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XXXIV.—*Preliminary Notice of Cephalodiscus, a new Type allied to Prof. Allman's Rhabdopleura, dredged in H.M.S. 'Challenger.'* By Prof. M'INTOSH, F.R.S.*

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A SHORT time ago Mr. Murray, Director of the 'Challenger' Expedition Commission, drew my attention to an anomalous organism which had been relegated to the Annelida; and though on examination it proved to be an ally of *Rhabdopleura*, Prof. Allman and Prof. Busk (both of whom had arrived at the same conclusion in regard to its systematic position) most kindly and disinterestedly insisted on my describing it, especially as *Phoronis* had just been the subject of investigation.

This remarkable form was dredged at Station 311 (in the Strait of Magellan †), January 11, 1876, in lat. $52^{\circ} 50' S.$, long.

* Communicated by the Author, having been read (with accompanying drawings) at the Southampton meeting of the British Association, August 1882.

† The Strait of Magellan appears to harbour several mollusoid rarities. Thus the remarkable *Goodsiria coccinea* of Prof. R. O. Cunningham (Trans. Linn. Soc. vol. xxvii. p. 489, tab. 58. fig. 3) is a social Ascidian with an elongate (above 2 feet) lobed, rooted, fibro-gelatinous mass of a vivid scarlet colour, "remining one in some measure of the fleshier Alcyonoid polyps," in which minute flask-shaped animals are imbedded in circumferential cells. The animals are about a line in length, and, so far as can be made out from the sketches, appear to be social Ascidians. From the same neighbourhood the curious *Pyura Molinæ* of Blainville also comes.

73° 53' W. Depth 245 fathoms. Bottom-temperature 7°·7 C. Sea-bottom composed of mud, which seemed to be fairly rich in other groups.

At first sight the flexible structure may readily be mistaken for a seaweed, since it is composed of a much-branched fucoid tissue tinged of a pale brownish hue and semitranslucent. Moreover the whole surface of the thickish stems is hispid with long spinous processes of the same tough secretion, and perforated here and there by somewhat large apertures with smoothly rounded edges. A more minute inspection reveals various opaque bodies in groups in the interior of the branches; and the appearance of these suggested the relationship of the structure to the Polyzoa or Ascidians. Prof. Busk, however, pointed out its distinction from the ordinary Polyzoa, and Prof. Herdman had stated that it was not an Ascidian. The following description is drawn up from a few fragments and three excellent slides mounted by Prof. Busk. Other points will probably be made out on the arrival of the larger examples, which have not yet reached me.

The cœnocœcium or polyparium of *Cephalodiscus dodecalophus** consists of thickish, irregularly rounded or flattened stems of the consistency of soft seaweed, and having a slight lustre like the semitransparent tubes of many annelids. The stems have a diameter varying from 4 or 5 millim. to double or treble that breadth in the flattened expansions; but the general size of many of the branches is nearly uniform. The main trunks seem to have arisen from submarine objects, such as stones or sponges; but instead of standing erect like soft Gorgonians, to which the inosculation of the branches give them some resemblance, they appear to have been more or less horizontal, since pillars of the tissue occasionally pass, like aerial roots, from the underside to the plane of attachment. The surface of the branches is everywhere studded with elevations and ridges, which terminate in long spines—simple, bifid, trifid, or multifid, and here and there bending downward to join the main stem, so as to form loops or arches, or inosculating with adjacent spines. Some of the spines are very large, and project far beyond the others, and occasionally they occur in groups. They generally taper a little towards the tip, which is often attenuate and of a deeper brownish hue than the rest of the cœnocœcium. The tips of the branches often show longer spines variously divided. The irregularity in regard to the distribution of the spines recalls the processes on the curious *Chondrocladia*, though it is much more marked than in the latter. All the spines are hollow

* κεφαλή, head; δίσκος, disk; δώδεκα, twelve; λόφος, plume.

and in connexion with the canals and cavities of the coenœcium.

