XIX. On the Structure and Development of Myriothela.

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GENERAL DESCRIPTION.

Myriothela, of which we have as yet no satisfactory evidence of more than a single species being known, consists of a solitary attached hydranth, carrying near its proximal or attached end the blastostyles or appendages which give origin and support to the gonophores (Plate 55).

Full-sized specimens (fig. 1) measure, when extended, nearly 2 inches in length. They are then cylindrical in form, with the mouth occupying the summit of a short conical hypostome, behind which the tentacles commence, and thence extend over somewhat more than one half the entire length of the body; while the proximal end of the body is bent at right angles to the rest, is invested with a chitinous perisarc, and gives origin to short sucker-like processes of attachment.

For some time after the animal has been removed from the sea and placed in the confinement of our jars, the tentacles will present the appearance of short papilliform processes (fig. 3). This condition, however, is that only of the tentacles in a state of contraction. When fully extended their form is very different; for they then attain a length of nearly half a line, and present a thin cylindrical stem, terminated by a large spherical capitulum, very well defined and distinct from the stem (fig. 2). In this state the tentacles are kept in constant motion, the animal perpetually depressing them and elevating them with a peculiar jerking action.

The tentacles are very numerous; upwards of two hundred may be counted in a single hydranth. For the greater part of their extent they are set close to one another; but as they approach their proximal limit they not only become smaller, but are separated from one another by greater intervals. Almost every tentacle carries a small purple pigment spot on its summit.

The hydranth when contracted (fig. 3) becomes club-shaped or conical, and the tentacles then pass into the state of short, thick, imbricated papillæ.

The contractility of the hydranth exists chiefly in the tentacular portion. In all that portion which carries the gonosome the contractility is much less marked. In the tentacular region the contractility is shown not only in the great extent to which this part of the hydranth can elongate and shorten itself, but in the loops and contortions, like the writhings of a worm, into which, when fully extended, it frequently throws itself (fig. 11).

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The blastostyles (a, a, a, a) spring from that portion of the hydranth which lies immediately below the tentacles. They form a dense group, surrounding the body on all sides. They are usually somewhat clavate, or of an elongated fusiform shape, but are very contractile and vary much in form. Towards their free extremity they carry several small scattered capitate tentacles; and at the proximal side of these are the gonophores (b, b, b), which belong to the type of simple sporosacs, and are large, of a globular form, and carried on very short peduncles, which spring without any regular, arrangement from the sides of the blastostyle.

From the same part of the body there also spring numerous very extensile filiform organs resembling tentacles (c, c, c). These arise for the most part close to the base of a blastostyle, where they occur mostly in pairs, though sometimes singly. They terminate distally in a truncated sucker-like extremity. It will be afterwards seen that these organs, which have been hitherto entirely overlooked, perform an important function in the economy of the animal. I shall designate them by the name of "claspers."

The section of the body from which the blastostyles and claspers spring is usually somewhat swollen, and is marked by close longitudinal shallow furrows. After continuing naked for some distance beyond the proximal limit of the gonosome, the body bends at right angles to itself, becomes clothed with a chitinous perisarc (d), and fixes itself by the extremities of short truncated processes (e) to some solid support.

The general colour of the animal is a pale straw-colour. The tentacles are almost all tipped with a brownish-purple spot, the same colour sometimes extending over the greater part of the tentacle, and generally also spreading in clouds and streaks over the tentacula-bearing portion of the body. The gonophores are of a dull white, with their distal poles encircled by a ring of purple pigment dots.

The genus Myriothela was instituted by Sars for an animal which he obtained off the coast of Norway, and described under the name of Myriothela arctica*. He has given an accurate, if not altogether adequate description of its external characters, and has correctly referred it to the Hydroida. Mr. W. Stimpson, however, has pointed out † that the Myriothela arctica of Sars is identical with an animal which Fabricius, in his 'Fauna Grænlandica,' has described under the name of Lucernaria phrygia, and for which De Blainville afterwards constituted a new genus, to which he assigned the name of Candelabrum. De Blainville, however, though he could have no difficulty in seeing that Fabricius's animal was not a Lucernaria, had notions of its affinities even less exact than those of the celebrated author of the 'Fauna Grænlandica.' He could see no relations between it and the Cælenterata, and asserts that its affinities are with Sipunculus.

If the laws of priority were rigidly enforced, SARS's name must yield to that proposed by DE BLAINVILLE; but as it is plain that DE BLAINVILLE knew nothing of the animal

^{*} SARS, Zoolog. Reise i Lofoten og Finmarken, 1849.

[†] See Agassiz, Cont. Nat. Hist. U.S. vol. iv. p. 341, note.

and was totally mistaken as to its affinities, while SARS, evidently unaware that the animal had been previously noticed, had an accurate conception of its true zoological relations, the name of *Myriothela* may fairly be accepted without any violation of the spirit which ought to regulate biological nomenclature. And though no less an authority than Prof. Louis Agassiz has felt himself compelled to restore De Blainville's name, I believe that further confusion will be avoided, and no injustice done, by adopting the later designation of the genus.

It is quite possible that the existing accounts of *Myriothela* include more than one species. At present, however, we have no evidence which would satisfy us in asserting that more than a single species has been observed; and the specific name assigned by Fabricius to the first known example of the genus must accordingly be accepted.

SARS'S description is entirely confined to the external characters of the adult; and the first account which takes us beyond these is given by Mr. Cocks*, who describes the young locomotive stage which he saw developed from specimens obtained on the coast of Cornwall. Mr. Cocks's observation has been confirmed by Mr. Alder, who, however, has left us no published account. Mr. Hincks, from an observation of living specimens, has given us an excellent description of the external characters of the adult, and has correctly pointed out the true composition of the colony, maintaining the zooidal significance of the appendages which support the gonophores.

