# NEW FORMS OF THE HEMICHORDATA FROM SOUTH AFRICA.

I. PHORONOPSIS ALBOMACULATA, g. et sp. n.

II. PHORONIS CAPENSIS, sp. n.

III. PTYCHODERA CAPENSIS, sp. n.

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### (With Plates XVI., XVII.)

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#### INTRODUCTION.

The three orders of the Hemichordata<sup>\*</sup> prove to be represented in South Africa: the Enteropneusta by the form here described; the Pterobranchia by a new species of Cephalodiscus †; and the Phoronidea by the two forms mentioned above.

A species of Phoronis is not uncommon in South African seas, and individual specimens are readily obtained in limestone and amongst incrustations of Polyzoa and worm tubes dredged from shallow water (15 to 30 fathoms).

A number of the animals were, however, obtained in a much simpler way. About the beginning of May, 1906, numerous specimens were observed in a tank at the Government Marine Laboratory, and there is evidence that they had been brought in with the supply water as larval forms. They were first seen in a small piece of limestone which had been procured from a depth of about 20 fathoms in False Bay some time previously, and it was thought that they had been brought in with the stone. Further search, however, in the tank resulted in the discovery of other

<sup>\*</sup> Adopting for the present purpose Harmer's subdivisions of this group (vide "Cambridge Natural History," vol. vii.).

<sup>+</sup> Vide "Marine Investigations in South Africa," vol. iv., pp. 173-192.

individuals, one in a large limestone rock which had been for some months out of water before being used to form part of the rock-work in the tank, three in a small piece of stone at the further end of the same tank introduced later, and a solitary specimen in another tank. Further evidence was afforded by the fact that a dried piece of limestone put into the tank for the purpose of confirmation had at least one Phoronis on it about eight months afterwards.

During the examination of the specimens in the limestone a single specimen (A) was observed which appeared to be a different species, being larger, of a somewhat different form, and pigmented. This was the only one of its kind then found, and special care was taken to observe its habits and behaviour in the living condition before preserving it for more detailed examination. It appeared to be thriving and specially active, and it was disappointing to find, on proceeding to examine it again, that this unique specimen had entirely disappeared, leaving only the end of the tube visible. After a time, however, the headless trunk of the animal was slowly protruded, and a month later the head region had apparently grown to its former dimensions. Fig. 2 is from a photograph of the animal at this time.

Only two other specimens (B and C) of this species have as yet been procured, but it will probably be found that the animal is not so rare as would seem to be indicated.

With regard to the first species (*Phoronis capensis*, sp. n.), there is little of special interest; but as the specimens, on account of their hardiness and their thriving so well in captivity in spite of somewhat severe handling, afforded excellent material for observation of their habits and certain features of the living animal, an opportunity was taken to add a few details to the little that is known on these points. Fig. 1 represents one of this species carrying eggs, and is from the living animal.

The second species is of more interest structurally. It shows an apparent advance on species hitherto described in the circumœsophageal nerve ring being partially sunk in an involution of the epithelium of the body, the single nerve chord being well developed, the nephridia somewhat modified, the longitudinal muscles of the body increased in number, and ova deposited in gelatinous mass in the tube instead of in the tentacles.

These distinctive features, especially the first, seemed to necessitate the separation of this form from others as a new genus— *Phoronopsis*.

The following description of this animal is necessarily somewhat incomplete on account of the limited material available, but I hope

to procure additional specimens to check and supplement it. Transverse sections were made of specimen A and longitudinal sections of B.

# I.-PHORONOPSIS ALBOMACULATA.

# (Plate XVI., fig. 2.)

# PHORONOPSIS, g. n.

The body is asymmetrical, muscles of body being numerous and more developed on left side, one nerve chord well developed, and nerve ring in an involution of the epidermis, ova deposited in gelatinous mass in the tube.

In all the species of Phoronis hitherto described the body is symmetrical or asymmetrical, as indicated by the development of the muscles and nerve of the left side; the muscles of the body are markedly less in number than in Phoronopsis, and there is no trace of any involution of the epidermis at the nerve ring; the ova and larvæ are lodged in the coils of the lophophore.\*

There seems little doubt of the necessity of separating this form from those hitherto described.

#### PHORONOPSIS ALBOMACULATA, sp. n.

Size.—The length of the animal removed from its tube was 18 mm., the diameter of the body 1 mm. immediately below the lophophore and 2 mm. at a distance of 4 mm. from the opposite extremity. The diameter of the lophophore from tip to tip of tentacles, when the animal was alive and completely expanded, was 7.5 mm.

Tube.—The tube is larger than that of P. capensis, being 1.2 mm. in diameter. It is not embedded—*i.e.*, it does not penetrate the substratum, but rather lies on it, being firmly attached by one side. The substance of the tube spreads over the substratum on the attached side, so that in sections it does not appear circular, but is flattened on one side.

The tube is about 30 mm. long, and, in the specimens, was irregularly curved, so that the two ends lay near each other. Its substance was apparently of the same nature as that of P. capensis, but firmer and of a much tougher consistency. It was covered by grains of sand and pieces of shell arranged in no definite manner.

\* Longchamps (8) observed the eggs of *Phoronis Mülleri* being discharged directly into the water, and suggests that this may be normal.

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Colour.—A pure white pigment of finely branching chromatophores occurs in spots irregularly placed on the tentacles. These spots were somewhat elongate in the direction of the length of the tentacles. To the naked eye each appears as a solid spot, but when examined with a lens is seen to be more or less divided longitudinally, and to consist in reality of two patches, one on each side of the tentacle. At the base of the tentacle they are more numerous, and form a continuous line along the lophophore near the oral region so as to form an incomplete circle. At the median point (that is, the mouth region) a strip of pigment passes backwards towards the anus (or along the dorsal aspect of the animal), and ends in a slightly enlarged circular patch. Whether or not this spot coincides with the anus, as it appears to do, could not with certainty be made out as the pigment was not visible in sections. The white pigment extends on to the body in few and irregular streaks below the lophophore.

Apart from this pigment the tentacle and lophophore were clear, transparent, and apparently colourless. The body, however, was of a faint yellowish colour.

Nervous System.—The single nerve along the left side of the body is well developed. The nerve cells are numerous and well developed, and are arranged so as to form a solid rod (cf. Caldwell (3), Cori (4), Longchamps (8). A transverse section showed that this nerve is not hollow, the centre being occupied by a clear, refractile, nonstaining substance. The nerve was thus, as a whole, partly differentiated from the epithelium, but not sinking away from it.

In following the sections upwards however it is seen that as they approach the duct of the nephridia the nerve gradually leaves the epithelium of the body, and when the duct (double, as it is here in the form of a loop) is cut the nerve is seen internal to it. Succeeding sections show that, after the nerve has thus passed over the duct on the inside, it again passes out between the two limbs of the duct before joining the circum-œsophageal ring of nerve tissue; in other words, on coming to the nephridial duct it passes over it on the inside in place of continuing on the outside, where the epidermis of the body is. This twisting of the lateral nerve may be associated with the marked distortion of the body. The anus, at one time terminal, has come to lie near and behind the mouth. The nephridial opening, at one time probably ventral and below the lateral nerve chord, has been carried upwards, necessarily passing over the lateral nerve chord, and finally attains a position near the anus.