The surface of the polyparium, moreover, is dotted, especially at the bases of the spines, with large rounded apertures, which lead into the interior of the stem, the latter being honey-combed from end to end by an irregular system of wide canals and cavities intersected by bridges and arches, which thus provide for the constant ingress and egress of sea-water throughout the entire system. The inner surface of these canals and chambers is as smooth and glistening as the outer, the secretion being perfectly homogeneous and evidently the product of the inhabitants. It cuts with great readiness and as cleanly as a soft *Fucus*. Microscopically it consists of numerous layers of a translucent and very fine membranous secretion, the sheen or lustre being doubtless due to this arrangement. The whole disposition of the tissue points it out as the secretion of the polypides, just as much as the tube of an annelid or *Phoronis*, the more regular and less bulky coenœcium of *Rhabdopleura**, and, it may be, the shell of a mollusk. Like the annelidan tubes it most approaches, it is little affected at first either by nitric acid or caustic potash, though the former by and by somewhat softens and bleaches it. This secretion of *Cephalodiscus* is paralleled by the curious investment or "house" of *Appendicularia*, and is therefore probably, like it, the homologue of the Ascidian test. The "house" has two funnel-shaped apertures, supported by a fibrous trellis-work, leading into the cavity containing the body.

It is not a matter for surprise that creatures so minute should secrete so conspicuous a home for themselves, or that it should preserve the algoid or zoophytic outline, especially when the productions of sponges and other forms are remembered, or when we reflect that even a transparent structureless fluid inside a smooth capsule (as in the Nemertean stylet-pouch) can produce, in countless examples of each species, precisely the same form of solid crystalline stylet. The enlistment of numbers in the present case supplies any deficiency likely to arise from minute size. The peculiar shape of the coenœcium, moreover, has probably been found that best adapted for the preservation of the animals, by its resemblance to the seaweeds in its neighbourhood, on the one hand, and, on the other, by its affording complete aeration, abundant supply of food, and security to the little architects and their delicate plumes.

In the interior of the cavities and canals of the semitransparent coenœcium numerous opaque masses (the polypides) and

* *Rhabdopleura Normani*, Allman, and *R. mirabilis*, Sars.

large ova are situated. The former often occur in groups, each individual, however, except in the case of buds, being perfectly free, at liberty to wander anywhere along the chambers or externally through the apertures. In some cases they are packed closely together in the cavity: but such may have been due to the condition on immersion in spirit; for thin partitions, bridles, and pillars of the transparent coenœcium often separate the individuals. Moreover, in turning out the latter, an operation performed with ease, owing to the friability of the coenœcium, at first sight it may almost be fancied that an ovigerous envelope containing embryos is before us, so remarkable is the profusion of eggs and animals, and apparently so active is the reproductive function. The aspect of the adults and their caudal buds, the proportionally large size of the ova, and other features, however, negative such a supposition.

Each adult polypide (and they are somewhat uniform in size) measures, from the extremity of the cephalic plumes to the tip of the pedicle, about 2 millim.; and of this length the body proper (that is, from the buccal disk to the posterior bulbous region above the pedicle) is rather more than 1 millim. The body in most is bean- or kidney-shaped, generally more rounded and bulbous posteriorly, since there is a tendency to a forward curve before the pedicle comes off. The dorsal surface is smooth and convex, a slight lateral constriction being evident just behind the anterior region bearing the red pigment-spots. The posterior end is generally bulbous and prominent; and in many a slightly elevated median ridge leading to the anus is evident. As the pedicle is often curved forward or projected outward at a small angle to the body, the ventral surface is comparatively short; indeed, in those which are much bent the base of the pedicle touches the buccal disk. This contour of the body is interesting in relation to the oblique direction of the cup-like body of *Loxosoma*. When the pedicle is extended the ventral surface is nearly straight and continuous with the pedicle, which leaves the body at the ventral edge, while the kidney-shaped mass of the body projects dorsally. The pedicle is shorter than the body, nearly cylindrical, and terminates apparently in a rounded end; it is marked ventrally by various longitudinal striæ from the muscular bands.

The anterior region of the body curves somewhat suddenly downward and backward, and forms a flattened surface on which the great buccal disk rests. On the ventral surface are two large and conspicuous pigment-spots or eyes, which are placed a little in front of the anterior margin of the oral

lamella, and in ordinary preparations are wholly covered by the disk. They are circular or irregularly rounded, of various shades of reddish brown, with occasionally a tinge of violet. In transverse section the eyes show a pale centre or a large clear globule, with an external ring of dark brownish cellular pigment. They lie over the ovary, and in dissection often remain attached to the eggs. They would appear to be mainly of service to the animal during the protrusion of the buccal disk and plumes. This form thus shows in the adult state what Prof. Vogt and Dr. Barrois found in the embryonic *Loxosoma*; for in the latter the double disk-like organ is connected with two eye-spots.