The only other notices we possess are a short one by Mr. Vigors‡, who, not aware of the previous descriptions by Fabricius and Sars, records the animal under the new generic and specific names of *Arum Cocksii*; and one by Mr. Gosse §, who also describes it as a new genus and species, under the name of *Spadix purpurea*.

The only published figures are one accompanying Mr. Cocks's description of the locomotive stage, a small woodcut outline by Mr. Gosse, and a characteristic figure by Mr. Hincks.

The specimens which have afforded the material for the present memoir were obtained at Lulworth, on the coast of Dorsetshire. They were attached to the under surface of large stones, close to the low-water level of spring-tides.

ANATOMY.

THE TROPHOSOME.—STRUCTURE OF HYDRANTH.

1. Endoderm.

The character of the endoderm varies according to the region in which it is examined. Throughout the whole of the main cavity of the body it constitutes a thick layer, composed of many cells in depth (Plate 56. figs. 1 & 2, a). The cells which form the greater part of this endodermal layer consist of simple round masses of clear protoplasm, about $\frac{1}{500}$ of an inch in diameter, in which a nucleus is frequently visible, and in which are immersed

^{*} Rep. of Roy. Pol. Soc. Cornwall, 1853, p. 34. ‡ Rep. Roy. Pol. Soc. Cornwall, 1849.

[†] Brit. Zooph. 1868, p. 75.
§ Ann. Nat. Hist. 1853, and Man. of Marine Zoology, 1855,

numerous refringent corpuscles and a few brown granules. No boundary membrane was evident in any of these cell-bodies. At the inner or free surface the endoderm of the whole of the gastric cavity, except in the region immediately below the mouth, forms long conical processes, which project like villi into the cavity (figs. 1 & 2, b). These processes, like the more external parts of the endoderm, are mainly composed of large cells, formed of clear protoplasm, with nucleus and refringent corpuscles; but besides these there exist also towards the free ends of the processes numerous smaller spherical cells (fig. 2, c), loaded with dark-brown granules. These cells are most abundant in the villi-like processes which are developed towards the proximal end of the body. They form a much less coherent tissue than the large clearer cells, and may be easily isolated under the microscope. Indeed they are constantly being thrown off, and may be often seen to be voided through the mouth of the living animal.

Extending over the free surface of the endoderm is an exceedingly thin stratum of a clear homogeneous protoplasm (fig. 2, d). This protoplasmic stratum is most obvious the villi-like processes, where it has the property of developing very minute, irregular, pseudopodial projections (e e e), which are constantly changing their shape, and may be seen under the microscope to be slowly protruded and withdrawn. The free surface of the endoderm carries also long, very slender vibratile cilia. I believe that the thin layer of protoplasm which extends over the free surface of the endoderm is continuous with an interstitial undifferentiated protoplasm which exists in small quantity between the endodermal cells. Its occurrence, with its pseudopodial extensions, on the gastric surface of the animal is full of interest, and suggests a close analogy between the absorptive action of the gastric surface and amæboid reception of nutriment; more especially when we bear in mind that the cells between and over which the semifluid protoplasm is spread are destitute of membrane, and that their protoplasm must be in direct relation with that of the pseudopodial stratum.

The cilia are extremely fine and difficult of detection. They do not appear to be continuous over the whole gastric surface, but to exist only at intervals. They probably originate directly from the proper surface of the endodermal cells, in which case they must traverse the pseudopodial layer. They may, however, be direct processes of this layer. Indeed it is difficult in either case not to regard them as modified pseudopodia. True vibratile cilia, like pseudopodia, can originate only from the surface of membrane-less protoplasm, which thus possesses, as one of its characteristic properties, the faculty of being able to develop two kinds of processes—the non-mutable vibratile cilium and the mutable pseudopodium.

From the gastric cavity the endoderm is continued in an altered form into the cavity of the tentacles (fig. 2, b, & 3). Here its condition differs strikingly from that of the tentacular endoderm of other marine hydroid trophosomes; for instead of forming the clear septate core which is so very characteristic of these, it consists of a single layer of small round cells surrounding an open axile cavity, and so loaded with opaque granules that the axis of the extended tentacle appears nearly white under reflected light.

2. Ectoderm.

Under this head I shall include, not only the proper cellular ectoderm, but the hyaline lamella which forms its internal boundary, and is composed of a fibrillated or muscular stratum, with a supporting structureless membrane.

The proper cellular ectoderm (Plate 56. fig. 1, c, & fig. 2, g, h) forms a much thinner zone than the endoderm. It is composed of two distinct strata—a superficial and a deep. The superficial stratum (fig. 2, g) consists of small round cells, several in depth. These are destitute of membrane, and contain abundance of yellowish corpuscles; while on the summit of the tentacles (fig. 3), and in irregular patches on other parts of the body, they contain dark brownish-purple pigment granules.

Lying irregularly among these ectodermal cells, and chiefly towards the free surface of the ectoderm, are the thread-cells (figs. 2 & 3). Two forms of thread-cells may be distinguished,—one oviform (fig. 4, a, a'), with the invaginated sheath occupying the axis; the other fusiform (fig. 4, b, b'), with a slightly curved axis, and having the invaginated sheath oblique. Both kinds of thread-cells are formed in the interior of certain cells belonging to the superficial layer of the ectoderm, and may be seen, some lying free among the true cells of this layer, others enclosed in their generating-cells, and either completely immersed in the granular matter of the cell or surrounded by a large clear vacuole (fig. 5). No facts, however, have come to my knowledge tending to throw further light on the mode of origin of the thread-cells.