The passing of the opening of the nephridial duct over the nerve

may also be associated with its separation from the epidermis at this point.

The most striking feature of the nervous system, however, is to be found in the character and position of the nerve ring. It is sunk in a comparatively deep involution of the epidermis, which is so intimately connected with the nervous system that it is most conveniently dealt with here. This involution or fold of the epidermis passes from the oral side of the animal round on each side, following the course of the nerve ring, till, on reaching the lophophoral opening, in or near which are situated the anal and nephridial apertures, it is continued round the body, passing outside these organs.

The fold can readily be seen with a low magnifying glass. It varies greatly in depth; outside the anus it is a mere ridge; it is deepest at the sides of the body, being about one-fourth of its diameter. Anteriorly, *i.e.*, in the oral region, it becomes somewhat shallower.

The general character of the histological elements of this fold is indicated in fig. 4. The external part is identical in structure with the general epithelium of the body—a layer of deep epithelium cells, including glandular cells. Towards the tip of the fold, however, these cells become smaller and lower, and at the tip somewhat abruptly change in character and become low, square, with comparatively large, round nuclei, and without distinct cell demarcations. These are continued down to the bottom of the fold, where they once more abruptly change into deep elongate cells, with punctated nerve substance. The nervous epithelium of the nerve ring does not, therefore, participate in the folding.

In some sections of the fold a few cells occur between the cubical epithelium and the epidermis, and apparently a space which is not coelomic. The existence of a space is doubtful, however, and may be an artifact.

In life, the small cubical epithelium of the fold is applied to the nervous epithelium, the lip of the folding not standing out as shown in the figure, which is from a specimen (B) killed and fixed in sublimate. In the other specimen (A), which was treated in practically the same way (fixed in sublimate with 1 per cent. acetic acid) before removal from the tube, the lip of the fold was closely applied to the body.

The epithelium of the nerve ring is not entirely covered by the fold, even when closely applied to it. In the region of the organs, which for want of a better name I have called "olfactory organs," it extends beyond the fold and is freely exposed. The nerve ring is

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therefore elongated, or broadened upwards towards the tentacles here, and, in the same region, elongated downwards in the lateral folds. This downward elongation comes in close approximation to the nephridia, as shown in fig. 5, which is a transverse section of specimen A.

With regard to the interpretation of this organ, the most obvious suggestion is that it is of the nature of an introvert, such as occurs in the Polyzoa and Sipunculoidea, and, if so, it might form another link between the Phoronidea and these groups. It seems probable from its size, structure, apparent absence of retractor muscles, and intimate relation with nerve ring, that it does not however act, to any great extent at least, as an organ for the withdrawal of the body, or any part of it—a function which is most efficiently performed by the numerous and powerful muscles of the body.

In specimen A we are dealing with a regenerated head, not mpossibly in B also, and it might be suggested that the fold is a stage in the complete separation of the nerve ring from the epidermis—a condition which might occur in a completely developed specimen, though the nature of the folding does not seem to support such a view.

If any phylogenetic significance is to be attached to the form of this organ, which is possible, it may be that it is the remnant of an ancestral introvert which has been retained with the new function of protection of the nerve ring.

*Muscles.*—The longitudinal muscles of the body were numerous and well developed, especially on the left side. In the region just below the nephridia there were 32 in the left oral chamber, 30 in the right, 18 in the left anal chamber, and 14 in the right, or, according to Longchamps' formula,  $\frac{32}{18}\frac{30}{14}$ .

Lophophoral Organ.—In specimen A this organ was not present but in specimen B it was very marked, being a deeply staining mass of glandular cells.

Tentacles.—The tentacles were numerous—126 in specimen A. They were a little over 3 mm. in length, and .08 mm. in diameter.

Septa.—The septa seemed to be of the usual number and disposition. The transverse septum was in part without basement tissue. In median longitudinal sections there appeared an offshoot towards the epistome—a condition which requires further examination and confirmation on other specimens.

Nephridia.—The two nephridial tubes are well developed, and in preserved material were bent on themselves, forming a loop, the limbs of which appeared of about equal length. As described above, the nephridial tube of the left side passes between the nerve and the

external epithelial layer of the body. Internally the nephridia opened in the lateral mesenteries, there being two very marked and wide openings to each. These openings were composed of deeply staining masses of cells, which extended up on to the transverse septum. They were not, as in other species, continued down on the lateral mesenteries.

Ova.—Specimen C was in all respects like in general form and colour to A and B, so far as could be ascertained by microscopic examination of the living animal protruding from its tube. There were no eggs or embryos in the tentacles, but, on one occasion, when the animal was retracted, a large number of ova were seen lining the mouth of the tube, and these were held together by a gelatinous substance. The eggs were slightly yellow in colour and '1 mm. in diameter. They were all in a very early stage of development. Both the animal and eggs were torn off, probably by a fish or other animal in the tank, only a part of the animal and tube being left, so that later stages of the eggs were not observed.

# II.-PHORONIS CAPENSIS, sp. n.

# (Plate XVI., fig. 1.)

There are no satisfactory features by which the various forms, which are here included under the genus Phoronis, to which this species belongs, may be separated from each other, and the description of a supposed new species cannot be drawn up on very definite lines, but rather with a view to affording details, some of which may subsequently be found to be of systematic value. Such particulars are size, form, colour, number of tentacles, tube, number and development of longitudinal muscles, nerve chord, &c.

Size, dc.—The body of this species is neither particularly large nor small. The largest specimen was not more than 1 mm. in diameter at the end of the body immediately below the lophophore. This might be reduced to about half this diameter when the animal was fully extended from its tube. The total length of a specimen removed from its tube was 21 mm., the smallest diameter of its body 1 mm., and the greatest  $1\cdot3$  mm. (near the basal end).

The living animal is clear, colourless, almost transparent. The tube in which it lives is circular and of a brown, horny-like substance, not easily ruptured, and is not confined to any special substratum, but may occur embedded in limestone or between any calcareous tubes of other animals, even among calcareous algæ. (See below for further details.)

*Nervous System.*—This is essentially as described in some other species. There are two very fine tracts of punctated nervous tissue running along each side of the body where it is joined by the lateral septa.

Beneath these, on or in the basement membrane, could be detected a very fine tube, such as has been described. No nervous tissue was found anywhere separated from the epidermis. The specially developed patches of nerve tissue at the base of the lophophore were present as described by Benham (2) for P. australis, and, for reasons stated further on, are perhaps to be considered as olfactory organs.

Another patch of nervous tissue, apparently representing a sensory organ, was found at the base of the epithelium of the floor of the mouth where it joins the transverse septum. The tissue is less developed and definite than in the previous case, but, taken in conjunction with the observations below, it would seem to be an organ of taste, or at least of discrimination of food particles, o which there is a very definite selection and rejection (fig. 6 ne').