The great buccal disk forms a thin plate with two slight and generally bilaterally arranged elevations in the centre anteriorly, and divided into two regions by a notch at each side, the anterior moiety being the larger and thicker. The surface of the latter is marked by an arch of brownish pigment-grains, which are densest in the centre of the curve, and shade off gradually on each side; while a very conspicuous and well-defined brownish-red band commences in the posterior division at the notch, and runs with a backward curve to the opposite side. Between this and the posterior margin a brownish pigment-belt (less developed than that in front) occurs. The two bands just mentioned form when complete a somewhat flattened ring. In many specimens, however, the brownish pigment is entirely removed by the spirit, leaving only the well-defined reddish posterior band. In transverse section the external or ventral surface of the disk is formed of finely granular and rather firm hypodermic tissue, closely marked with vertical striæ. As we pass deeper (*i. e.* towards the dorsal surface) there is a tendency to form cells; while near the dorsal margin ovoid granular cells are very evident. These gland-cells are tinged in this region of a brownish hue by transmitted light. A basement-layer, possibly with a few muscular fibres, intervenes between the thin median hypoderm and the free parts of the disk on the dorsal aspect. The structure of this organ accords in most respects with the careful researches of Prof. Allman on the organ in *Rhabdopleura**. It seems chiefly to be a glandular hypodermic structure with discerning powers of great activity, probably in relation to the remarkable cœnœcium.

This disk differs from that in *Rhabdopleura* by its much greater size and its thickness. In the form just mentioned the organ is more nearly allied to the truncated and thickened opercular process of certain annelids; while in *Cephalodiscus*,

* Journ. Linn. Soc. Zool. vol. xiv. p. 585.

instead of forming a mere anterior appendix, it overlaps the adjoining parts to a great extent. In *Cephalodiscus* it is attached to the anterior end of the body, in front of the mouth, by a central pedicle, but its broad scale-like margin is quite free all round and can readily be raised. Transverse sections show that the pedicle of the organ has three main pillars, viz. two lateral and one central. The outer surface of the lateral is covered by the hypoderm continued from the dorsal surface of the disk, and which passes to the basal region of the branchiæ. Beneath the basement tissue, under the foregoing, strong bands of muscular fibres pass along each side of the pedicle to radiate into the outer region of the disk. The central pillar is composed mainly of what seems to be elastic tissue, which is continued upward to a granular glandular area, which fills the space between the ovaries. The upper region of the latter space is angular, the lower convex and rounded, and having the foregoing pillar connected with the elastic tissue which bounds the entire area. The central region of the latter is filled with granular glandular tissue, and probably is an anterior process of the buccal region. Whether any space exists on each side of the central pillar or lamella is an open question; but in some of the preparations a finely granular substance like coagulated fluid occurs.

Attached to the posterior part of the disk, and apparently running from edge to edge so as to become connected with the broad apron-like lamella on each side of the mouth, is the basal tissue of the plumes, most of which remain fixed to the disk on its removal, only one or two clinging externally to the margin of the lamella. This basal collar is tinted of a brownish hue by transmitted light; and twelve plumes* arise almost in linear series from its dorsal edge, six on the one side of the median line and six on the other. The plumes are nearly of uniform size, and consist of a central stem, slightly crenate posteriorly, and furnished with a series of longitudinal muscular fibres; while distally it has a peculiar bulbous enlargement, which at first sight resembles the tip of certain medusoid tentacles, bristling with dart-cells and pigment. The rugose appearance, however, is due to large gland-cells containing granules and globules; and the tissue seems to be a further development of the somewhat large hypodermic granules of the tips of the pinnae. The bulbous end of the stem shows a rather regular disposition of these cells and globules, in transverse section, especially at the circumference; indeed the appearance of such a section recalls that of the

* Hence the specific name *dodecalophus*.

tip of a tentacle of *Coryne* or the spine of an Echinoderm. The ventral surface and sides of the stem are rendered plumose by a large number of long slender filaments having slightly bulbous extremities, and with a linear streak from base to tip, apparently from a groove, though traces of a septum also occur. These pinnæ apparently do not taper, and for the most part, in section, are composed of granular hypoderm with a few brownish pigment-cells. It is probably the latter which give in some a light pinkish or pale violet blush to the feathery plumes, which in life must have been finely tinted; and it is further interesting that the same pigment occurs in *Rhabdopleura*.