The deep layer of the cellular ectoderm (fig. 2, h) is formed by a very remarkable tissue, to which I shall refer under the designation of the *claviform tissue*. This is composed of cells consisting of a yellowish granular protoplasm, entirely destitute of membrane, and each drawn out into a long caudal process. They are frequently provided with an obvious nucleus. By the union of their caudal processes groups of claviform cells (fig. 6, a) are produced whose common stalk runs to the hyaline lamella, where it loses itself in the fibrillated stratum (b). The whole forms a very soft, pulpy, and somewhat glandular-looking tissue, easily broken down under the compressor.

Caudate cells, of apparently the same significance, were first made known by Kleinenberg*, who discovered them in Hydra, where he believes that he has followed their caudal prolongations into direct continuity with the fibrillæ of the muscular lamella. He regards the body of the cell as destined for the reception of stimulus from without, and, looking upon the whole cell with its fibrilliform continuation as representing a combined nervous and muscular system, he gives it the name of "neuro-muscle-cell." According to this view Hydra would represent in the phylogenesis of animals a form in which the nervous and muscular tissues are as yet but imperfectly differentiated from one another.

I believe that we are quite justified, with our present data, in attributing to the claviform tissue the general function of a nervous system. Indeed I do not see what other place it is possible to assign to it in the economy of the animal. In *Myriothela*, however,

^{*} Hydra, eine anatomisch-entwickelungsgeschichtliche Untersuchung. Leipzig, 1872.

I have never succeeded in tracing a direct continuity of the caudal processes of the cells with the fibrillæ of the muscular lamella. There is no doubt that the stalks of the claviform tissue pass into the muscular layer and become intimately associated with it; but I do not believe that any more direct continuity with the individual fibrillæ can be here demonstrated.

KLEINENBERG has further described the bodies of the caudate cells in *Hydra* as united laterally with one another, and forming the outer surface of the body, while the spaces which must necessarily lie between their caudal prolongations are occupied by a tissue composed of small non-caudate cells, to which he gives the name of "interstitial tissue," and in which he maintains that the thread-cells and the generative elements are formed.

I can find nothing like this interstitial tissue in *Myriothela*; and I believe that its place is here taken by an undifferentiated protoplasm, through which the prolongations of the caudate cell-clusters make their way to the muscular layer.

If we except the case of the long transitory arms of the actinula or free locomotive stage, which will be afterwards described, the claviform tissue does not in *Myriothela* come to the surface of the body. Throughout the whole of the body of the adult it forms a deep zone, intervening between the hyaline lamella and the superficial layer of the ectoderm, and very distinct in sections made from specimens hardened in chromic acid.

The hyaline lamella (fig. 2, i) forms the internal boundary of the ectoderm, and is found everywhere between the endoderm and the cellular ectoderm. It consists of two layers,—internally (fig. 6, c) a perfectly transparent, thin, structureless membrane, and externally (b) a layer of fibrillæ, which adheres closely to the structureless membrane.

Special attention was first called to the presence of the structureless membrane in other hydroids by Reichert*, who named it "Stützlamelle;" but he refused to admit the existence of a true fibrillated layer. The fibrillated layer, however, is extremely distinct in almost all hydroids. In Myriothela it can be separated, after a short maceration in water, from the underlying structureless membrane. It is here composed of longitudinal fibrillæ, which adhere to one another by their sides in a stratum of a single fibre in thickness, which forms a continuous lamella, even after detachment from the supporting structureless membrane. The fibrillæ are about $\frac{1}{12,000}$ of an inch in diameter, soft, and compressible, very transparent, with a very minutely granular structure, but otherwise apparently homogeneous. They show a convex surface when seen in profile on the folded edge of the lamella. That they are contractile elements, forming by their union a muscular lamella, there would seem to be little reason to doubt. They do not, however, possess the character of true muscle-cells. So far as I was able to trace them, they retain a uniform diameter, and show no appearance of nuclei.

As already said, I have failed to find any direct continuity between the fibrillæ and

^{*} Ueber die contractile Substanz &c. Berlin, 1867.

the caudal prolongations of the claviform tissue. These prolongations run to the surface of the muscular lamella, and become there intimately united with it, so that it is perhaps impossible to detach them without laceration; but I cannot affirm any thing further regarding the nature of this union. But though *Myriothela* does not seem to afford any evidence of the direct continuation of the muscular fibrillæ with the caudal prolongations of the claviform tissue, it cannot be regarded as in any way contradicting the hypothesis that this tissue is destined for the reception of external stimulus—in other words, that it represents a nervous system.

The general structure of the ectoderm of the Myriothela hydranth is that which has been now described; in the globular capitula of the tentacles, however, we have a most singular modification of those structures which lie external to the hyaline lamella. Here the place of the caudate cells is taken by a remarkable tissue, composed of closely appressed transparent prisms, or, to speak more exactly, of greatly elongated pyramids (fig. 3, a, & fig. 7), which are attached by their inner or apical ends to the hyaline lamella of the capitulum to which they are perpendicular, and thence radiating outwards terminate at some distance from the outer boundary of the capitulum in a curved surface, which occupies somewhat more than a hemisphere. The distal or basal extremity of each pyramid is formed by a curve of greater convexity than that of the general surface formed by their combined bases; and this surface thus acquires a minutely papillose appearance. The whole organ thus constituted caps the hyaline membrane and endoderm of the summit of the tentacle. In its structure it strongly suggests the rod-like tissue which in higher animals we know to be associated with special organs of sense.

Radiating from its convex surface are a multitude of slender filaments, which make their way among the cells of the ectoderm, and terminate distally at a short distance within the outer surface of the capitulum, where each carries on its summit an oviform, transparent, very thin membranous sac (fig. 3, b, b & fig. 8). This sac bears, close to its distal end, a minute bristle-like process, and is completely filled by a firm refringent capsule, within which may be seen a transparent cylindrical cord wound in two or three coils. The capsule (fig. 9) is easily liberated from its enveloping sac, and under slight pressure the contained cord may sometimes be ejected through its distal end (fig. 10). The whole assemblage of sacs, with their included capsules, forms a zone parallel to the surface of the capitulum and a little within it (fig. 3).