Musculature.—The longitudinal muscles of the body are fairly well developed. Near the nephridial region they are symmetrical, that is, an equal number on the right and left of the median septum. According to the convenient formula of Longchamps they would be  $\frac{12}{4} \frac{12}{4}$ , that is, 12 in the right and left anterior chamber, and 4 in the right and left posterior. This, however, was not constant, and  $\frac{12}{4} \frac{11}{4}$  and other combinations were observed.

Lophophoral Organ.—This organ in *P. capensis* appears to be essentially similar to that in other described species.

In view of the observations on this organ in the living animal, two parts are to be distinguished. First, the glandular epithelium at the base of the lophophore below the tentacles forming the lower part of the brood chamber. This glandular epithelium extends up on the inner side of one or two of the tentacles, that is, into the region where the more developed embryos lie. It is readily seen in sections that the mucus from the epithelium envelops the eggs, and the mucus with which the mass of developing eggs and embryos are held together is very apparently from this source. Secondly, a free continuation of the epithelium out from the lophophore. The cells here assume rather the characteristic of ordinary epithelium (ciliated). Though in sections little more than a slight projection or fold, this part in the living animal is broad and leaf-

like, and functions as an organ for conveying the eggs from the nephridial opening to the brood chamber as described below.

*Tentacles.*—The number of tentacles in specimens with eggs, and therefore probably full grown, is about 90, though much fewer were observed in others with rejuvenating (?) heads and in small specimens.

The number of coils of the lophophore when contracted (in sections) was at most one and a half on each side, and, when fully extended, one, that is, in the circle of tentacles, the course from a point in front of the middle of the mouth to a corresponding point behind, was about circular with a slight re-entering curve in which the eggs were lodged (*vide* fig. 1). The coils were flat, that is, not in a turreted form as described in *P. australis* (2) and *P. buskii* (7).

Septa.—A transverse septum exists in P. capensis, but it is not of the same character as in P. australis (2). In the latter it is composed of a homogeneous dense matrix with embedded cells and spaces lined by cells. This condition, which I have also found in section of P. hippocrepia, may have been brought about by the invasion of the septum by the gelatinous basement membrane of the body wall. In P. capensis only a part on each side and behind is so invaded, the rest of the septum being composed of the closely applied coelomic epithelium of the supra- and infra-septal cavities, so that in longitudinal section near the right or left body wall the septum appears of the character found in P. australis, while in a median longitudinal section the septum is in the form of cells without basement tissue. The characteristics of the septum in this respect would probably be of value in specific determination, but it has not been described for most species.

The mesenteries of the cavity below the transverse septum are of the same character. Gaps, however, occur in them, and the two layers are not always evident. In the nephridial region of the lateral septa the basement tissue, however, appears.

Nephridia.—There are two nephridia. In addition to the large opening into the rectal chamber, there is a smaller into the lateral chamber. The rectal opening is continued down the mesentery for a considerable distance, as described in *P. australis*, and other species.

Circulatory System.—Some of the details of the course of circulation were made out by examination of sections, but chiefly by observations on the living animal. They showed that the circulation was apparently different from that of P. australis (2).

In sections, the afferent vessel was seen to be divided into two

branches, but these do not pass into "circular" vessels only, but lead by a large vessel (often swollen up into a large cavity full of blood corpuscles) directly into the two branches of the efferent vessel, so as to effect a direct communication between afferent and efferent vessels.

This was confirmed by observation on the circulation in the living animal as given below, where the circulation is more fully discussed.

Affinities of P. capensis.—The species seem nearest to P. hippocrepia. It differs from specimens of this species which I have examined in the structure of the transverse septa, as already indicated, and in the number of tentacles. The latter characteristic is, however, very variable, and the value of the former as a specific characteristic is not yet proved, and it is by no means certain that the forms are distinct.

The wide geographical separation of the species can reasonably be accounted for by the habits and modes of occurrence of the animals as here described. If they can be conveyed through a pump, a long pipe, with a fall of about a foot into a tank of water, and become affixed to a stone, it is more than probable that they will lodge in the material which accumulates on ships' bottoms, or floating pieces of wood, and be carried great distances in this way.

# OBSERVATIONS ON BEHAVIOUR AND HABITS OF PHORONIS CAPENSIS.

There is still some considerable doubt on many points connected with the general habits and certain physiological phenomena of Phoronis. Its formation of what might be called "pseudo-colonies," in which there is apparently no co-operation or advantage to its individual members; how the animal apparently penetrates solid limestone; how the tube is formed; how food is ingested; function of the "lophophoral organ" and of epistome; nature of sense organs, if any; whether the movement of the blood is real circulation or merely oscillation—these and other points still remain somewhat obscure.

The following notes are based on observations for a year on a "colony," and on specimens occasionally procured by dredging, and also on repeated observations made under the microscope on specimens living in as normal conditions as possible. For convenience, I have arranged these under the following heads :---

(a) Mode of occurrence, formation of tube, boring (?), colony formation.

(b) Tentacles, muscular and ciliary movements.

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(c) Eggs, larvæ, oviposition, breeding season.

(d) Lophophoral organ, lophophoral gap, epistome.

(e) Sensory organs.

(f) Circulation.

(a) Mode of Occurrence, Formation of Tube, &c.-Most of the animals examined were found in a limestone of recent origin which occurs on the shore and on the sea-bottom in False Bay. It contains a large quantity of rounded sand-grains embedded in a calcareous matrix, which is made up of recent shells. It is bored through by worms, lamellibranchs, and sponges. It seemed at first pretty conclusive that the Phoronis had bored into this limestone, as, in most of the cases, where they were chiselled out or the limestone broken, they were found to fit closely the cavities in which they lay, and as the tubes were coated on their outside with a layer of sand-grains apparently pushed aside when the limestone itself was dissolved. The presence, however, of numerous sponge spicules in this coating of the tube seemed to indicate that the cavity had originally been made by a sponge. Further, the fact that other specimens were found in the interstices of Polyzoa and worm tubes, in one case in the tube of a Serpula which had left or been ejected, and in another case in the loculi of the base of a barnacle shell, is evidence in the same direction. I may add also that no acid reaction was obtained from living specimens. On the whole, the balance of evidence seemed to indicate that this Phoronis is not a limestone-boring animal, and that colony formation, which, however, is not a very characteristic feature of this species, is merely due to local conditions favouring growth at a particular point.

The part of the tube projecting from the material in which the animal occurred varies much in length, being usually about 4 to 6 mm., but sometimes much longer, or entirely absent. This part of the tube was very flexible, and covered with a substance similar to that of its surroundings. The stone was found to be covered with a greyish coating of  $d\dot{e}bris$ , held together by a sticky substance. On one or two occasions large starfish, which were in the tank, were observed to remain for some time in the stone and clear off this coating without, however, injuring the Phoronis. It would appear that this coating may be produced by the action of the Phoronis themselves. Sections of the projecting part of the tube showed that the  $d\dot{e}bris$  was not only adherent to the outside of the tube, but was included in the substance and particles, see below. In some species the foreign substance adhering to the tube has been described as the

excreta of the animal. In this species the excreta were observed to be ejected in long, solid, cylindrical masses, falling clear of the animal and tube. Growing on the tube were often to be observed solitary stalked Protozoa with horseshoe-shaped nucleus.

