained at Ilfracombe; and P. ovalis, found in a decayed oyster-shell, inhabited also by Cliona celata, dredged near Inchkeith in the Firth of Forth. Of P. hippocrepia an excellent description is given, so far as the structure could be made out in the part of the animal protruded from the membranous tube. This account includes an accurate description of the hippocrepian lophophore, the number of tentacles being given as about sixty; of the descending œsophagus and the ascending rectum, the position of the mouth, epistome, and anus being well described; of the blood, containing red corpuscles; and of the principal vessels, including the afferent and efferent trunks, the tentacular vessels, and some of the lophophoral vessels. The structure of P. ovalis is described in less detail, but stress is laid on the form of its lophophore, which is oval but slightly flattened on one side. The tentacles were eighteen in number, and the blood-corpuscles were noticed. The entire animal was about half an inch in length, and the gullet terminated in a globular gizzard, which communicated with a thick-walled stomach. Good figures are given of the oral ends of both species, the body of P. ovalis being figured as protruding from a delicate tube, embedded in the substance of the oyster-shell. The examination of Strethill Wright's figures and description leaves no doubt that the specimens described in the present paper belong to P. ovalis.

Although the eroded appearance of the outer surface of the Neptunea-shell furnished the clue which led to the discovery of the Phoronis, it does not appear to have been caused by the presence of this animal. The outer layers of the shell, both on the outer and on the inner side, are traversed by a number of branching hypha-like threads, which reach a diameter of as much as 24μ; and it appears probable that these are the principal cause of the erosion noticed on the outer surface. This is in accordance with the statements of Bornet and Flahault (1889), who give an account of various Algæ and Fungi which bore in the shells of Molluscs. According to these authors the organisms in question commence their work by extending horizontally in the epidermic layer of the shell, subsequently sending branches vertically into the shell-substance and others parallel with the first set. These become so numerous and their branches so close together that the interposed calcareous substance finishes by disappearing, and the plant thus comes into contact with the external water, and is able to discharge its reproductive cells. The surface of the shell is thus rendered rugose and uneven. This process is supposed to be the principal cause of the disappearance of empty shells in quiet bays.

I have not succeeded in determining the vegetable organisms found with the Phoronis ovalis, though they appear to have some resemblance to the Alga described by Bornet and Flahault as Gomontia polyrhiza. The hyphæ of this plant are said to have a maximum diameter of 12 μ—a size which is considerably exceeded in the largest filaments found in the Northumberland material.

The thickness of the Neptunea-shell varies between about 2 and 4·5 mm. In the neighbourhood of the columella it reaches its greatest thickness, while it is much thinner in the middle of the whorls. The diameter of the tubes of the majority of the Phoronis individuals is from ·250 to ·275 mm. Even in the thinnest part of the shell the diameter of the burrow of the Phoronis is thus not more than about one-eighth of the thickness of the shell, and there is accordingly plenty of room in the substance of the shell to accommodate a large number of these burrows.

The general arrangement of the cavities inhabited by the Phoronis may be indicated by comparing the shell with a mass of wood excavated by the burrows of Teredo. The Phoronis is present in very large numbers, its burrows passing in all directions through the shell, and opening to the exterior either on the outer side or on the inner side. The distal end of the burrow is commonly placed at right angles to the surface, but in some cases part of the tube lies in a superficial groove of the shell. In addition to the Phoronis and the Alga already mentioned, the substance of the shell is inhabited by other boring organisms, and particularly by the Sponge Cliona and a Polychæte which is probably Polydora. The Sponge forms much larger cavities than those produced by the Phoronis, and these naturally have a form corresponding with the lobes of the Sponge, being quite different in shape from the cylindrical Phoronis-tubes, which remain of approximately the same diameter throughout their course. The Polychæte tubes are larger than those of the Phoronis; and, instead of having the hyaline character of the tubes of this organism, their transparency is affected by the presence in them of numerous granular particles.

The tubes of the Phoronis are represented in several of the figures (e.g. Pl. 8, fig. 15; Pl. 9, fig. 37). It will be seen that they are by no means uniform in shape, but that they are generally curved in various ways. The thin membranous tube is closely applied to the inner surface of the excavation in the shell, and the burrows are accordingly curved in correspondence with the form of the tubes seen in a decalcified preparation.

The most superficial examination of a number of the tubes set free by decalcifying the shell shows that there is an extraordinary amount of variation in the included organisms. It is hardly going too far to say that it is difficult to find two individuals alike on a slide containing a large number of individuals. The length of the animal varies within wide limits, while differences in the transverse diameter of the specimens are also marked. The most striking differences are seen, however, in the extent of the development of the lophophore. While some of the individuals are provided with a lophophore bearing well-developed tentacles (Pl. 7, figs. 1–3), the lophophore is completely absent in others (Pl. 9, figs. 29, 30). In others again a lophophore in an early stage of development can be made out at the distal end (Pl. 8, fig. 13); while all stages between this and the fully-developed lophophore can be found without difficulty among the other individuals on the slide (Pl. 7, figs. 5, 4, 8). It is impossible to interpret these appearances on any other supposition than the assumption that regeneration of the lophophore takes place with great readiness in this species of Phoronis. Although it is probable that this regeneration may be no more than the replacement of the lophophore previously present, there is reason to suppose that in other cases it indicates the occurrence of a process of asexual reproduction, the regenerating lophophore being formed, in such cases, at the distal end of a proximal part of the body separated off from the remainder by a zone of transverse fission. Before considering the evidence in favour of this view it will be convenient to notice previous observations bearing on this subject.

The power of regeneration possessed by Phoronis early attracted the attention of observers of this animal. Dyster (1858, p. 251) states that "an abstracted head [of P. hippocrepia] is renewed within forty-eight hours, not completely developed, but with a serviceable mouth and its covering valve and stumpy tentacles which do their work of providing food." In the same year Van Beneden (1858[1], p. 460, Plate, figs. 4-6, and 1858[2], p. 18, Pl. v, figs. 4–6) describes and figures the spontaneous loss of the lophophore and its subsequent regeneration in P. gracilis. Cori (1890, p. 502), in describing P. psammophila, mentions the same phenomenon, which occurs spontaneously, although he refers to the belief of the fishermen of Messina that the "heads" are bitten off by small fishes. In the course of a paper dealing with Cœlenterates, Cerfontaine (1902, p. 262) records some interesting observations on P. kowalevskyi,[1] which occurs at Naples in a very restricted situation under a bridge in the "arrière-port de Naples." The animal forms large colonies in this locality, and these are found in a flourishing condition during a certain part of the year, namely from May to November. They are provided, at this period, with lophophores, among the tentacles of which occur numerous

[1] De Selys-Longchamps (1907, p. 173) points out that this form is indistinguishable on anatomical grounds from P. hippocrepia, but that its tubes are encrusting, while P. hippocrepia is a boring species.

eggs and developing embryos, a great number of larvæ being set free from time to time. At the end of this season the lophophores are lost and the colonies then consist of blackish "cakes" of matted tubes, from 1 to 2½ cm. in thickness. At the recommencement of the favourable season these cakes become covered by "une riche végétation de Phoronis." The tubes, examined during the "mauvaise saison," were found to contain remains of the body of the Phoronis, with lophophores in all stages of regeneration. Actinotrocha is said to occur rarely in the plankton at Naples at any time in the year, and Cerfontaine points out that it is difficult to suppose that the innumerable Phoronis which appear on the surface of the old cakes in a few days, at the commencement of the favourable season, can have been derived from larvæ. He concludes, therefore, that P. kowalevskyi possesses a mode of spontaneous annual regeneration.