The close resemblance of the capsule, with its contained cord, to a thread-cell is abundantly obvious; and even the external sac, with its bristle-like process, has its parallel in the generating-cell of certain thread-cells. But besides the presence of the filiform peduncle there are other points in which these remarkable bodies differ from true thread-cells. The included cord does not, like the contents of an ordinary thread-cell, consist of a wider portion continuous with a narrower one, which during ejection becomes invaginated in the wider, but, on the contrary, possesses a uniform diameter considerably greater than that of the filament of an ordinary thread-cell; and instead of

presenting a vast multitude of coils rolled together into a complicated mass, as in the latter, it has only two or three such coils. Further, when ejected from the capsule (while it still holds on by one end to the point of exit) it does not, like the filament of a thread-cell, straighten itself and shoot across the field of the microscope, but immediately on becoming free coils itself again into a spiral (fig. 10). Indeed I believe that the significance of these pedunculated capsules is something very different from any which has been hitherto assigned to the thread-cells; and it is scarcely possible not to recognize a special apparatus of sense in the whole structure just described, including the rod-like tissue in which the peduncles of the sacs have their roots, and which is plainly but a modification of the structure which forms the claviform or nervous tissue in other parts of the body. Indeed it is impossible to overlook the striking resemblance between these pedunculated sacs, with their enclosed capsule and cord, and the Pacinian bodies of the Vertebrata. If this be a correct view of the nature of the structures here described, we have now for the first time evidence which would justify us in assigning a special apparatus of sense to a hydroid trophosome.

But with all this the resemblance between these pedunculated capsules and true thread-cells cannot be ignored, and indeed makes us hesitate, even more than we may have hitherto done, in regarding the latter merely as urticating organs. It is possible that the pedunculated capsules may throw new light on the function and significance of thread-cells; but with no facts beyond those at present before us, we are scarcely in a position to speculate further on this subject.

The best display of the capsules, with their investing sacs and peduncles, was obtained from specimens which had been for twenty-four hours immersed in a solution of osmic acid of 0·1 per cent., and afterwards placed in a mixture of 100 parts of glycerine with 5 parts of acetic acid; while the most beautiful demonstration of the rod-like tissue was found in sections which had been simply macerated in water for twenty-four hours, and then examined, without further preparation, under the compressor. The more external tissues of the capitulum had been softened and disintegrated by the maceration, and were now easily separated by the simple action of the compressor; while the firm, rod-like tissue, offering more resistance to the decomposing action of the water, remained beautifully isolated, with its component rods looking almost like the radiating acicular crystals of certain forms of zeolite.

External to the zone of pedunculated capsules is a thin layer of ectoderm, which forms the most superficial portion of the capitulum (fig. 3). This is composed of small round membraneless cells, containing refringent corpuscles, while the summit of the capitulum is almost always occupied by a group of small cells, containing dark brownish-purple pigment granules. The two forms of true thread-cells already described are here developed in greater numbers than elsewhere, and may be seen scattered, without any definite order, among the more superficial cells of the ectoderm.

THE GONOSOME.

The gonosome of *Myriothela* (Plate 55) consists of blastostyles with their gonophores and of claspers.

The blastostyles (fig. 2, a, a, a) arise from the hydranth towards its proximal or attached extremity. They may be followed over a section occupying about one fifth of the entire length of the extended hydranth, and spring from this region on all sides without any very definite arrangement. They are very contractile, somewhat fusiform in shape when extended, but more clavate in various states of contraction. Towards their free extremities they carry several scattered tentacles resembling those of the hydranth, but much smaller; and where the tentacles cease to be borne the gonophores (b, b, b) commence, and continue with an irregular scattered disposition to within a short distance of the attached end of the blastostyle.

The structure of the blastostyles resembles, in all essential points, that of the hydranth, with the exception of their being entirely deprived of a mouth. Their gastric cavity communicates with that of the hydranth which bears them; the villi-like processes of the endoderm are extremely well developed, and the spherical cells, loaded with brown granules, which enter into the composition of these processes are very abundant (Plate 57. fig. 14, a). The muscular lamella is well developed, and the structure of the tentacles is quite the same as in the hydranth, the rod-like tissue and pedunculated capsules being similar in both*.

The claspers (Plate 55. fig. 2, c, c, and Plate 57. fig. 14, b, b), as already mentioned, are long tentacle-like organs of a cylindrical form, slightly enlarged towards their distal extremity, where they terminate in a sucker-like disk. They spring, like the blastostyles, from the body of the hydranth, and mostly in pairs from two points close to the base of a blastostyle. They have, however, no definite arrangement; many blastostyles have no claspers at their base, and solitary claspers occur, not only at the base of a blastostyle, but here and there at some distance from it on the body of the hydranth.

The claspers are very contractile. Their structure differs considerably from that of the blastostyle. The endoderm (Plate 56. fig. 11, a) is composed of an external layer of closely applied large cells with clear contents, and an internal looser layer of small round cells filled with brown granules, this internal layer surrounding a very narrow axile cavity. There are no villi-like processes. The ectoderm, except in the terminal enlargement, essentially resembles that of the blastostyles and hydranth. The muscular

* Before I had an opportunity of examining specimens of Myriothela, I regarded the appendages which carry the gonophores not as true members of a zooidal colony, and therefore not as proper blastostyles, but as mere peduncular organs like those which carry the gonophores in Tubularia (Gymnoblastic Hydroids, p. 383). In thus viewing them I differed from Mr. Hincks, who looked upon them as true zooids, having a reproductive function, and forming with the hydranth from which they spring a compound colony (Hincks, Brit. Hydroid Zoophytes, p. 76). I must now abandon my former view and declare my entire agreement with Mr. Hincks as to the true zooidal significance of these bodies.

lamella (b) is very well developed, and is succeeded externally by a zone of claviform tissue (c) overlaid by a zone composed of small round cells with nearly colourless granular contents, and lying two or three in depth (d). Among these the oviform and fusiform thread-cells are scattered in considerable abundance.