The exposed part of the tube was readily injured, and occasionally individuals were seen protruding through an aperture in the injured tube.

The substance of the tube was semi-transparent, brownish, and of a tough consistency where embedded; in this region there were no inclusions in the substance of the tube. There was evidence that the tube is secreted by glandular epithelium of the body generally. Thus, if the animal is removed from the tube, there is an active secretion of mucus, which soon causes the body to be covered with any loose particles that may be in the neighbourhood. In one case a fairly large active copepod was observed to become entangled in the viscid secretion, and was soon rendered quite helpless. The mucus is at first clear and transparent, but soon becomes whitish and opaque.

None of the tubes were straight, but had a more or less irregular curve, sometimes even forming a loop. When tubes were removed from the limestone by decalcifying, they were found to be densely coated with firmly adherent quartz grains, not arranged in any definite manner. These sometimes deeply indented the substance of the tube and the body of the animal. The posterior end of the animal apparently exercises some penetrating though not boring function.

The body of the animal varied much in diameter according to the extent to which it was protruded. Under certain conditions, which could not exactly be determined, the animals were greatly extended from the tube. The body and tentacles were then mostly rigidly extended. They sometimes slowly rotated in themselves—both lophophore and body—but did not, as described for some species, bend or wave from side to side. This latter movement was sometimes observed, however, when the animals were under observation in small vessels, especially when being examined by transmitted light.

Tentacles, Muscular and Ciliary Movement, &c.—The method at first adopted in microscopic examination of the living animals was to remove it from its tube by cutting away the limestone, or to suddenly cut off a protruded head, when after a time it often again expanded fully. The tentacles were then observed to be well provided with long cilia (about one-fourth the diameter of the tentacles). In these cases, however, the cilia were never observed to be in motion

(cf. van Beneden's observations (2), in which he describes the cilia as non-motile).

Other observations were then made on animals projecting over the edge of the stone so that transmitted light could be used. In this case the cilia were observed to be very active, though, if the animal were disturbed, they suddenly ceased before the animal withdrew into the tube. On one or two occasions the cilia were observed to remain at rest when the undisturbed animal was fully extended. Expansion of the lophophore was not as described in some species, viz., after the extension of the body, but the tentacles began to spread out at the very commencement of the protrusion.

The currents of water were best observed under the microscope. It was found that what might be called the inset current, as is to be expected, was into the space between the outer and inner circle. Particles in suspension in the water were carried into this region even from a distance equal to the length of the outstretched tentacles. The particles, especially the larger, were carried to the mouth on the tentacles, evidently by the active cilia. It was surprising, however, to find that in many cases, after reaching the base of the tentacles or margin of the mouth region, the same particles were returned on the same tentacles, and travelled as rapidly in the opposite direction to the distal end of the tentacle. The tip of the tentacle was then slowly bent backwards, and the particle dropped off on to the stone. the cilia at this part of the tentacle during the process ceasing all movement. In such cases, the particle was observed to have a coating of mucus, by a thread of which it often hung on to the tentacle for a time. In a few cases the particles were dropped off in the same way without first travelling to the mouth. This was observed to occur not only in the outer circle of tentacles, but also in the inner, in which case they were dropped into the centre of the inner circle when there was a constant and very strong current passing upwards and away from the animal. The disposal of particles in this way seemed as much a function of the cilia as the conveying of them to the mouth. I at first supposed that it was effected by a reversal of the movement of the cilia, but this was never observed. It was afterwards observed, however, that if a tentacle be carefully examined, looking towards it from the direction of the mouth region, the cilia on each side showed the ciliary movement in opposite directions.\* This occurred on all the tentacles, both those of the inner and outer row. The apparent movement may best be described as upwards on the left side and downwards on the right of

\* I do not know whether such ciliary motion has been recorded in any of the Polyzoa, but I have observed it in some.

each tentacle when it is viewed from the oral side of the animal and with the lophophore fully expanded. The result would be, of course, that particles, in contact with the one side only, would be carried in a direction outwards or inwards, and opposite to that of the apparent motion of the cilia (due, of course, to the slower stroke in that direction). The cilia on either side could be brought into contact with the particles by rotation of the tentacle, which was observed in a few cases to occur, but this point was not conclusively established, as exact observations are not here easily made. It is certain, however, that the propulsive action of the cilia is not only towards the mouth, as has been supposed, but is largely concerned in carrying away any rejected particles. Particles of a diameter about equal to a sixth of that of the tentacle, and larger, are carried off in this way, as are also irregular masses of *débris* that may be caught up in the inhalent current. Smaller particles are got rid of in another way. If an actively feeding animal be viewed laterally, so that the outer and basal part of the tentacles is seen, a large number of particles is observed to be escaping between the bases of the tentacles over the edge of the "membrane" connecting them, and then to fall in a continuous shower on to the edge of the tube, to which some were observed to adhere (probably the origin of the inclusion seen in the substance of the protruding part of the tube).

Another and different action of the tentacles was observed when the animal was feeding actively. This was a sudden bending in towards the mouth of the distal free end of the tentacle both of the inner and outer row (cf. fig. 1, in which one tentacle of the outer row shows the nature of this bending). Single tentacles, independently of the others immediately next them, showed this movement, which was sharp and definite both in the action and recovery to the normal position. At times this movement was repeated by different tentacles at very short intervals, and in the case of Phoronopsis, in which this movement was more marked, on several occasions it appeared as a quite continuous jaculatory movement all round the lophophore. It might be suggested that the result of this movement is to throw or sweep particles of food towards the mouth, but only in a few instances was this actually seen, and the possibility is not excluded that these cases were accidental. This movement might be compared to the reaction on stimulus of the tentacles of some sea anemones and polyzoa.

The inhalent current, which sets in towards the mouth region, passes off in two directions, viz., between the outstretched tentacles of the outer row and downwards, and between the tentacles of the inner row and inwards, where there is formed a very strong current

upwards, stronger than the inhalent current (being more confined). It might be expected that a part or all of this current would also flow out over the anus and nephridial openings by the large space which forms the open part of the horseshoe-shaped lophophore, and, indeed, Masterman (6), who, however, had not the living animal, describes and figures such a current as existing. If the living animal is carefully observed, however, it can be seen that not only does no such current exist, but that there is a current leading inwards not outwards at this aperture, so that it passes first over the two pillar-like sides of the lophophore which are characterised by the special development of nervous tissue at this place, then over the nephridial openings and the anus, and joins the strong exhalent current of the inner circle of the lophophore. Benham (2) has accurately described this patch of nervous tissue, and regarded it as structurally the only approach to an appearance of a sensory organ in Phoronis, but expresses his doubts on account of its proximity to the excretory openings. The existence of such a current of water however, passing in turn over the nervous epithelium, the renal openings and the anus, removes this objection, and renders the case quite similar to that of the current, for instance, in the palleal chamber of some Mollusca, which passes first over the osphradium, then the renal aperture, and finally the anus. It has been repeatedly observed that the animal seems very sensitive to the condition of the water in which it lives, and I cannot but think that the two special patches of nerve tissue represent a sensory organ similar in function to the osphradium of molluscs, and it may be called for want of a better name the olfactory organ.