A more detailed account of the process of regeneration is given by Schultz (1903[1]), who describes the spontaneous loss of the lophophore in P. mülleri at Heligoland, and compares it with the loss of the calyces in the Polyzoa Pedicellina and Urnatella, or of certain parts in Compound Ascidians (Diplosomidæ) and Hydroids. He states that the process occurs, in Phoronis, whenever the conditions become unfavourable; and that it is followed by the regeneration of the lophophore as soon as better conditions return. The loss of parts of the body under unfavourable conditions is regarded as a physiological necessity which has become a normal process in various animals and plants (as in the loss of leaves by deciduous trees); this "reduction" being explained as the loss of parts which can be dispensed with temporarily during a period of hunger, thus leaving fewer structures to be nourished during times when nutriment is not abundant. Schultz points out that a reduction-process of this nature, in an animal which has a high capacity for regeneration, may lead to transverse fission, "and so indirectly to budding," although he does not prove that an asexual method of reproduction occurs in Phoronis.

On dividing a Phoronis transversely with a pair of scissors Schultz found that regeneration took place readily in both the pieces thus separated. Although he did not determine the minimal size of the fragments which were capable of regeneration, he states that this process occurred, in both the proximal and the distal portions, wherever the cut was made. The distal portion regenerates a proximal end, for instance, even if the part separated consists only of the lophophore and a part of the body containing the commencement of the œsophagus and the extreme end of the rectum. The proximal portion regenerates a new distal end whether the cut be made through the commencement of the œsophagus, or at practically any lower level, while the distal end regenerates a new proximal end with a similar disregard of the region where the section has been made. The details of the process of regeneration are described.

In a later paper (1903[2]) Schultz shows that regeneration takes place in the Actinotrocha larva of Phoronis, similarly divided by transverse cuts, although it proceeds at a much slower rate than in the adult animal.

None of the papers so far quoted contain any suggestion that the regeneration in Phoronis may be associated with a process of reproduction by fission.

In his monograph of the Phoronidea of the Gulf of Naples (1907, pp. 161–) de Selys-Longchamps gives further information with regard to the regeneration of species of this group. No evidence was obtained that the lophophoral end spontaneously thrown off was capable of regeneration. The lophophore may be thrown off several times in succession by the same individual, which regenerates this portion after each reduction. The proximal end of the body, or "ampulla," is incapable of regeneration, a process which appears to be confined to the muscular region. On cutting this part, in P. psammophila, into six pieces of approximately equal size, each of these pieces regenerated so as to become a complete individual, while the lophophore and the ampulla did not regenerate. Fragments hardly longer than wide in which the lophophore was being regenerated were found in certain colonies.

On p. 164 of his monograph, de Selys-Longchamps makes the significant remark that it is difficult to believe that the numerous individuals which compose a colony of P. kowalevskyi can have been derived from as many Actinotrocha larvæ. It seems most unlikely that these larvæ, which lead a pelagic existence, can assemble at the time of their metamorphosis in sufficient numbers to build up a colony of the kind characteristic of this and other species. Allusion is made to the observations of Cerfontaine, who found numerous regenerating fragments in colonies of Phoronis which appeared to be dead and decomposing; and to others by Ikeda (1901, p. 580), who had found young animals which he supposed—probably wrongly—to have been derived from larvæ, in the débris of old colonies. De Selys-Longchamps believes that fragmentation of the individuals is a normal process, and, as this is followed by regeneration of the pieces, that it is a method of asexual reproduction. The correctness of this conclusion is borne out by my own observations on P. ovalis.

Specific Characters of Phoronis ovalis.

It has already been pointed out that P. ovalis has not hitherto been recognised since its original description by Strethill Wright in 1856. As doubts have been cast on its claim to be regarded as an adult form (cf. de Selys-Longchamps, 1907, p. 188), it is important to notice that the Northumberland material includes specimens possessing fully developed ovaries (Pl. 7, fig. 2) or testes. The following diagnosis of the species may be given :

Size very small compared with that of other species of the genus. Total length reaching at least 6 mm., the diameter of the body being about 250 μ, and of the tube, in large specimens, about 250–350 μ. Tube delicate, hyaline, embedded in the substance of shells of molluscs. Lophophore oval, not much broader than long, one of the longer sides of the oval indented, thus indicating the hippocrepian form of the lophophore in other species. Number of tentacles very small, about twenty-two. Metasome (body) sharply divided into two distinct regions, the distal portion with strong longitudinal bundles of muscles, the proximal portion with an extremely thin body-wall in which muscles are absent or at most very slightly developed. The proximal end of the muscular region is slightly invaginable, so that in contracted specimens this portion forms a shallow cup surrounding the more distal part of the muscular region. About fourteen bundles of longitudinal muscles occur on each side in the distal portion of the body. Regeneration of the lophophore occurs with great facility, and this regeneration is frequently the result of transverse fission.

Phoronis ovalis differs from other species in its relatively minute size, in the remarkably simple character of its lophophore, which is, however, hippocrepiform, in the very small number of its tentacles, and in the sharp differentiation of its body into two regions, the proximal end of the muscular region being slightly invaginable. As the occurrence of functional gonads in some of the specimens indicates that it is really an adult form, the claims of the species here described to be regarded as a distinct species seem to be incontrovertible.

P. ovalis has often been referred to in literature, but as no subsequent observer has hitherto succeeded in obtaining it, these references are all based on Strethill Wright's original account. De Selys-Longchamps (1903, p. 32) has stated that he considers the claims of P. ovalis to specific rank not improbable, and that Actinotrocha pallida, Schneider, may be its larva.