The arrangement of these numerous tentacular plumes wholly differs from that in *Rhabdopleura*, in which they form two symmetrical tentacular arms from which the pinnæ spring. Both the latter and the new form widely diverge from the ordinary Polyzoa in this respect, both having very mobile pinnæ that curve gracefully in all directions, instead of the somewhat stiffish corona and straight tentacles of the other Polyzoa. In *Cephalodiscus* they are probably of great tactile service; but there is little evidence from their minute anatomy in support of their branchial function, at least of the ordinary kind. They thus present a much more elementary structure than in *Phoronis*. They do not appear to be of much value as exciters of food-currents, as Prof. Lankester suggests in the case of *Rhabdopleura*; at least they could only produce currents in the cavities of the cœnœcium without special reference to the mouth. Both *Rhabdopleura* and *Cephalodiscus* differ from the ordinary Polyzoa in the absence of the tentacular web at the base. Both have very long pinnæ; but the new form excels *Rhabdopleura* in this respect. *Cephalodiscus* also diverges in regard to the thin postoral lamella, which, instead of being a simple triangular peak on each side, as in *Rhabdopleura*, forms a free apron-like process. Moreover it is not simply continuous with the tentacular arms as in *Rhabdopleura*, but the broad lamella seems rather to arise at each side, at the point of insertion of the basal tissue of the plumose arms, and it is boldly curved outward therefrom. The oral region thus has a different environment from that in *Rhabdopleura*, though the plan of structure is not very divergent. The distinct circular aperture of the mouth lies in the middle line at the anterior margin of the foregoing lamella, and is thus concealed between the opposed surfaces of the latter and the disk; and if these are ciliated, their influence on the conveyance of food into the aperture must be considerable. The oral lamella in some preparations passes straight up to the sides of the mouth

and forms a transverse margin anteriorly. The edges of the mouth are slightly raised laterally and posteriorly, the latter often being spout-shaped; anteriorly it is devoid of any well-defined boundary, and leads directly upward into the alimentary canal.

There are no special organs in connexion with the mouth, which leads by a canal with frilled walls into the stomach, situated on the ventral surface of the body. At the posterior end of the latter the intestine turns upward and advances along the dorsum, to open by a large anus on the anterior projection of the body behind the plumes. No part of the alimentary canal enters the pedicle. In minute structure the canal resembles that in the Nemerteans, the first or pharyngeal region, however, being perhaps less firm than the gastric. The folds of the latter show numerous and somewhat regular vertical streaks and granules from the arrangement of the gland-cells; indeed the smooth, firm, gastric ridges have a characteristic granular striated appearance. The canal throughout has proportionally thick walls. Externally is a firm investment, probably containing muscular fibres. Internally the surface seems to be covered by a fine limiting membrane, through which the contents of the glands have in many cases escaped. In the interior of the stomach are cellulo-granular matter, grains of sand, minute spicules, and bodies resembling minute *Thalassicollidæ*. The canal agrees with that in *Rhabdopleura* in having no differentiation into regions as in the Polyzoa proper. It is probably ciliated during life, after the manner of canals of similar structure.

The body-wall is composed externally of a thin hypodermic layer (for no distinct cuticular coat can be demonstrated in the preparations), within which is the elastic coat, bounded internally by the longitudinal muscular layer. The wall is much attenuated over the distended ovigerous region anteriorly. There is no other investment of the alimentary canal than the foregoing wall, which is probably homologous with the "thin glassy skin" of Sars, surrounding the digestive canal in *Rhabdopleura*. As with the latter, the preparations give no evidence of perigastric fluid.