Still another movement may be observed, but with greater difficulty. It occurs on the upper part of the body just below the insertion of the lophophore. No current of water was observed, but merely a movement of particles apparently entangled in mucus and in contact with the body. These were slowly carried upwards away from the mouth of the tube. Very small cilia were on occasions observed. This action may account for the fact that no foreign particles, such as might fall into the tube, were found included in its substance where embedded in the stone.

Eggs, Larvæ, Oviposition, Breeding Season, &c.—The eggs and embryos are very conspicuous, and could be readily observed mostly within the lateral bends of the inner circle of tentacles though occasionally projecting outside these bends. Those nearest the body were apparently held together by the mucus which is secreted by the glandular part of the lophophoral organ; those near the free ends of the tentacle were further developed, some attached to the

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tentacles and still in the delicate egg capsule; others, however, were in some cases observed to have hatched out, and to have reached the stage at which the pre-oral hood and the body formed two approximately equal portions. Some embryos at this stage were observed to exhibit a fairly active opening and closing motion of the two limbs thus forming (pre-oral hood and the body), suggesting that the relatively large development of the hood at this stage may have an important physiological function (respiration? attachment? nutrition?).

The discharge of the ova from the body and lodgment in the brood chamber can readily be observed. Throughout the whole breeding season of about 11 months eggs could be seen in the particular group under observation at any time, in one or other of the specimens, passing up the body cavity singly or in rows of usually about 6 or 8. If a specimen projecting over the edge of the stone (so as to allow of microscopic examination by transmitted light) be examined, the movement of the eggs upwards in the body can readily be observed. At each expansion of the blood vessel from below upwards the eggs or row of eggs was shifted a little further towards the nephridial opening, and on the contraction and emptying of the blood-vessel they were carried back again, though not so far. No evidence of any slow forward movement, such as might be caused by cilia, was apparent. In a typical case the eggs were observed to pass in this manner from the point in the body where it projected from the tube upwards to the nephridial duct in about 10 minutes. Here they became grouped together, remaining thus for 6 minutes. One of the eggs was then seen assuming an elongate slightly bent form (apparently entering the nephridial tube). It was then observed to travel upwards slowly and at a uniform rate inside the nephridial tube which was closely applied to the base of the lophophore. The nephridial tube was then apparently elongated, its opening being covered by the leaf-like part of the lophophoral organ so that on its escape from the opening of the duct the egg was safely carried upwards to the base of the brood pouch and took its place along with the others. It here again assumed a circular form, 0.22 mm. in diameter. Almost immediately after the discharge of the ovum by one nephridial duct the same process took place by the other duct, and so on alternately till all of the group of ova were discharged (in about 15 minutes).

At the upper end of the mass of developing eggs the larvæ were well advanced. In a larva which was observed escaping no trace of tentacles was seen (cf. Longchamps' observations (8)). In one or two cases the larvæ were observed swimming about freely, but

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retained by a bending in of the tips of the tentacles of the inner circle.

In the particular group of animals under observation nearly all the individuals carried eggs and larvæ when first found in the beginning of May. A few had them up to the end of June. On November 10th one specimen was observed to have an egg in the body, and by the 20th of the same month more than 90 per cent. had conspicuous clusters of eggs and larvæ in the tentacles. The comparatively sudden and simultaneous appearance of these was somewhat striking.

Soon all of the specimens bore eggs and larvæ, and this continued up to about the beginning of March of the following year, when a few were seen without them. By May 12th none of the group under observation had eggs. In some of the individuals which were more carefully watched a peculiar occurrence, for which I cannot suggest an explanation, was observed. The animal which had remained with body and lophophore with its egg mass fully extended for months, totally disappeared, leaving only the projecting tube. This seemed a confirmation of the suggestion of the annual dying off of the Phoronis. A few days (8–10) afterwards, however, the same animal was observed projecting (to a less extent) from the tube, but the lophophore was much smaller, the tentacles being only about twothirds their former length and without eggs.

Lophophoral Organ, Lophophoral Gap, Epistome.—From the observations just described on the method of discharge of ova, it is apparent that the projecting leaf-like fold of the lophophoral organ acts in such a way as to form a closed passage from the aperture of the nephridial duct to the brood cavity, the glandular part supplying the mucus in which the eggs are enveloped and bound together. The whole organ might be described, therefore, as a glandular oviducal furrow.

Contrary to what has been observed in other species, I have not found this organ absent in any specimen with eggs, though sections of a large number of individuals might show that this is true of P. capensis also.

The lophophoral gap between mouth and anus has received a good deal of attention, and there has been some speculation as to its function. It is a very striking opening in the circle of tentacles as seen in sections, but it does not exist as such in the expanded living animal, in which the gap is no larger than the spaces between the tentacles. This will be made clear from fig. 1, which is from the living animal. It seems quite out of the question that the inhalent current of water directed by the epistome escapes by this "gap" into the inner circle as has been suggested (Masterman (6)).

It is merely the point of origin of the tentacles, which in this region are of all sizes; two sometimes scarcely projecting have been seen at each side touching each other across the "gap," and following these 5 or 6 on each side rapidly increasing in length till they join the fully developed tentacles of the inner circle. These smaller tentacles on each side often overlap at their tips, preventing any wide opening between the regions of the inhalent and exhalent currents.

The contraction of these small tentacles and of the tissue in the neighbourhood of the gap, along with the approximation of the tentacles in preserved material, doubtless bring about the appearance of a large gap in sections of this region.

The epistome could be readily observed in the living animal in certain positions. In contrast to the other organs of the body it showed a constant and active movement. This occurred at its free edge. Observations were, of course, only possible when the lophophore was fully extended. In this condition the epistome was usually held back against the inner circle of tentacles, the mouth being widely open. Occasionally, however, the epistome descended over the mouth, closing or partly closing it. Various suggestions have been made as to its action, directing the currents of water (Masterman (6)), preventing a direct passage between mouth and anus through the lophophoral gap (Benham (2)). These, though quite justifiable deductions from a study of sections, do not seem probable in view of what has been noted above with regard to the behaviour of the animal in the living condition. So far as observations went, the function appeared to be the obvious one of closing the mouth, and its lateral extension on each side; it is doubtless also partly sensory.

*Circulation.*—Though the closed vascular system with red blood of Phoronis is one of its most striking characteristics, there is still some doubt as to whether there is actual circulation or merely oscillation of the blood. This is probably to be accounted for by the difficulty in obtaining accurate observation of the course of the blood. In a recent paper Enriques (5) describes a unique type of circulation which he has observed in *Phoronis psammophila*. He was enabled to examine the circulation microscopically by removing the animal from its tube by a method which he considers would not injure the animal to such an extent as to upset its normal circulation. Briefly, his conclusions are that there is an oscillatory movement of the blood plasma, and that, during this process, the

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corpuscles accumulate in the distal or lophophoral region, from which they are finally expelled by a strong contraction of the median vessel into the general vascular system, there being thus a circulation of blood corpuscles but not of plasma. I have also observed something similar to this in specimens of *P. capensis* which have been removed from their tubes, and also similar movements in the vascular system of individuals which have thrown off the lophophoral region, with the exception in this case, of course, that the blood corpuscles, while accumulating at the distal or regenerating end, cannot pass off again by a circulatory movement into the system.