The only description which might refer to the same species is Van Beneden's account of Crepina gracilis (1858[1], 1858[2]). This was described as having from twenty-four to forty tentacles, and as reaching a length of 8–10 mm. The epidermis is provided with numerous stiff hairs, the points of which project to the exterior. The lophophore, as shown in the original figures, has a simple structure, its ends not being in-rolled. In this respect it agrees with P. ovalis; but Van Beneden's figures represent animals with about forty tentacles, a number which is considerably in excess of that given by Strethill Wright for his species, and of that found by myself in the Northumberland material. De Selys-Longchamps (1903, p. 25) has found a form at Heligoland, which he refers to Van Beneden's species; and in support of this conclusion he emphasises the occurrence, in the Heligoland specimens, of very numerous epidermic structures (see his Plate ii, figs. 22–26), which he identifies with Van Beneden's "hairs." This resemblance is certainly a striking one, especially as the author points out that he has not found these structures in any other species. The number of tentacles found by de Selys-Longchamps was, however, greater than that given by Van Beneden, being commonly fifty to sixty, but sometimes as much as eighty. The length of the tube of the Heligoland species is said to be 10–20 mm.

It may be remarked that P. hippocrepia, P. gracilis, and P. ovalis are all found in burrows in the shells of Molluscs, or in other calcareous substances. They appear to differ from one another in size and in the number of their tentacles; P. hippocrepia having the largest dimensions and the greatest number of tentacles, P. ovalis occupying the other end of the series in both respects, and P. gracilis taking an intermediate position.

P. mülleri, also described by de Selys-Longchamps (1903, p. 6) from Heligoland, does not form colonies. It reaches a length of 40–80 mm. and has fifty to sixty tentacles, of which those on the oral side of the lophophore are specially short.

Structure of P. ovalis.

The general structure of the members of this genus is so well known[1] that it will not be necessary to describe that of

[1] See especially the elaborate monograph of de Selys-Longchamps (1907), who gives full references to the literature of the subject.

P. ovalis in great detail. I confine myself, therefore, to a description which is sufficient to show that the subject of this paper is rightly referred to Phoronis, and also brings out some of the more noteworthy features of P. ovalis.

Tube.

The characters of the tube can be readily examined after decalcification of a fragment of the shell containing the animals. The single shell which furnished the whole of the material must have contained hundreds of individuals, whose tubes penetrated the substance of the shell in all directions. Although accompanied by other boring animals (Cliona, Polychæta) there is not the slightest reason to suppose that the Phoronis inhabits burrows excavated by other organisms. The diameter of its tubes is distinctly smaller than those of its associates; and each Phoronis-tube closely lines the burrow in which it lies, along the whole of its course. De Selys-Longchamps (1907, p. 28) thinks that the tube is secreted by the proximal end of the ampulla, and that its growth takes place at this end. I have no observations to indicate how the boring is effected, but I am inclined to think that the main increase in length takes place as suggested by that author. The set of tubes shown in Pl. 8, fig. 15, seems to prove, however, that this explanation is not sufficient, and that the faculty of boring and secreting a tube is not restricted to the region of the ampulla. The figure shows that secondary deposits of tube-material may be formed inside the original tube. Some of these are more or less curved transverse septa (*E*, *B*, *H*), occurring on the proximal side of the ampullar region. Others may be formed in an irregularly longitudinal direction, as at *L*. In three places (*C*, *G*, *J*) a lateral opening has been formed on the proximal side of a transverse septum, and a new tube has grown out at an angle with the original tube. These lateral tubes, which will be considered below in the section dealing with regeneration, can hardly have been formed by the proximal end of an individual; and it seems necessary to assume that the faculty of producing a tube and of boring in the shell is possessed by a considerable part of the body-wall.

Structure of the Animal.

Owing to its small size many of the principal points in the structure of this species can be made out in stained preparations of the entire animal mounted in Canada balsam. The frequent occurrence of regenerating lophophores gives rise to an extraordinary want of uniformity in the appearance of the individuals. The even more striking variation in size, as exemplified, for instance, by Pl. 7, figs. 2 and 5, appears to be due to the reduction in length produced by transverse fission.

A specimen with expanded lophophore is represented in Pl. 7, fig. 1. The small number of the tentacles is at once apparent, and it constitutes one of the most characteristic features of the species. How striking is the difference between P. ovalis and some other species of the genus may be illustrated by the comparison with P. buskii, the number of whose tentacles is estimated by de Selys-Longchamps (1907, p. 33) at about one thousand.

In the great majority of the specimens the tentacles lie in their retracted condition inside the tube. This condition of the tentacles is shown in Pl. 7, fig. 3, and other figures. In favourably prepared specimens (Pl. 9, fig. 40) the epistome (*ep.*) can be seen as a distinct lip overhanging the mouth and surrounded by the bundle of tentacles.

The distal part of the body-wall is thick (Pl. 7, fig. 3), a condition which is largely due to the presence of strong bundles of longitudinal muscles. These end abruptly at about the middle of the length of the body in this particular individual, although the proportion which the muscular part of the body-wall bears to the non-muscular part is highly variable. In Pl. 7, fig. 2, for instance, the muscular region is not more than a quarter of the entire length, although absolutely of about the same length as in Pl. 7, fig. 3. In many of the specimens the proximal region of the muscular part of the body is slightly invaginated (Pl. 7, figs. 4, 8), thus forming a sort of shallow cup surrounding the base of the remainder of the muscular portion. The cavity of the cup faces distally, towards the lophophore.

The remainder of the body-wall is extremely thin and transparent. In some individuals (Pl. 7, fig. 8) the extreme proximal end has the ampulla-like form usually found in Phoronis. The absence of a typical ampulla in other specimens is doubtless due to the loss of this region when transverse fission takes place; but the ampulla is probably regenerated in due course by the distal individual formed by fission. Muscles have not been detected in the "non-muscular part"; and if they occur they must be excessively thin.

The alimentary canal has the form usual in the genus. The first part of the descending limb is formed by an œsophagus, sharply marked off from the succeeding part, and occupying from half to a quarter of the length of the muscular part of the body (Pl. 7, figs. 3, 8). The remainder of the descending limb, constituting the proventriculus (*pr.*), is relatively narrow throughout the muscular region, but it gradually dilates in the non-muscular part, reaching its maximum size in the ampullar region, but before the extreme proximal end is reached. From the dilated stomach (*st.*) thus formed (Pl. 7, fig. 8) a short section of the descending limb, of distinctly smaller size than the stomach, continues to the proximal end of the body, where it curves round into the ascending limb (*int.*). This portion is for the most part of small diameter, though its size depends partly on the amount of the remains of food (commonly Diatoms) or the fæces which it contains. The last part of the intestine is of small size, and opens by the anus (Pl. 9, fig. 40, *an.*) close to the lophophore, and on the side corresponding with the base of the epistome.

In a few individuals (Pl. 7, fig. 2) a number of large eggs may be seen lying in the body-cavity of the non-muscular region. These no doubt constitute the ovary, and the occurrence of this organ is of importance as evidence that animals in this condition are mature.