The terminal enlargement (e) of the clasper differs from its narrower portion chiefly in the great development of the claviform tissue which constitutes the principal mass of its substance. The caudal prolongations of the cells (fig. 12) composing this tissue are very long, and do not unite with one another, so as to constitute botryliform groups to the same extent as in the corresponding tissue in the ectoderm of other parts of the hydroid; they radiate from the hyaline lamella, and possess a considerable resemblance to the constituent elements of the rod-like tissue in the tentacles. On the summit of the clasper, where this organ exercises a special function of adhesion, the thread-cells so well developed in other parts of the ectoderm are deficient.

The function of the claspers, as we shall see more particularly under the head of development, is that of seizing, on its escape from the gonophore, the plasma mass which is to become developed into an embryo.

The gonophores (Plate 55. fig. 2, b, b, b, and Plate 57. fig. 14, c, c, d) show nothing like a medusal conformation. They are simple sporosacs of a spherical form, supported on very short peduncles, which spring without any definite arrangement from the sides of the blastostyles. They show no definite order of arriving at maturity, the more mature gonophores being sometimes at the distal side of the younger ones, sometimes at their proximal side, and sometimes scattered among them. Their law of maturation is thus strikingly different from that of the gonophores of most other hydroids, in which we find either a constant centripetal or a constant centrifugal order in the periods of their first appearance and of their arrival at maturity.

Myriothela is also extremely exceptional in carrying on the same hydranth, and even on the same blastostyle, both male and female gonophores. So far, however, as my observations extend, the male gonophores are borne at the distal side of the female ones. No external difference between the two can be detected beyond the fact that the mature males are much smaller than the mature females.

In the walls of the mature gonophores (Plate 57. figs. 7, 10, 12), whether male or female, several distinct structures may be demonstrated. Most externally is a zone of spherical cells (fig. 12, a), which for the most part contain clear colourless granules; but towards the summit of the gonophore some of these cells are filled with purplish pigment granules, and form a coloured circle surrounding the distal pole of the gonophore (fig. 14, c, c, d). Passing from without inwards, this is followed by a zone of clavate tissue (fig. 12, b), and this by the structureless lamella (c) overlaid by muscular fibrillæ. These three zones are direct continuations of the corresponding elements in the ectoderm of the blastostyle.

Lying immediately within the hyaline lamella is another cellular layer (fig. 12, d). In its thickness this layer corresponds to the depth of a single cell. Most of the cells

composing it contain only clear colourless protoplasm, with some clear granules; but towards the distal pole of the gonophore the cells increase slightly in size, and contain purple granules, which form a coloured ring internal and parallel to that belonging to the outer layer (figs. 7 & 10, a). In the centre of this internal ring the layer now under consideration is perforated by a narrow aperture, which thus lies immediately under the distal pole of the gonophore, which is itself quite imperforate.

The last described layer encloses the mass of the generative elements (figs. 7, 10, & 12), from which, however, it is separated by a very thin structureless membrane (fig. 12, e), by which the whole generative mass is surrounded, and which becomes reflected over the spadix where this is plunged into the midst of the mass of ova or spermatozoa.

DEVELOPMENT.

The first appearance of the gonophore shows itself in a minute offset of the gastric cavity of the blastostyle. This pushes itself outwards into the ectoderm of the blastostyle, carrying with it the endoderm, which continues to form its immediate boundary, separated from the cellular ectoderm by the hyaline lamella; but no well-defined external projection has yet become apparent.

The endoderm (Plate 57. fig. 1, a), which lies over the distal end of this gastric diverticulum, soon becomes excavated by a cavity of a nearly spherical shape (b). This cavity, which I shall speak of as the *gonogenetic chamber*, is separated from that of the diverticulum (c) by a considerable thickness of the endodermal layer; but the endoderm, which bounds it distally, forms a cellular membrane of only a single cell in thickness. The cavity, which as yet appears quite closed, is filled with clear contents, in which no formed matter beyond minute granules can be detected.

In the next stage the diverticulum from the cavity of the blastostyle has increased in size, and continuing to press the endoderm and ectoderm before it, the whole has begun to form a well-defined hernial projection from the side of the blastostyle, while the floor of the gonogenetic chamber has become convex; and the chamber, which has at the same time increased in size, presents in longitudinal section a crescentic shape. A minute orifice has now become visible in the summit of the chamber; and the endodermal cells, which immediately surround the orifice, have become somewhat larger, and are seen to be filled with brown pigment granules. The ectoderm continues imperforate, the orifice being entirely confined to the thin layer of endoderm which forms the immediate roof of the gonogenetic chamber.

Up to this point there is nothing by which the male and female gonophores may be distinguished from one another. We soon, however, observe a differentiation of the contents of the gonogenetic chamber. In the female gonophore a layer of more consistent protoplasm has accumulated on the free surface of the walls of this chamber (fig. 2, b), more especially on its proximal wall or floor. Minute, clear, nucleus-like bodies may be seen scattered through the protoplasm, and a few similar bodies float free in the more liquid contents which still occupy the centre of the chamber.