I cannot but suspect that these interesting phenomena observed by Enriques, are mainly due to injury or irritation produced in removing the animal from its tube, and might be compared from their mechanical aspect at least to clot formation.

The method adopted in making the following observations was to select for microscopic examination specimens projecting over the edge of a piece of stone so that they can be examined by transmitted light. The animals sooner or later began to expand, often to a very considerable extent, and an account of their habit of occasionally rotating slowly in the tube, first in one direction then in another, presented different aspects of the vascular system. The method is rather tedious, but probably ensures normal results.

On the first protrusion of the tentacles, the movement of the blood was readily observed in a few, and, in full expansion, blood was seen to course up and down in all the tentacles. The intervals between such pulsation varied much (4–10 seconds). The inflow of the blood into the blood-vessels of the tentacles was slow, and apparently caused by pressure from behind; the outflow was more rapid and apparently caused by contraction of the vessels.

The inflow and outflow of blood was never synchronous in all the tentacles, but was irregular, though occasionally a few neighbouring tentacles showed pulsation at the same time. Each of the blind tentacular vessels opened into a common circular vessel in which the course of the blood was sometimes in one direction, sometimes in another.

Two such circular vessels were seen lying not far from each other. These were, however, not recipient and distributing vessels such as occur in *P. australis* (2), but were merely the single connecting or circular vessels of the inner and outer circle of tentacles. In both, the movement of the blood was to and fro without any regularity. The outer circular vessel was continued round on the oral side, but

the inner circle was interrupted at this point thus (()).

The blood flowed away from each side of the lophophore, from the right by a vessel which passed round by the oral region and joined that from the left to form the large vessel on the left side of the descending limb of the alimentary canal. In all these there was observed to be an almost continuous stream of blood downwards away from the lophophoral region.

As in some other species, the efferent vessel at a little distance from the lophophoral region gives off a number of blind vessels into the body cavity. These were occasionally very distinctly seen in the living animal, and were then observed to be contractile, receiving blood from the main vessel and expelling it exactly as in the case of the tentacular vessels.

The tentacular vessels apparently expelled the blood by contraction. It would be difficult to say if the circular vessels were contractile. The vessels by which the blood leaves the lophophoral region were not contractile (*i.e.*, the vessel on the left side of the alimentary canal and its two branches).

The centrally placed vessel between the ascending and descending limbs of the alimentary tract showed, however, a very marked contraction from below upwards. This was observed to occur, always in the same direction, through the entire course of so much of the vessel as could be seen (sometimes 10 mm.) under normal conditions, without removing the animal from its tube, in which case the movement was abnormal. A large volume of blood (corpuscles and plasma) was seen to be thus conveyed to the lophophoral region and to pass to either side by two short branches of the main vessel. Each of these branches opened directly into a vessel which seems capable of great expansion, and is lodged in a cavity of the lophophore very apparent in section. The blood passed into the tentacles in its immediate neighbourhood, and to the tentacles further removed by the circular vessels. There was no evidence of any true circulation through the tentacles nor of circular distributing and recipient vessels, the whole of the blood-vessels of the lophophoral region being merely a complex form of the simple blind vascular diverticula seen on the large vessel within the body. The greater part of the stream of blood thus never entered the tentacles, but passed on directly to the two branches of the efferent vessel which joined each other to form the single vessel situated in the left side of the descending limb of the alimentary canal. There was thus a true circulation, the blood being driven forward by a vessel lying over what in Phoronis corresponds to the dorsal aspect of the alimentary canal. On reaching the anterior end it passes by two vessels round the alimentary canal (cf. the "hearts" of annelids) which join to-

gether on the left side (ventral?) of the alimentary canal to form the efferent vessel. This passes downwards and joins the contractile afferent vessel, by which the blood is again driven through the same circle. Blind diverticula occur in the course of this vascular system, viz., the tentacular vessels, a group of vessels floating freely in the body cavity some distance below these, and finally a number of vessels penetrating the gonads at the other end of the body.

The intervals between the contraction of the dorsal vessel were very uniform in any one individual under observation, but varied much in different individuals. In some they were three seconds, in others as much as ten. They appeared also to differ in the same individual at different times.

If the movement of the blood be carefully observed in a favourable position of the animal it is found that after each contraction of the dorsal vessel is completed there is a very slight return of the blood in its upper part, the quantity returned however being infinitesimal as compared to the large volume passed upwards, and it is only in the upper part of the afferent vessel and carried forward again in the next flow. The same thing happens in the commencement of the efferent vessels. This may be expressed more definitely in the time observations in a particular case. Thus in one case the interval between the contraction of the dorsal vessel was ten seconds. In the afferent vessel the flow of blood continued from the first to the sixth second, in the seventh and eighth there was complete contraction and emptying of the vessel (both of corpuscles and plasma), in the ninth and tenth there was a slight return of blood in the upper part of the vessel. The efferent vessel was never without blood corpuscles. A more decided flow began in the second second and lasted till the eighth, and between such intervals there was a slight return.

The lumen of the afferent vessel is less than that of the efferent, but the proportions of blood corpuscles to plasma in each seemed the same. The peristaltic contractions of the dorsal vessel were always towards the free or lophophoral end of the animal in normal conditions.

In injured or regenerating animals there is an oscillatory or toand-fro movement of the blood in the afferent and efferent vessels, and often a crowding together of blood corpuscles into patches which remain stationary for a time in the free or distal region of the body.

# III.-PTYCHODERA CAPENSIS, sp. n.

I have from time to time, in shore collecting found specimens of this Enteropneust chiefly at or near low water, and generally in coarse sand or gravel. It appears to belong to a species not hitherto described, and, in recording its occurrence in this region, I add a brief description of its external features, which I hope to supplement at a later date by anatomical details and a figure of the animal.

The length of the specimens procured varied from about 80 to 130 mm. in the normal expanded condition. Individual specimens, of course, varied much at times when disturbed, but when left in fresh sea-water and coarse sand seemed to assume about the same proportion. The relative size of the various regions of the body did not vary much. Even the caudal region, which in other species has been found to vary so greatly, was in these specimens about the same proportionate length, probably owing to the fact that this species does not show the tendency to break up so markedly as in other species. Some imperfect specimens were procured, but they seem to have been injured in the securing of the animals. None of the specimens kept alive or preserved were observed to break up.

*Proboscis.*—The proboscis is of the usual size and shape. It was mostly somewhat longer than broad, egg-shaped, slightly tapering to the anterior end. When prying among the sand and shells, it was somewhat longer and often bent in various directions. A slight notch occasionally appeared on its posterior dorsal surface. In some conditions the longitudinal muscles of the proboscis were seen in distinct bundles.

The colour of the proboscis was pale chrome-yellow, uniform, except when this organ was expanded so that the longitudinal muscles appeared as distinct stripes.