In most of the specimens a considerable amount of granular tissue is visible, lying in the body-cavity, principally of the non-muscular region, between the alimentary canal and the body-wall (Pl. 9, figs. 29, 33, *ad.*). This is the "adipose body" or "vaso-peritoneal tissue" of other authors; and, as in other species of Phoronis, a part of this tissue commonly has the histological characters of a testis. I have not convinced myself that ovary and testis may occur in the same individual, and it is possible that P. ovalis is diœcious. If this difference really occurs between P. ovalis and other species (which are usually hermaphrodite) it is perhaps the result of the small size of the animal.

Some of the anatomical features have been examined in sections; but the material, contained as it was in the burrows in the shell, is not sufficiently well preserved to show the finer details.

Pl. 8, fig. 14, an approximately sagittal section of the distal end of the animal, shows the muscular region of the body-wall and the cup-like invagination (*inv.*) at its base. The strong muscular bands (*l. m.*) are clearly seen, as well as the origin of the bundles from the body-wall in the region of the invaginated part. The epistome (*ep.*) is visible, surrounded by the tentacles, while the œsophagus (*œs.*) is cut along the whole of its length, and is separated from the proventriculus (*pr.*) by a circular valve. The terminal portion of the intestine (*int.*) is seen by the side of the œsophagus; and the position of the anus (*an.*), which opens into a depression of the body-wall close to the lophophore and the base of the epistome, is indicated.

A few sections from a series cut transversely to the long axis of the body have also been figured. In the first of these (Pl. 8, fig. 16) the tentacles are seen to be arranged in the form of a horse-shoe, though the ends of the lophophore are not drawn out to the extent found in species with numerous tentacles. Twenty-two tentacles can be counted, and this was the full number present in this individual. The tube (*t.*) is seen to consist of several superposed cuticular layers.

In the next section shown (Pl. 8, fig. 17) the bases of the tentacles have become confluent on the anal side, and the lophophore is now clearly seen to be hippocrepian in form. Some indication of the tentacle-vessel can be seen in several of the tentacles, in addition to the cavity of the tentacle. The tip of the epistome is cut at *ep.*

In Pl. 8, fig. 18, the union of the tentacle-bases is more complete, and a considerable part of the epistome (*ep.*) is visible. The next figure (Pl. 8, fig. 19) shows the epistome at its largest part. In Pl. 8, fig. 20, the tentacle-bases have all united, so that the mouth (*m.*) is completely outlined. The anus (*an.*) opens into a depression between a lobe of the metasome and the lophophore, and a part of the nerve-ring (*n. r.*) is visible between it and the mouth. The two nephridia are seen in one or two of the sections which come next in the series; but they have not been drawn, as the preparations are not very favourable for showing their details. In Pl. 8, fig. 21, the œsophagus (*œs.*) and the intestine (*int.*) are seen, as well as the oral part of the nerve-ring (*n. r.*). The afferent blood-vessel (*a. v.*) occurs between the œsophagus and the intestine, and some of the longitudinal muscles of the body-wall are visible.

Pl. 8, fig. 22, shows a complete median mesentery (*mes.*) supporting the two limbs of the alimentary canal; and both the afferent (*a. v.*) and the efferent (*e. v.*) blood-vessel. The longitudinal muscles of the body-wall are now well developed. In Pl. 8, fig. 23, the longitudinal muscles (*l. m.*) are still stronger, and about fourteen bundles can be seen on each side of the median mesentery. Both the longitudinal blood-vessels are still visible. Pl. 8, fig. 24, is through the proximal end of the muscular part of the body-wall, and shows part of the shallow invagination (*inv.*) above described. Pl. 8, fig. 25, represents a section passing through the non-muscular part of the body, and shows the thin character of the body-wall in this region.

Pl. 8, fig. 26, is from another series of sections, and it represents a section through the distal end of the body, not far from the lophophore. A considerable part of the nerve-ring (*n. r.*) is visible, as well as both nephridia (*neph.*). The small lobes projecting into the body-cavity, near the tubes of the nephridia, are probably parts of the funnels of these organs.

Regeneration and Fission.

In the material under consideration there is no need to make a careful search for evidence of regeneration. It is more difficult to find a lophophore provided with tentacles of the full length than to find one with immature tentacles. It is, moreover, a striking and most obvious fact that the dimensions of the individuals vary to such an extent as to be unintelligible on any hypothesis of orderly growth from the immature to the mature condition. It may further be noted that there is no relation between the condition of the lophophore and the size of the specimen. It will be convenient to analyse the facts under the following heads:

(*a*) Regeneration of the lophophore.

(*b*) Direct evidence of transverse fission.

(*c*) Method by which the tube of the proximal segment is completed.

(*d*) Size of regenerating individuals as indirect evidence of fission.

(*e*) Position of the zones of fission.

(*a*) Regeneration of the Lophophore.

Assuming provisionally that transverse fission is a process of normal occurrence, it is obvious that the conditions under which a new lophophore is formed is not quite the same in the two individuals formed by the fission. In the case of the proximal individual, the entire lophophore has to be formed de novo from a region which is far removed from the original lophophore. In the distal individual, regeneration, if it takes place, presupposes the loss of the original lophophore. This latter process is of the same nature as that which has been described in other species, where the lophophore is thrown off, the wound closes, and a new crown of tentacles is formed from the extreme distal end of the animal.

Many of the specimens figured illustrate the regeneration of the lophophore at the distal end; and where the relations of the tube give no indication of the previous occurrence of fission in this region (cf. section (*c*)) the regenerating lophophore appears to be a replacement of the original lophophore. But as none of the regenerating specimens figured are as long as the fully adult specimen shown in Pl. 7, fig. 2, it may be considered probable that they are all fractional portions of individuals produced by the metamorphosis of larvæ. Neglecting for the moment the differences in the length of the individuals, the regeneration of the distal end may be illustrated by the following cases:

In the distal individual shown in Pl. 9, fig. 32, the thick-walled muscular region of the body is clearly indicated, with the collar-like partial invagination (*inv.*) characteristic of the proximal end of this part. The new lophophore is represented merely by the thickened body-wall at the extreme distal end.

In Pl. 9, fig. 36, the distal thickening indicating the new lophophore is more distinct, and is separated by a slight annular constriction from the beginning of the muscular part of the body-wall.

In Pl. 8, fig. 13, the lophophore is still more distinct and shows distal lobulations which will become the new tentacles.

Further stages in the growth of the tentacles are shown in Pl. 8, fig. 11, and Pl. 7, figs. 5, 4, and 8; and in the last of these the formation of the new lophophore is practically complete.

For a more detailed description of the growth of the regenerating lophophore reference should be made to the memoir of Schultz (1903[1]).