Following now the female gonophore in its development, we find that in the next stage (fig. 3) both it and its included gonogenetic cavity have increased in volume, while the floor of the cavity projects further into its interior in the form of a hollow conical core. This is easily recognized as the spadix; on the free surface of the cavity of the spadix (c) villi-like processes similar to those which occur in the general cavity are abundantly developed. The gonogenetic cavity has now become uniformly filled with a plasmatic mass (b), which is seen to consist of a multitude of nuclei (fig. 5) about $\frac{1}{3500}$ of an inch in size, each enclosing a minute nucleolus, and immersed in a minutely granular protoplasm. An extremely delicate structureless hyaline membrane (fig. 3, d) can now be traced over the whole surface of the generative mass, which it thus separates from the proper endodermal walls of the gonogenetic chamber.

As yet no distinct cell-boundaries can be detected in the contents of the gonogenetic chamber, and the nucleolated nuclei afford the only evidence of cell-differentiation. With the enlarging gonophore, however, the protoplasm which surrounds the nuclei increases in volume, and we soon begin to discover in it manifest cell-boundaries (fig. 4). Every nucleus is now surrounded by a differentiated mass of protoplasm, and the cavity of the gonophore has thus become filled with bodies which possess all the characteristic features of true ova, each with its well-defined germinal vesicle and germinal spot and its surrounding vitelline protoplasm.

These ova-like bodies continue to increase in size with the growth of the gonophore. They remain for some time closely pressed against one another, having thus acquired a polyhedral form (fig. 6); but they gradually become looser, assume an oval shape (figs. 7 & 12, f), and may be easily isolated by the needle or by the mere action of the compressor. Their germinal vesicle is now very large and distinct, and within the large germinal spot a well-defined spherule or nucleolina may be easily detected. Though their subsequent history differs in some points from the characteristic development of the ovum such as is met with in other animals, we should yet be scarcely justified in denying to them the significance of true ova.

They have no sooner attained their complete independence and acquired their full size in the sporosac, than they begin to present a very remarkable phenomenon. They lose their independent existence, and begin to undergo a fusion into one another; and when the contents of the sporosac are now liberated by rupture under the microscope, many of these nucleolated protoplasm masses may be seen united to one another by irregular pseudopodia-like extensions of their substance (fig. 8). By the gradual shortening and thickening of these processes the little masses which they connect are drawn closer to one another, and end by becoming completely fused together into a common protoplasmic mass (fig. 9). In this mass the cell-boundaries are completely lost, but numerous nucleolated nuclei are scattered through its substance. These are almost certainly the nuclei with their included nucleoli of the original independent protoplasm masses or ova.

The fusion commences among the ova which lie in the immediate vicinity of the spadix, to which the masses formed by their union continue for some time to adhere by

a considerable extent of their surface (fig. 7); while those ova which lie more towards the periphery of the cavity continue longer distinct, but ultimately follow the same course as the others by coalescing into compound masses.

Several such masses (fig. 10), eight or more, will thus be formed from the coalesced ova. They detach themselves more and more from the spadix. They are now of an oval form; and some of them may still be seen to be connected with the spadix by a narrow easily ruptured protoplasmic prolongation. They do not, however, entirely fill the cavity of the gonophore; and the narrow intervals between them, as well as the small space which separates them from the walls of the gonophore, is occupied by a matter which appears to consist chiefly of free nuclei and of dwindled and degraded ova, all apparently undergoing a process of liquefaction, and doubtless an unused residuum of the bodies by the coalescence of which the compound masses had been formed.

If in this stage the gonophore be laid open, and the protoplasm masses, whose formation we have been tracing, be liberated under the microscope, we shall often succeed in witnessing very minute bristle-like processes of clear protoplasm which have become developed over their surface (fig. 11). These little processes, however, are not permanent structures, and they will often become entirely withdrawn while the object is under examination. They are, in fact, true pseudopodia, and are probably employed in the nutrition of the masses from which they arise.

The contents of the gonophore, however, are intended to undergo further changes before the period of their liberation has arrived. The separate protoplasm masses increase in size, the residual matter which had surrounded them disappears, having probably afforded material for their nutrition; they begin to coalesce with one another, and there is ultimately formed a single large plasmodium, which entirely fills the cavity of the gonophore. When this plasmodium is examined under the compressor, the same nucleolated nuclei which had hitherto characterized the products of the coalescence of the ova are seen to be scattered in great numbers through its substance (fig. 13). These nuclei, however, have already begun to suffer a change; for while in some the nucleolus is still distinct, in others it has quite disappeared; and while in some the contents consist of a minutely granular matter, in others they are quite homogeneous.

When the separate protoplasm masses have all united with one another, but generally a little before they have become so completely fused together as to have their original distinctness entirely lost, the time has arrived when the contents of the gonophore are to be expelled. The walls of the gonophore now begin to contract on these contents; and here the use of the muscular layer, which is well developed in them, becomes at once apparent. The contained plasmodium is thus gradually forced out through the summit of the gonophore (fig. 14, d).

The orifice in the endodermal wall of the gonogenetic chamber is ready to aid in giving exit to the plasmodium, but the ectoderm has been hitherto imperforate. This, however, appears to have been becoming gradually thinner on the point immediately over the endodermal orifice, and it is now easily ruptured at this spot by the pressure

from within. By the continued contraction of the gonophore-walls the plasmodium is at last entirely expelled, completely enveloped, however, in a transparent structureless membrane. This is apparently the membrane which at a very early stage had shown itself lining the gonogenetic chamber; it is at first of great tenuity, but it soon acquires considerable consistence. The empty gonophore may now be seen retracted in the form of a shallow thick-walled cup with everted edges upon the summit of its short peduncle (fig. 14, e)*.