As previously mentioned, the short ventral surface of the body is continued into the cylindrical pedicle, whereas the dorsal outline rises abruptly above the pedicle. The stomach and the dorsal curve of the intestine would alone require considerable space. The hypoderm on the ventral surface of the body appears to be somewhat thicker than on the dorsal, and in the preparations is generally thrown into bold transverse wrinkles, evidently from the strong muscular

fibres passing from the oral region backward to the pedicle. The same hypodermic layer covers the latter, which is likewise ringed all round by rather regular transverse furrows, the coat, moreover, being thicker dorsally than ventrally. Within the foregoing is a thick elastic coat continuous with that on the body, and which in a line with the narrow (ventral) margin is bent inward at a sharp angle, so as to form a longitudinal ridge along the pedicle. Internally are numerous bundles of longitudinal muscular fibres, which are especially dense on each side of the ridge. In longitudinal sections these fibres form large coarse fasciculi; and their origin is as in *Rhabdopleura*, viz. near the oral region. In transverse sections the centre of the pedicle is occupied by a little connective tissue and granules, and there does not seem to be evidence of a distinct canal. At the tip, however, in longitudinal sections a central cavity is sometimes seen—containing cells and granules, and which may be homologous with the peduncular gland of *Loxosoma*. The buds arise from the latter region, often from the ventral aspect. It is interesting that Prof. Allman found at the end of the funiculus of *Rhabdopleura* a somewhat reniform dark-brown body, which he considered a statoblast. The spot from which the buds arise in *Cephalodiscus* is likewise towards the tip. No trace of a nervous system was observed.

In most of the specimens a pair of large rounded whitish masses conspicuously distend the body-wall anteriorly under the eyes; and, indeed, one or other of the latter generally clings to the undeveloped ova adjoining it. In transverse section through the ovary one of the ova is found to be considerably larger than the other, often twice the size; and thus the outline of the body is asymmetrical. Each shows germinal vesicle and spot, and is surrounded by a transparent investment. Moreover each has developing ova of various sizes abutting on it ventrally; and since the extension of the large ova is mainly external, the smaller ova and their clear globules are compressed towards the middle of the body as well as ventrally. A fine membrane (ovisac?) appears to surround the large and the small ova in common, while each of the latter has its own hyaline investment. On extrusion (whether by anus, mouth, or otherwise is yet unknown) the large and somewhat pyriform ovum is provided with a well-formed pedicle of the transparent investment—truncated at the extremity for attachment. An ovum is occasionally found amongst the tentacular plumes, as in *Phoronis*, with its swarms of minute eggs; but such is probably accidental. The ova are filled with the usual granular contents, and each is

attached to the wall of the chamber by the pedicle ; but many seem to have become detached and lie loose in the cavity. The products of these ova are yet unknown, though in all probability they are motive embryos which would carry to fresh sites the construction of the cœnocœcium. Their comparatively large size recalls the condition in the *Artisca*, in which the great ova produce embryos about a third the size of the adult.

Prof. G. O. Sars found in *Rhabdopleura mirabilis* (between the dorsal wall of the gullet and the anal region) a clear cellular body, in which several nuclei were visible. He was of opinion that it could scarcely be a nervous ganglion, since it did not lie in the substance of the body itself, but only within the external skin. There would seem to be little doubt that this cellular body in *Rhabdopleura* is the homologue of the ovary in *Cephalodiscus*.

The large ovigerous bodies over the eyes appear to be the homologues of the remarkable organ which occurs on the dorsal side of the œsophagus in the young *Pedicellina* (and which, according to Dr. Hatschek, is mesoblastic), and more especially of the double organ of the same kind described by Prof. Vogt and Dr. Barrois in the embryo of *Loxosoma*. The lamented Prof. Maitland Balfour was in doubt about Dr. Hatschek's interpretation of the remarkable dorsal organ as a bud, since, "owing to the deficiency of our observations on the attachment of the larva, this suggestion has not received direct confirmation ; yet the relations of the dorsal organs in *Pedicellina* and *Loxosoma* respectively strongly confirm Hatschek's view of their nature"*. The very great development and unequivocal condition of the double organ in *Cephalodiscus* place the subject in a fair way for solution. There cannot be much doubt as to their being ova in this form, while, again, the great distance from and independence of the actual buds on the distal end of the pedicle negative any close relationship between them. It is also worthy of note that in *Cephalodiscus* the eye-spots are so closely related to the surface of these organs that they are generally removed with them in dissection. It is further interesting that the buds in *Loxosoma* arise from a region corresponding more or less to that containing the foregoing ova in *Cephalodiscus*, and not from the pedicle. The objection of Prof. Allman † to Oscar Schmidt's view that the apparent buds in *Loxosoma* are really detached from the ovary and developed on the body of the parent is clearly shown to be right, not only because the immature buds

* Comparative Embryology, i. p. 245.