(*b*) Direct Evidence of Transverse Fission.

It has not been very easy to obtain unmistakable evidence of the occurrence of this process, but several specimens have been found which appear to be demonstrative in this respect.

Pl. 9, fig. 31, represents what may be regarded as the commencement of this process. At the extreme distal end of the non-muscular part of the body an annular layer of tube-substance has been formed, projecting into the cavity of the tube, and slightly constricting the body-wall, which does not as yet show any indication of transverse division.

In Pl. 9, fig. 29, a similar process of constriction is taking place in the non-muscular region, at some distance from its distal end. The tube lies in very close contact with the body of the animal, but a constricting lamina can be seen on the left side of the figure. The body-wall now shows evidence of being constricted, and it may be noticed in particular that the mass of adipose tissue (*ad.*) which fills up most of the proximal region of the body-cavity is being divided into two parts by the constriction. This specimen furnishes the most direct evidence which has been obtained of the occurrence of the process in question.

In Pl. 9, fig. 32, two individuals lie in the same tube, the cavity of which has been divided by a transverse septum. The proximal end of the distal individual has a bilobed character, differing from the evenly rounded surface which characterises the normal ampulla. This lobed appearance of the proximal end has been noticed in many of the individuals, and may be taken as evidence of the occurrence of fission, the rounded form of the ampulla not being yet reconstituted. The figure shows that the mesentery of the alimentary canal is attached to the emargination between the two lobes. The distal end of the individual on the proximal side of the septum is also lobed, and this region shows indications of regeneration, particularly in the commencing differentiation of an œsophageal portion of the descending limb of the alimentary canal. It appears to be practically certain that this specimen represents a stage not long after the occurrence of transverse fission.

In Pl. 9, fig. 37, there are also two individuals in what may be considered one original tube. The individual on the proximal side of the septum already shows a recognisable lophophore and œsophagus, but it is constituting a new distal end to its tube by growing out laterally from the original tube.

(*c*) Method by which the Tube of the Proximal Segment is completed.

The specimen last described furnishes the evidence required, and the explanation it suggests is fully confirmed by a number of other cases which have been noticed. In most of the specimens referred to, a tube makes a sudden bend outwards, immediately on the proximal side of a transverse septum; and this outwardly bent portion contains the distal end of an individual. This is represented, for instance, in Pl. 8, fig. 9, and Pl. 9, fig. 34; and the natural interpretation of the conditions shown is that the portion of the tube containing the proximal end of the individual in question is part of an original tube, from the rest of which it is separated by the transverse septum; and that at the formation of this septum the proximal part of the tube, being cut off from the exterior by the septum, has grown out laterally so as to form a new opening for itself. It may be noted that the formation of these laterally growing tubes makes it almost impossible to accept the view of de Selys-Longchamps, alluded to on p. 12, that the tube is secreted only by the ampullar end of the animal.

The system of empty tubes represented in Pl. 8, fig. 15, may be taken as distinct evidence, in the light of the facts already recorded, that the process of fission may be repeated several times in one original individual and its products. The tube *A–K* appears to be part of a tube originally inhabited by a single individual, and added to from time to time as the result of successive transverse fissions of its inhabitants. *A* is the proximal end, and *K* the distal end of the portion represented. The transverse septa at *B*, *F*, and *I*, may be taken as indications of as many transverse fissions The segment of the tube between *B* and *F* has been occupied by an individual which has formed a new distal end to its tube at *G*, and has restricted the size of the rest of its tube by the formation of the irregular, longitudinal, secondary deposit of tube-substance seen at *L*. The septum *H* may indicate merely a part of this process of reducing the size of the tube, but fission may have occurred at this point, in which case it must be assumed that the segment of the animal which occupied the portion *B–H* had not succeeded in forming a new distal end to its tube. The portion of tube situated proximally to the septum *I* has grown out into the irregular tube *J*. On the proximal side of the septum *B* a considerable length of the distal part of a tube has been formed at *C*. This individual occupied only a short portion of the original tube, a septum having been formed at *M*; and it then appears to have grown out proximally, in the direction *D*, a further fission of the inhabitant of the tube being indicated by the septa *E*. It is not impossible that the fragment of the individual left in *D* may have turned completely round in its tube, so that *E* became the proximal end and *D* the distal end of its tube, but of this there is no evidence.

The appearances presented by this system of tubes, together with the evidence brought forward in the next section (*d*) suggest that fission occurs repeatedly in this species, and it seems not improbable that all the numerous individuals found in a given area of the shell may have been derived by fission from a single metamorphosed larva, or from a small number of individual larvæ which succeeded in effecting their metamorphosis in the neighbourhood of the shell.

Further evidence of the correctness of the interpretation of Pl. 8, fig. 15, suggested above, is furnished by Pl. 8, figs. 9, 28, and Pl. 9, figs. 34, 37, which show individuals, in varying conditions of regeneration, in which the distal part of the tube arises laterally from another tube, and, usually, immediately on the proximal side of a tube-septum which appears to indicate the position of the zone of fission.

(*d*) Size of regenerating individuals as indirect evidence of fission.

The variation in length of the regenerating individuals is a very striking fact. The individual shown in Pl. 7, fig. 2, is about 6 mm. long, while that represented in Pl. 7, fig. 7, is only ·3 mm. long. If what is here described as regeneration were really explainable as the various stages by which a metamorphosed larva reaches its adult condition, there would be some definite relation between the size of the specimen and the stage of development of the body and lophophore. Nothing of the kind can be made out. The earliest stages in the development of the lophophore may be found in very long individuals, as in Pl. 9, fig. 36; and, conversely, very small specimens (Pl. 7, fig. 5) may have a well-grown lophophore. The only legitimate explanation of the facts seems to be that regeneration of the lophophore may occur indifferently in large and in small specimens; and from the evidence which has already been brought forward it appears to be fair to conclude that this process is commonly the result of fission. In cases where no tube-septum can be discovered on the distal side of a regenerating specimen, the process appears to be the consequence of the spontaneous loss of the lophophore, as has been described in other species of Phoronis. But in cases like Pl. 9, figs. 32, 33, the new lophophore is clearly being developed as the direct result of the formation of a fission-zone. Pl. 9, fig. 35, represents what appears to be an unusual condition. The position of the fission-zone which cut off the small individual shown is clearly indicated by the annular tube-septum. But in this case the regenerating distal end is growing into the part of the original tube situated distally to the septum, instead of growing out laterally to form a completely new opening. Perhaps the septum was not a complete one ; but if not it must be assumed that the central part of the septum has been absorbed by the regenerating fragment. It is not more difficult to make this assumption than to assume that in other cases a lateral part of the tube can be absorbed, in order to allow the proximal fission-segment to form a new orifice to its tube.