The liberated plasmodium closely enveloped in its delicate structureless capsule is of a nearly spherical form, and now lies upon the retracted gonophore, where it is usually retained by the spadix plunged for a short distance into its mass (fig. 14, f). It does not, however, continue long in this position, for the function of the claspers is soon brought into play. These curious organs now stretch themselves out towards the liberated plasmodium; and as soon as they reach it they attach themselves (f) by their sucker-like extremities to its capsule, and then by contracting pull it entirely away (g) from the remains of the gonophore.

Sometimes the plasmodium will be seized by only one clasper; very often, however, two or even three will fasten on it (Plate 55. fig. 2); and the plasmodium will sometimes be seen more or less distorted by the tension thus exerted on it at the same time in different directions.

Leaving for a while the further history of the female elements, we may now trace the development of the male. The male gonophore resembles the female in all points except in being about half the size of the latter; and I could detect no difference as to origin between the matter which in one case is to become differentiated into ova, and that which in the other is destined for the formation of spermatozoa. In every young gonophore I have examined, the first appearance of the matter in which sexual elements are afterwards to show themselves is within the gonogenetic chamber which has become excavated in the substance of the endoderm; and it is only when the ovarian nuclei become differentiated in the one case, and the spermatic cells in the other, that we obtain any decided indication of the sex of the gonophore.

As we have already seen, the primitive plasma which fills the gonogenetic chamber in the female presents after a time scattered nuclei-like bodies, which are to become the germinal vesicles of the ova. In the male, on the other hand, such nuclei never make their appearance, and the primitive protoplasm becomes changed into minute cell-like bodies, which entirely fill the chamber (Plate 57. fig. 15). These little bodies are the vesicles within which the spermatozoa originate; but in what way the latter are produced from them I have not succeeded in discovering. After a time the vesicles have disappeared, and are replaced by mature spermatozoa, which now fill the cavity of the gonophore, and which may be liberated by rupture of the latter. When thus set free they are seen to consist of a very minute oval head, with a vibratile tail of extreme tenuity (fig. 16).

^{*} In a single instance a gonophore with two such plasmodia ready to escape from it came under my observation.

They are more minute than the spermatozoa of any other hydroid with which I am acquainted.

By what means the spermatozoa naturally escape from the gonophore I have not been able to determine with certainty. I could find no external orifice, nor could I detect a thinning of the summit of the gonophore like that which in the female precedes the escape of its contents; and when the mature male gonophore was subjected to pressure it was always by the rupture of the spadix and the escape of the spermatozoa through the peduncle, which would thus carry them into the cavity of the blastostyle, that the gonophore became emptied. It is not improbable, as we shall afterwards see, that this is their natural mode of escape.

Returning now to the contents of the female gonophore which, just after their escape, we had left in the grasp of the claspers, we find that by this time the coalescence of the separate plasma masses into a single spherical plasmodium has been completed; and it is probable that fecundation now takes place. Hitherto we have seen nothing which can be compared to any phenomena which we would be justified in regarding as the immediate consequence of the action of the male element on the female; but soon after the liberation of the plasmodium and its seizure by the claspers, we find that the whole has become broken up into a multitude of small round or irregularly shaped masses (Plate 57. fig. 17). Some of these may be seen still connected to one another by narrow isthmuses of their substance, while others are quite free, and can be isolated under the microscope. They all consist of a granular protoplasmic matter without any distinct boundary membrane, and with numerous nucleus-like bodies immersed in their substance. The common external structureless membrane is distinct, but it is still thin and weak.

I must regard this breaking up of the plasmodium into separate masses as representing a true segmentation, such as in the simple ovum occurs as the immediate result of fecundation. I have not, however, succeeded in witnessing its earlier stages, and I cannot say whether it proceeds in accordance with the ordinary binary law of vitelline segmentation.

How far this breaking up of the plasmodium is continued before a true histological differentiation becomes apparent, I am unable to say, for the next stage which showed itself (Plate 58. fig. 1) presented a marked advance on the previous ones. The segmented condition had now entirely disappeared, and the developing mass had acquired a true cellular structure, while it had become further differentiated into two distinct layers—an external (a) layer, ectoderm, in which the cell-boundaries were with some difficulty made out, and an internal (b), endoderm, composed of very obvious cells larger than those of the ectoderm, and each with a clear nucleus and granular protoplasm. This internal layer formed the boundary of a cavity (c) produced apparently by lique-faction of the more central parts of the mass.

The developmental stage to which we have now arrived is thus represented by a hollow spherical body, whose walls are formed by two layers, an ectoderm and an endo-

derm, and which plainly corresponds to the planula of other hydroids. It is, however, entirely destitute of cilia, and is still confined within its external structureless capsule (d), which has now acquired considerable thickness.

We next find that the planula presents numerous minute pits distributed without any definite arrangement over its surface (fig. 2, b, b). These are points where the walls of the planula have begun to invaginate themselves; and if at this time a section be made of the planula (fig. 3), its cavity will be found to be occupied by numerous hollow conical projections (b, b), which radiate into it on all sides from the inner surface of its walls. These projections are simple involutions of the walls, and are therefore composed, like the walls themselves, of an ectoderm and an endoderm, but in an inverted order.

If an uninjured planula in this stage be dissected out of its external structureless capsule, which now lies loosely over it, and be subjected to carefully moderated pressure, the internal projections will become suddenly evaginated, and will shoot out in all directions over the outer surface in the form of hollow cylindrical arms.

The evagination which has thus been effected by artificial pressure takes place naturally in the progress of development; and in the next stage (fig. 4) we find that the arms which had been formed internally by a process of involution have become external, the embryo being still enclosed within its capsule. The ectoderm had already, by the multiplication of its cells and the development in it of the clavate tissue, increased considerably in thickness, and the hyaline lamella may now be seen on its inner boundary.