† Journ. Linn. Soc., Zool. xv. p. 2.

both in *Loxosoma* and *Cephalodiscus* bear other buds, but because the position of the large ova in the latter cannot be confounded in any respect with the buds either in their early or subsequent stages.

No differentiation was noticed in regard to sexes; and there seems to be no dimorphism of the zooids, as in Prof. Ehlers's remarkable burrowing form (*Hypophorella expansa* *). Nothing is more striking, however, than the profusion of buds and the abundance of ova, one of the chief ends of the species apparently being propagation. The chambers of the cœnœcium are loaded with the large ova; and almost every adult bears one or more buds attached near the tip of the pedicle.

The early buds consist of minute and somewhat pale clavate or pyriform bodies attached by the narrow end to the pedicle. They are situated either on or near the tip. Very soon the pedicle is differentiated from the disk, the young animal consisting of a large, flat, and somewhat thick disk and a short, broad, and sometimes crenate pedicle attached to the parent. The disk is shield-shaped, broader distally than proximally. Two ovoid opaque thickenings are observed dorsally. The hypoderm of the bud resembles that of the adult. At this stage no trace of the tentacular plumes exists.

As development proceeds the anterior or disk-bearing region of the body increases much more in proportion than the posterior. The disk is rapidly enlarged, and shows traces of the broad arch of pigment anteriorly and the reddish band posteriorly, as well as the two median elevations on the ventral surface. The posterior moiety of the disk is especially large. Moreover the body superiorly begins to project outward, and first one or two and then four or five rounded papillæ indicate the commencement of the tentacular plumes. These papillæ form a slightly curved row in front of the dorsal projection of the body.

In the next stage the disk is almost completely formed, though of smaller size and thicker than in the adult. The pigment bands are well developed. So little has the pedicle advanced, that the free posterior margin of the disk almost touches the pedicle of the parent to which the bud is attached. The anterior dorsal projection of the body has greatly increased, forming a large rounded boss. The tentacular or branchial plumes are now more numerous; and form an irregular and prominent double row from side to side above the disk. The short pedicle almost immediately follows the anterior dorsal projection of the body; and as a peculiar bending of the latter has now taken place, the tip of the pedicle hardly

* Abhandl. der königlichen Gesellschaft der Wiss. zu Göttingen, 1876.

projects beyond the margin of the disk. The tentacular plumes soon exhibit a symmetrical series of filaments on each side, the general outline of each process being still abbreviated and rounded. Shortly after this stage the bud separates from the parent (the plumes being still small). The pedicle is fairly developed; and as soon as it is detached (and sometimes before) a little bud appears near the tip. The pedunculated bud in *Rhabdopleura* somewhat resembles this form, though the tentacular plumes greatly diverge.

Cephalodiscus thus differs from *Rhabdopleura* in regard to the coenœcium, in the much greater size of the buccal shield, in the remarkable branchial or tentacular plumes, in the structure of the pedicle, and in the perfectly free condition of the polypides.

Cephalodiscus and *Rhabdopleura* agree in the absence of the calyciform membrane connecting the bases of the tentacles, in the position of the mouth, which opens ventrally behind the buccal shield, in the general structure of the alimentary canal, and in the position of the anus. The development of the young buds is similar. Both connect the ordinary Polyzoa with *Phoronis*.

Cephalodiscus naturally falls under Prof. Allman's section Polyzoa Aspidophora, and further demonstrates the correctness of that author's opinion in regard to the systematic position of these anomalous forms. Prof. Lankester's designation "Pterobranchia," as applied to *Rhabdopleura*, is less suitable than the foregoing.

CEPHALODISCUS, n. g.

Coenœcium consisting of a massive, irregularly-branched, fucoid secretion resembling chitine, hispid with long spines of the same tissue, and honeycombed throughout by irregular apertures, channels, and spaces, in which the separate and independent polypides occur singly or in groups.

Lophophore richly plumose, with an enormous buccal shield and large oral lamella, the mouth opening between the two. Anus on the anterior dorsal prominence, behind the plumes. Two large eyes abutting on the ovaries. The homologue of the funiculus is short and quite free, its tip serving for the development of buds.



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