The great capacity for transverse fission possessed by P. ovalis is indicated by the very small size of the regenerating fragments. The smallest specimen shown (Pl. 7, fig. 7) is only ·3 mm. long, but it shows clear signs of regeneration in the differentiation of a new muscular region of the body-wall, indicated by a greater thickness of this part distally, and by the formation of a distinct line of separation between it and the future non-muscular portion. The appearances here shown give reason to suppose that a fragment no more than ·3 mm. long can regenerate a complete individual. The complicated arrangement of the tube-septa in this case implies that the cavity of the original tube has been reduced in size several times, probably in correlation with the small size of the living fragment left in this section of the tube.

(*e*) Position of the zones of fission.

The direct evidence obtained on this subject points to the non-muscular part of the body as the region where fission may occur. This is illustrated by Pl. 9, figs. 29–31. It may be noted that this is not in agreement with the statement of de Selys-Longchamps (1907, p. 163), according to whom it is the muscular region that is specially capable of regeneration. The observation by this author that, having cut the muscular region of a Phoronis psammophila into six fragments, each of these regenerated a complete individual, is too precise to be disputed. But in P. ovalis I have found no certain evidence that the muscular region shares the power of division which is undoubtedly possessed by the non-muscular region. It is possible that Pl. 8, fig. 10, indicates that fission may occur in the muscular region, since in this case the longitudinal muscles are well differentiated in a fragment which is only just beginning to develop a new lophophore. Pl. 9, fig. 35, may also imply that the fission-zone was formed just distally to the junction of the two regions of the body-wall. But in most of the specimens drawn, the muscular part is at first indicated merely by a thickening of the body-wall, and no distinct muscle-fibres can be recognised in the early stages. The regeneration of the distal end in fact commences, as has already been pointed out, with the regeneration of a muscular region, and the lophophore appears subsequently at the distal end of the muscular region.

The general result of these observations is that fission may occur in P. ovalis at practically any point of the non-muscular body-wall, and that very small fragments separated off in this way are capable of complete regeneration. No certain evidence has been obtained that the muscular part can form fission-zones, though this possibility is not excluded. A lobed condition of the proximal end of the body, as shown in Pl. 9, figs. 32, 36, 39, appears to indicate that the ampullar region has not been completely reconstituted since the last fission took place.

Many of the individuals, whether regenerating or not, show a great development of the adipose tissue which accompanies the two longitudinal blood-vessels. In many cases, as in Pl. 7, fig. 6, Pl. 9, fig. 29, the body-cavity of a regenerating fragment contains a large quantity of this tissue, which may probably be regarded as a reserve of nutrient material, at the expense of which the fragment can continue to survive until it has reconstituted its alimentary canal and has formed a new orifice to its tube. Larger specimens which have developed a considerable amount of this tissue are probably in a favourable condition for undertaking fission; and it may be noticed that the specimen shown in process of dividing in Pl. 9, fig. 29, is well provided with adipose tissue. The regeneration of the lophophore without fission may also be facilitated by the previous deposition of a sufficient reserve which can be drawn on for the nourishment of the other tissues during the temporary closure of the alimentary canal. It may be noted that the intestine of a regenerating fragment without a functional lophophore frequently contains the remains of Diatoms, which must have been taken in during a period when well-developed tentacles occurred.

The presence of a large amount of adipose tissue is not, however, a necessary prelude to fission, even though it may favour this process. Some of the specimens of full length are remarkable for being of smaller diameter than usual, their tissues being more transparent than in other cases, and the adipose tissue being deficient in amount. These seem to be ill-nourished individuals, and their occurrence probably accounts for certain abnormally slender regenerating fragments, of the kind shown in Pl. 9, fig. 38, which are sometimes found. The muscular part of the body-wall has commenced to differentiate in Pl. 9, fig. 38, and although its small diameter points to a want of vigour, this individual, and others like it, may have been in a condition to complete the regeneration.

The Occasional Complete Invagination of the Muscular Part of the Body-Wall.

In several cases individuals have been found in the peculiar condition shown in Pl. 9, figs. 41 and 39. In Pl. 9, fig. 41, the partial invagination which normally occurs at the proximal end of the muscular body-wall has become so complete as to result in the invagination of the whole of the lophophore and of the tentacles. The invaginated muscular wall is now turned entirely inside out, forming a sheath opening distally (*or.*), containing the tentacles (*tent.*), and having its epidermal portion lining the cavity of the introvert and its longitudinal muscles on the outer side of the epidermis. The junction between the muscular and non-muscular parts of the body-wall now lies at the distal end of the introvert, and the outermost layer in this region is the part of the non-muscular wall into which the more distal part has been invaginated. The invagination has resulted in the formation of a loop of the alimentary canal which passes distally along one side of the invagination.

Pl. 9, fig. 39, is in a similar condition, except that the introvert contains no tentacles. In their place may be seen a projection which obviously consists of a regenerating muscular part of the body-wall, terminated by a commencing lophophore.

I am unable to give a satisfactory explanation of these appearances, although the fact that three or four specimens have been found in this condition shows that the complete invagination of the muscular body-wall happens not infrequently. It is perhaps one of the methods by which the lophophore may be regenerated, as it seems probable, from a comparison of the two specimens figured, that Pl. 9, fig. 41, is the earlier stage in the process, and that the invaginated tentacles would have been thrown off somewhat later, the wound closing, and the body-wall in that neighbourhood then growing out into the part seen inside the introvert in Pl. 9, fig. 39. It is not obvious what the later course of the regeneration would have been, though it is possible that the introvert would have been evaginated and the muscular wall reconstituted, partly from the old wall and partly from the portion which is being regenerated in Pl. 9, fig. 39. It does not seem probable that the loss of the original lophophore always takes place in this way. It is not easy to explain the mechanism by which the complete invagination of the muscular part of the body-wall takes place in these cases.

The condition shown in Pl. 9, fig. 41, resembles that found in Ectoproct Polyzoa during the retraction of the tentacles, though the Phoronis has no retractor muscles comparable with those of the Polyzoa. The resemblance does not appear to me, however, to lend any support to the view maintained by some authors of a relationship between these two groups. The Phoronidea differ from the Polyzoa in their embryonic development, as well as by striking morphological characters, and in view of these differences the resemblance of the invaginated body-wall to the tentacle-sheath of the Polyzoa seems to be merely a fortuitous one. The formation of an introvert containing the retracted lophophore might perhaps be compared with more reason with the similar introvert in Sipunculoid Gephyrea, though the affinity of the Phoronidea to that group has not been established with any certainty. The introvert of these specimens of P. ovalis is not unlike that which occurs in certain Gasteropoda (e.g. Buccinum), but it would hardly be maintained that this resemblance is any indication of affinity.

The Larval Form of Phoronis ovalis.