Collar.—The dimensions of the collar were also normally fairly constant, its length being usually equal to that of the proboscis. Its breadth was slightly less than its length, being narrow in the middle. The free anterior margin was always somewhat folded. This region, which occupied nearly a half of the total length of the collar, was of a paler yellow than the succeeding part, which was in the form of a narrow ring. This was followed by a thin band of white pigment in the form of a circular streak, a little further back another thin band or yellow streak, and somewhat behind this, where the collar joined the body, another.

The collar often showed longitudinal corrugations thicker in the

middle, but none occurred between the two last-mentioned yellow streaks. No distinct circular furrow was seen in this region in the living animal.

In one living specimen, which happened to have the lip of the collar widely expanded, the two legs of the skeleton were seen lying at an angle of about 50° to each other. In the apex of the angle was observed what appeared to be a small opening—apparently that of the "notochord."

Genital Wings.-These were well developed both in length and breadth. Their greatest breadth was at the posterior end of the gills. It was, when spread out, a little over twice the length of the proboscis. The posterior extremity could not be exactly determined, as from this point they gradually diminish in size and lie alongside the hepatic coeca as mere ridges. The place of transition from distinct folds to ridges is about the middle of the hepatic coeca. Here also the brilliantly coloured gonads ended in most specimens. There was, however, no abrupt transition, as in some other species. The free edge of the genital wings are always in contact with each other where they join the collar. They are transparent throughout, in marked contrast to the gonads. Towards the body they meet each other above the intestine behind the gills, and this region is also clear and transparent. A fine genital streak (apertures of the gonads) occurs along the centre of each, and is of a dark reddish colour, the colour of the gonads themselves being a bright yellow. The genital folds usually met each other dorsally over the body, though often folded outwards, so as to expose the gills; their point of origin is the dorso-lateral region of the body.

Gills.—The gill region is comparatively small, being equal to the combined length of the proboscis and collar. This length did not vary in any of the specimens examined. In breadth it was fairly uniform till near the posterior end, when it abruptly tapered off to a point and was often observed to pass under the joined bases of the genital pleuræ, about one-seventh of its total length being thus hidden. At its widest anterior part it was about half the length of the proboscis. About fifty gill-slits or pores were counted in the deep furrow at each side of the gill. In the living animal the anterior of these were slit-like, being more than twice as long as broad. Towards the posterior part of the gill they became more circular, and the most posterior were almost circular, sometimes square. In preserved specimens all the openings were decidedly elongate.

Hepatic Coeca.—These are about sixty in number, and are arranged in pairs. Anteriorly they are less definite and more widely set

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apart, about twelve of them being between the genital folds, by which a few of the anterior of the twelve may be hidden. Further back they are normally in pairs, one on each side of the body opposite each other, but in extensions of the body they were often seen to interdigitate, thus alternating on each side. Posteriorly they gradually diminished, the whole length of the hepatic tract being about half the length of the genital ridge, or one-third of the tail region.

In colour the hepatic coeca varied considerably, being, however, always dark brown in the central region. Anteriorly and posteriorly they were more or less light in colour, sometimes pinkish.

Tail Region.—The tail region was a little over half the total length, and did not vary much in thickness, being about equal to that of the middle of the hepatic region, which was a little over half the diameter of the collar. The most prominent feature was the presence of three lines running along nearly the whole length of the upper surface, the central one of these being the dorsal nerve chord, and one on each side being a thin yellowish streak, which commenced about the middle of the hepatic region and continued to near the extremity of the tail. In other species in which such streaks are described they are situated in a groove which passes through the "islet" like cross-bands of glandular tissue. Here, however, these bands pass over them so that epidermal furrows were absent on the dorsal surface, one of the most distinctive external characteristics of this species.

On the ventral side the yellowish ventral nerve chord occurs, and interrupts the glandular patch throughout its whole course from the collar to the anus; in contrast to the dorsal nerve it thus lies in an epidermal groove.

On the dorsal side of the tail these glandular patches of the epidermis are of no great length transversely to the body, but on the ventral side they appear almost like annulations.

### SUMMARY.

(1) Phronopsis, a new genus of the Phoronidea, differing from Phoronis chiefly in having an involution of the epidermis with definitely differentiated (cubical) cells. The involution occurs below the nerve ring, which it partly covers; it passes round the body, encircling the mouth, anus, and nephridial apertures.

(2) Phoronis capensis, a new species, closely related to P. hippocrepia.

(3) In Phoronis capensis the following observations, some of

which are probably applicable to other species of Phoronis, have been made :—

a. Currents of water with food and other particles pass in between the outer and inner circle of tentacles towards the mouth. They pass out between the expanded tentacles, downwards between those of the outer row, and inwards and upwards between those of the inner.

b. Another current of water passes in succession over two special patches of nervous epithelium, the nephridial openings and the anal opening, and joins the last-mentioned current.

c. Most of the particles in the first current come in contact with the tentacles, and are carried on them to the mouth region; some of these are then carried back on the same tentacles on which they came and dropped off.

d. The two special patches of nerve tissue on the nerve ring are in a position with regard to currents of water similar to the palleal olfactory organ of Mollusca and probably exercise a similar function.

e. The nervous tissue at the commencement of the digestive tract appears from the definite rejection of particles after reaching this region to be an organ for the discrimination of food particles, and may be called an organ of taste.

f. The lophophoral gap between mouth and anus is in the living and expanded animal no wider than the spaces between the tentacles, and plays no special part in the passage of currents of water.

g. The projecting free part of the lophophoral organ is relatively large and leaf-like in life, and in discharge of ova overlaps the nephridial opening conveying the ovum to the brood cavity in the tentacles. The more glandular part probably supplies the mucus in which ova and embryo are enveloped. The whole organ may be called a glandular oviducal furrow.

h. The blood (corpuscles and plasma) in the normal condition of the animal passes successively through a median (dorsal?) vessel, two circumœsophageal dilatable vessels, a lateral (ventral?) vessel, and on again to the median vessel. That is, in these vessels there is a true circulation which, however, becomes oscillatory or partly so under abnormal conditions.

*i*. The movement of the blood is oscillatory (to and fro) in the vascular diverticula of the tentacles, the body cavity and the gonads. It is also oscillatory in the small circular vessel at the base of the tentacles.

j. Reproduction may take place throughout the year, but is much more marked in the summer months.

k. This species does not die off annually.

(4) Ptychodera capensis, a new species of the Enteropneusta.

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### EXPLANATION OF PLATES XVI., XVII.

FIG. 1.—*Phoronis capensis* in nearly complete expansion. The eggs are indicated in the inner circle of tentacles, the jaculatory movement of tentacles by a bent tentacle on the left, the nerve ring by white lines, and the digestive tract by a longitudinal white band.

FIG. 2.—*Phoronopsis albomaculata*, viewed from above (from a photograph of the living animal in complete expansion).