Although the observations here recorded do not throw any direct light on this question, one or two remarks on the subject may not be out of place. P. ovalis is known from Strethill Wright's original account to occur in the Firth of Forth, while the large number of individuals found by me in a single shell from the Northumberland coast suggests that the species is common along the eastern coast of the northern part of England, although it has hitherto been overlooked owing to its retiring habits. Actinotrocha has more commonly been found in these regions than the adult Phoronis; and it is, for instance, of frequent occurrence at St. Andrews.

The adult characters of P. ovalis seem to be so distinctive, particularly the small number of the tentacles and the restriction of the bundles of longitudinal muscles to a small part of the metasome, that a recently metamorphosed Actinotrocha belonging to this species might well be recognisable. It should, however, be pointed out that the characters of the individual produced by the metamorphosis of a larva may differ from those of any of the specimens examined from the

Northumberland material. Reproduction by fission appears to take place so frequently in these specimens that all the observed individuals may well have been produced in this way. It would thus be unsafe to assume that primary individuals metamorphosed from larvæ have so restricted a muscular region as that of their fission-products. This may, however, be the case; and it would be desirable to bear in mind the short muscular region and the tendency for its proximal end to be slightly invaginated, should the opportunity occur of examining recently metamorphosed specimens from this part of the British coast.

Observations which I have attempted to make on this subject have led to no definite result. By the kindness of Prof. W. C. M'Intosh, F.R.S., I have been able to examine specimens of Actinotrocha branchiata from St. Andrews; and amongst them I have found one or two specimens which have recently completed their metamorphosis. There appear to be no sufficient reasons for referring these specimens to P. ovalis. I have also examined three recently metamorphosed Phoronis kindly lent to me by Prof. J. Graham Kerr, F.R.S., who obtained them on the West Coast of Scotland, off the Island of Arran. The number of tentacles in these specimens seems to be not less than twenty-eight to thirty, and there is no obvious differentiation of muscular and non-muscular portions in the metasome. The evidence thus appears to indicate that the specimens in question do not belong to P. ovalis.

De Selys-Longchamps (1903, p. 43) has convinced himself that Actinotrocha branchiata is the larva of P. mülleri, a species described by him from Heligoland, but not, so far as I am aware, at present recognised as a member of the British fauna. In the same memoir (p. 47) he has advanced reasons for believing that A. pallida, Schneider, is not the larva of either P. hippocrepia or P. gracilis; and he suggests that it may belong to P. ovalis, if that form is really a distinct species. His statement (p. 47) that the worm produced by the metamorphosed larva of A. pallida has eighteen bundles of longitudinal muscles appears to be significant in this connection, though it should be remarked that the number of muscle-bundles which I have found in P. ovalis (cf. Pl. 8, figs. 22, 23) appears to exceed eighteen.

Actinotrocha pallida was described by Schneider (1862, p. 64, Pl. ii, fig. 12) from Heligoland, where it is said to be as common as A. branchiata. It is stated to have not more than ten tentacles, which are broader and shorter than those of A. branchiata. It possesses only a single mass of larval blood-corpuscles, while A. branchiata has a pair of these masses, one in connection with each of the nephridia. De Selys-Longchamps (1907, p. 190) has found A. pallida at Wimereux (Pas-de-Calais) as well as at Heligoland, and he represents two young stages in Pl. xi, figs. 21, 22. He states that there are never more than six pairs of larval tentacles, and that the length of the larva does not exceed ·6 mm., while that of A. branchiata (p. 189) is as much as 2 mm.

The evidence at present available thus seems to point to A. pallida as being the larva of P. ovalis, and the small dimensions of this larva are in accordance with the small size of the adult form to which it is supposed to belong.

Summary.

Phoronis ovalis, which has usually been regarded as the immature form of some other species, is shown to be a well-characterised adult form. It inhabits burrows which it excavates in the shells of molluscs. It possesses in a high degree the faculty of regenerating the distal end, which is of common occurrence in the genus. Its gregarious habit is probably the result of its power of reproducing by transverse fission, a process which takes place repeatedly and profusely. There is reason to believe that a similar process occurs in certain other species which are found as colonies consisting of numerous individuals, though it is uncertain whether other species have the power of reproducing by fission.

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EXPLANATION OF PLATES 7, 8, AND 9,

Illustrating Mr. Sidney F. Harmer's paper "On Phoronis ovalis, Strethill Wright."

Reference Letters.

ad. Adipose tissue, or vaso-peritoneal tissue. *amp.* Ampulla. *an.* Anus. *a. v.* Afferent blood-vessel. *ep.* Epistome. *e. v.* Efferent blood-vessel. *f.* Fission-zone. *int.* Intestine, or ascending limb of the alimentary canal. *inv.* Invagination of the proximal end of the muscular part of the body-wall. *l.* Lophophore. *l. m.* Longitudinal muscles. *m.* Mouth. *mes.* Median mesentery. *musc.* Muscular part of the body-wall. *neph.* Nephridium. *n. r.* Nerve-ring. *œs.* Œsophagus. *or.* Orifice of invaginated body-wall. *ov.* Ovary. *pr.* Proventriculus, constituting the greater part of the descending limb of the alimentary canal. *s.s*^{1}., Septum of tube. *st.* Stomach. *t.* Tube. *tent.* Tentacles.

[All the figures refer to Phoronis ovalis. The sections, Pl. 8, figs. 14 and 16–26, were drawn with a Zeiss C Obj.; the remaining figures with a Zeiss A Obj. All the figures have been reduced two-thirds.]

PLATE 7.

Fig. 1.—The expanded lophophore of an adult specimen. Eighteen tentacles can be counted. Slide L.

Fig. 2.—A fully adult specimen with expanded tentacles. The ovary (*ov.*) is developed. The lobed character of the proximal end of the body probably indicates, as in other similar cases, that the ampulla (*amp.*) has not been completely reconstituted after transverse fission. Slide O.

Fig. 3.—A smaller specimen with retracted tentacles. Slide M.

Fig. 4.—A small regenerating fragment. The marked angle between the axes of the proximal and distal parts of the body probably indicates, as in fig. 3 and other specimens drawn, the lateral outgrowth of the new distal part of the tube necessitated by the closure of the original tube by the septum formed during the process of transverse fission. Slide O.

Fig. 5.—A smaller regenerating fragment. Slide N.

Fig. 6.—A small regenerating fragment in which the lophophore is not yet developed. The muscular part of the body-wall (*musc.*) is already indicated. The adipose tissue (*ad.*) fills most of the body-cavity. Slide M.

Fig. 7.—An extremely small fragment in about the same stage of regeneration as the preceding figure. The cavity of the tube is restricted by a complicated system of septa (*s.*). Slide Q.

Fig. 8.—A regenerating specimen resembling those shown in figs. 4 and 5, but more completely developed. Slide M.

PLATE 8.

Fig. 9.—A completely regenerated individual. The original tube has been subdivided by septa (*s.*), and the new distal end of the tube has been developed as a lateral outgrowth starting immediately on the proximal side of the septa. Slide Q.

Fig. 10.—A small regenerating fragment in which the muscular part of the body-wall is unusually long; *l.*, the commencing lophophore; *l.m.*, longitudinal muscles. Slide M.

Fig. 11.—The appearances of this specimen suggest that a small fragment produced by fission on the distal side of the septum (*s.*) has formed a new distal end to its tube by lateral outgrowth instead of making use of the original distal end of the tube. Slide P.

Fig. 12.—Another small fragment. The muscular part of the body-wall (*musc.*) is already invaginated at its base (*inv.*); *l.*, the commencing lophophore. Slide N.

Fig. 13.—A specimen with strongly marked invagination (*inv.*) of the proximal end of the muscular region (*musc.*) and a commencing lophophore (*l.*). Slide M.

Fig. 14.—A sagittal section passing medianly through the distal end of the body. *inv.*, invaginated part of body-wall; *ep.*, epistome; *œs.*, œsophagus, separated by a circular valve from the proventriculus (*pr.*); *an.*, position of anus. (Zeiss C Obj.) Slide F.

Fig. 15.—A system of empty tubes from which the course of the transverse fissions of the animal can be inferred. For explanation see text, pp. 12, 20. Slide K

Figs. 16–25.—From a series of sections transverse to the principal axis of the body of an adult specimen. (Zeiss C Obj.)

Fig. 16.—Through the retracted tentacles, of which 22 are present, arranged in the form of a horse-shoe. Slide A^1.

Fig. 17.—The tentacles have united at their bases on the anal side (*l.*); *ep.*, the tip of the epistome. Slide A^1.

Fig. 18.—A more proximal section; *ep.*, epistome. Slide A^1.

Fig. 19.—The epistome (*ep.*) is cut at the level where it reaches its greatest size. Slide A^1.

Fig. 20.—The tentacles have completely united at their base, and the mouth (*m.*) is thus outlined. The anus (*an.*) lies between the lophophore (*l.*) and a lobe of the metasome; *n.r.*, part of the nerve-ring. Slide A^1.

Fig. 21.—Through the commencement of the metasome. The afferent blood-vessel (*a. v.*) is visible; *n. r.*, the part of the nerve-ring on the oral side. Slide A^1.

Fig. 22.—A more proximal section. Both limbs of the alimentary canal are supported by the median mesentery (*mes.*). Both longitudinal blood-vessels (*a. v.*, *e. v.*) are visible. Slide A^1.

Fig. 23.—A more proximal section. The longitudinal muscles (*l. m.*) form strong bundles. Slide A^1.

Fig. 24.—Showing part of the invagination (*inv.*) at the proximal end of the muscular part of the body. Slide A^2.

Fig. 25.—Through the distal part of the non-muscular region of the body. Slide A^2.

Fig. 26.—From another series of "transverse" sections, through the region close to the base of the lophophore; *n. r.*, part of the nerve-ring; *neph.*, nephridia. (Zeiss C Obj.) Slide B^1.

Fig. 27.—A small regenerating fragment which is not yet provided with an orifice to its tube. Slide M.

Fig. 28.—Regeneration practically complete, the distal end of the tube having been formed as a lateral outgrowth developed on the proximal side of the septum (*s.*). Slide Q.

PLATE 9.

Fig. 29.—A regenerating specimen which is commencing to divide. At the distal end, the muscular part (*musc.*) is developing, while the lophophore (*l.*) is recognisable owing to the presence of a septum dividing its body-cavity from that of the metasome; *f.*, zone of transverse fission, accompanied by the formation of a tube-septum. The adipose tissue (*ad.*) is present in large quantity. The proximal end is lobed, indicating a previous fission, further evidence of which is afforded by the tube-septum (*s.*). Slide L.

Fig. 30.—A larger specimen in the same condition. Slide O.

Fig. 31.—The first indication of fission is afforded by the formation of the annular tube-septum (s^1.), which in this case occurs at the commencement of the non-muscular part of the body. Slide Q.

Fig. 32.—A later stage in the fission-process. The two products of fission are completely separated, the distal one showing a lobed proximal end, and the proximal one showing signs of regeneration distally. Slide N.

Fig. 33.—The proximal member of the result of the occurrence of fission, the evidence of which is the tube-septum (*s.*) and the lateral outgrowth of the tube (*t.*) on its proximal side. Slide Q.

Fig. 34.—A similar specimen of much smaller size. Slide N.

Fig. 35.—A very small regenerating fragment, the distal end of which is growing through the annular tube-septum (*s.*) which presumably indicates the previous occurrence of fission. Slide Q.

Fig. 36.—A large specimen, of a kind frequently observed, in which the alimentary canal is thin and occupies only a small part of the body-cavity: a condition which is probably due to deficient nutrition. Regeneration of the distal end is taking place. Slide O.

Fig. 37.—The two specimens here shown have probably been separated from one another by fission, as indicated by the septum (*s.*) and the lateral outgrowth of the tube on its proximal side. The lophophore (*l.*) of the proximal individual is in an early stage of development. Slide N.

Fig. 38.—A very slender and presumably ill-nourished regenerating specimen. Slide N.

Fig. 39.—The significance of the condition here shown has not been ascertained. The entire muscular region has been invaginated, forming an introvert opening to the exterior at *or.* The introvert contains a regenerating distal end, in which the new muscular region (*musc.*) and lophophore (*l.*) can be distinguished. By the formation of the introvert the alimentary canal has been thrown into a loop, the portion of which belonging to the descending limb (*pr.*) is seen to the right of the introvert. The ascending limb of the alimentary canal probably has a similar course, but it was not observed in this specimen. The outgrowth of the proximal end of the body in a direction at right angles to the axis of the original tube probably indicates a lateral extension of the proximal end of the tube in order to provide room for the elongation of the corresponding region of the body, the growth of which, in this direction, would otherwise be prevented by the septum *s.* Slide N.

Fig. 40.—Lateral view of the distal end of a mature specimen, showing the epistome (*ep.*) inside the group of retracted tentacles. Slide M.

Fig. 41.—Another stage of the condition shown in fig. 39. The introvert contains a bundle of fully developed tentacles. This may be either an earlier stage than fig. 39, in which case the original lophophore has been completely retracted into the introvert, and was destined to be thrown off later; or a later stage, in which the new lophophore has been completely regenerated. In this specimen there is evidence that the ascending limb of the alimentary canal, as well as its descending limb, forms a loop passing up one side (left in the figure) of the proximal end of the introvert. Slide M.