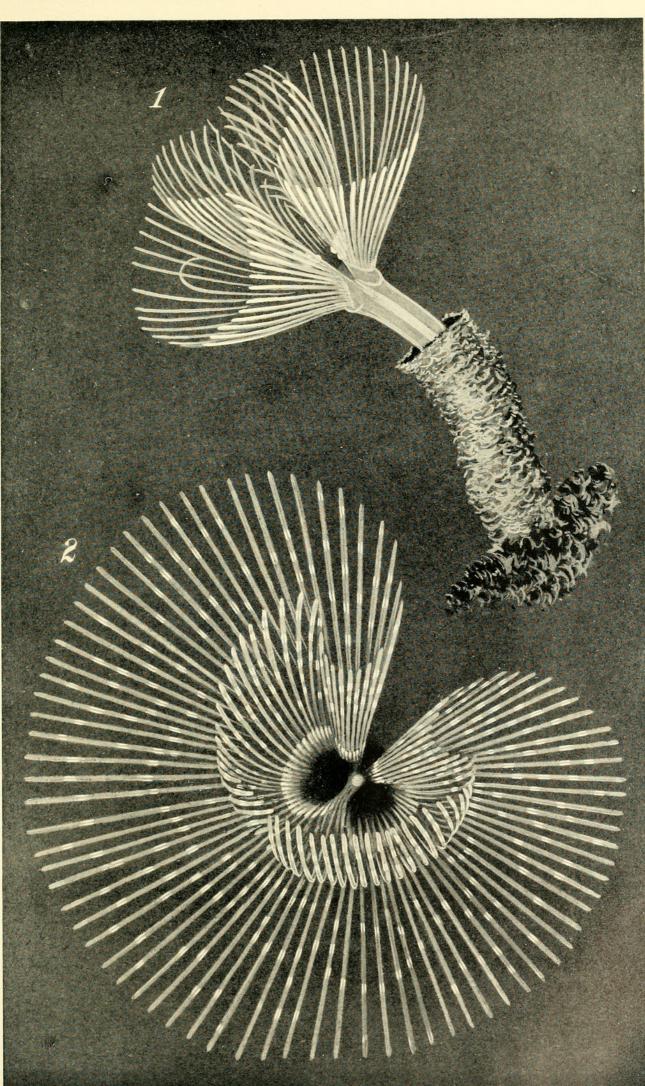
FIG. 3.—Longitudinal section of *Phoronopsis albomaculata* (specimen B), showing fold of epidermis and nerve ring. *bl.* Blood-vessel. *bt.* Basement tissue. *ep.* Epidermis of body. *ep'.* Modified epidermis of fold. *eps.* Epistome. *int.* Tangential section of wall of intestine. *lo.* Lophophoral organ. *n.* Nervous tissue. *neph.* Section of duct of nephridium.

FIG. 4.—Enlarged view of nerve ring with epidermal fold shown in fig. 3. bt. Basement tissue. coe. Coelomic epithelium. ep. Epidermis of body. ep'. Modified epidermis of fold. n. Nervous tissue. neph. Section of duct of nephridium. ts. Transverse septum.

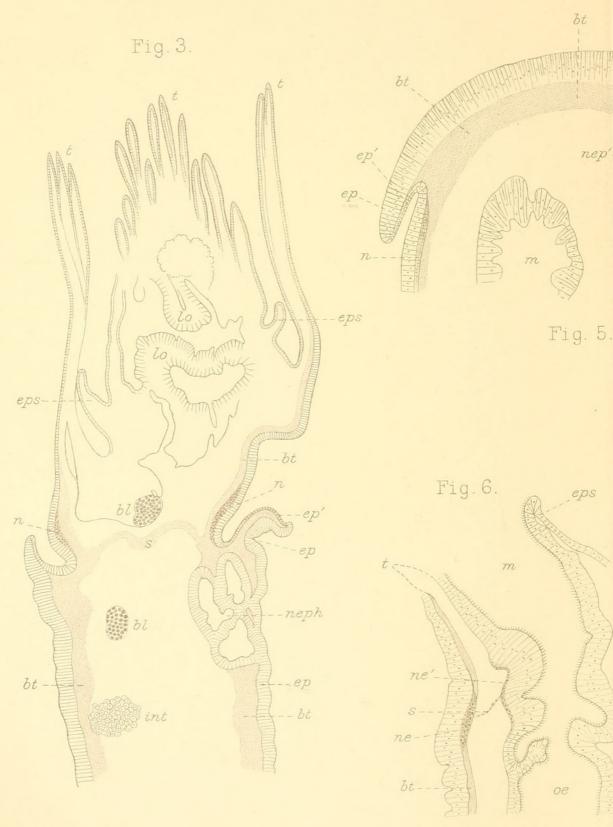
FIG. 5.—Transverse section of *Phoronopsis albomaculata* (specimen A). The section is in reality oblique, as the organs of the left side were at a lower level than those of the right. Figuring as in Fig. 4 with the addition of a. Anus. m. Mouth. nep'. Cells of internal opening of nephridium.

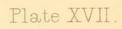
FIG. 6.—Median longitudinal section of *Phoronis capensis*. b.t. Basement tissue. *eps.* Epistome. *m.* Mouth. *n.e.* Sub-epidermal nerve tissue of nerve ring. *n.e'*. Nerve tissue near mouth (organ of taste?). *oe.* Œsophagus. t. Tentacle.

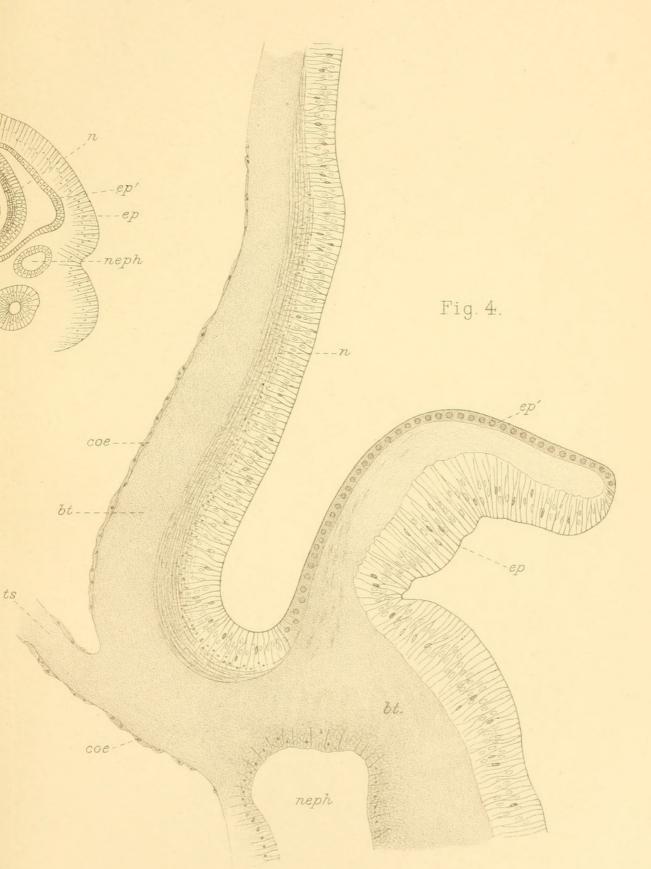
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