Up to this period the embryo had retained its nearly spherical form; but it now begins to elongate itself, and assumes an oval shape (fig. 5). From its surface there project on all sides the tubular arms, which, from their original position within the cavity of the body, had become external by evagination; while at one extremity of the greater diameter the body has become truncated, and here numerous short papilliform processes (a) have become developed from its surface.

The arms continue to elongate themselves, and soon present a well-defined terminal capitulum. The papilliform processes, too, increase in number, and extend further back on the body of the embryo, which has become still more elongated. It is probably at this stage that the mouth is formed in the truncated end. The embryo is now ready to escape from its enclosing capsule, which has all along remained adherent to the extremity of the clasper, and which now becomes ruptured, and allows the little animal to enter on a free life in the surrounding water (Plate 55. fig. 2, dd).

The free embryo of *Myriothela* (Plate 58. fig. 6) is very contractile, and when fully extended is of nearly cylindrical form, about a quarter of an inch in length, slightly attenuated at one end so as to form a short conical hypostome (a), which carries the mouth on its summit, and more decidedly so at the opposite end, where it terminates in a little sucker-like disk (b). The papilliform processes (c) have now attained the form of the permanent tentacles, presenting a short stem with a terminal enlargement.

They commence just below the hypostome, and extend for some distance backwards on the body. Springing from between the short permanent tentacles, and from a considerable portion of the body which lies at their proximal side, are the long arms (d, d, d) which made their appearance at an early period of embryonic development, and which are destined to disappear entirely before the arrival of the animal at maturity. They are about twenty in number, capable of great extension, and when stretched out to their utmost (fig. 6) are in the form of long straight filaments slightly tapering towards their distal extremities, where they terminate in a well-defined spherical capitulum. In complete retraction they are short, somewhat ovoid bodies marked by strong transverse ruge.

In accordance with the terminology I have already adopted in describing the early stage of *Tubularia**, I shall designate the free locomotive embryo of *Myriothela* by the name of actinula. It moves about by the aid of its long arms, whose terminal capitula are capable of being used as suckers of attachment; while the proximal end of the body, like that of a hydra, also admits of being temporarily attached by means of its little suctorial disk.

After the actinula has enjoyed for some days its free locomotive existence it begins to fix itself (fig. 7). This fixation is effected by means of the proximal sucker-like extremity (b). After it has thus become stationary it continues to manifest great contractility, becoming sometimes much extended, and at other times contracted into a nearly spherical mass. The long arms now undergo a rapid degradation (d, d, d); they lose their terminal capitula, become much shortened, and ultimately entirely disappear (fig. 8).

In the mean time the short papilliform tentacles become more numerous, extending further backwards on the body. The proximal extremity of the animal becomes bent at right angles to the rest of the body so as to form a sort of horizontal stolon-like foot, from which small fleshy processes with sucker-like extremities, and having a considerable resemblance to the claspers, are emitted. The function of these processes, however, is very different from that of the claspers; they serve to attach the animal permanently to some solid support, to which they fix themselves by their extremities. Along with the stolon-like foot they become clothed in a chitinous perisarc, and the actinula has thus acquired all the essential characters of the adult trophosome.

The gonosome has not, however, as yet begun to develop itself; but it soon makes its appearance by the budding of the blastostyles and claspers from the hydranth at the proximal side of the tentacles. From the blastostyles the gonophores are subsequently developed in the manner already described, and the animal thus attains its complete maturity (Plate 55).

In the histological structure of the actinula there are several points which deserve special consideration. In the very young animal, at the time when the arms are about to become changed from internal to external appendages, the endoderm and ectoderm can be everywhere followed without difficulty. The endoderm is composed of clear

^{*} Gymnoblastic Hydroids, p. 90.

cells, several in depth, the most internal presenting convex surfaces to the gastric cavity, but forming no villi-like projections. The ectoderm already consists of two zones besides the muscular lamella—a superficial zone composed of several layers of small round cells with clear granular contents, and a deeper zone of claviform tissue. The hyaline lamella with its muscular fibrillæ lies everywhere between the claviform tissue and the endoderm. All these elements can be followed from the walls of the body into those of the arms. In these the endoderm, composed of small, round, clear cells, surrounds a wide axial cavity.

When the arm has acquired its terminal capitulum, we find that the zone of claviform tissue, hitherto simply continued into the arm from the walls of the body, has become specially developed in the capitulum (Plate 56. fig. 13, c), and here envelops the endoderm in a nearly spherical cap, which takes exactly the place of the rod-like tissue in the permanent tentacles. The tissue composing this cap, moreover, is intermediate in its form between the ordinary clavate tissue and the rod-like tissue; for its component elements do not form branching groups as in the clavate tissue of other parts, but consist of radiating, simple, greatly elongated clavate cells, very similar to those already described as forming the claviform tissue in the distal extremity of the clasper, and thus affording further evidence that the rod-like tissue is only a modified claviform tissue.

The capitulum of the actinula arm further resembles that of the permanent tentacle in the presence of the pedunculated capsules. These differ, however, in some points from the corresponding organs of the permanent tentacles; for they are not more than half their size, while the included cord is finer and longer, and is wound into closer and more numerous coils (Plate 56. fig. 14, a). Like the cord of the larger capsules, it continues after its emission to form a spiral, instead of straightening itself out in the field of the microscope like the filament of the true thread-cells. The spiral, however (fig. 14, b), is more open and more elongated than that formed by the cord ejected from the stalked capsules of the permanent tentacles. The styliform process of the external sac is long and slender.

When the transitory arms of the Actinula have attained their full growth, the ectoderm of their stem (fig. 13, a) no longer presents the two zones which were present in their younger stages. It is the superficial zone which appears now to be wanting, so that the clavate tissue comes to the surface. In thus becoming superficial the distal ends of the cells composing this tissue have become wider, and lie more closely on one another, and very often contain a large vacuole excavated in the midst of their granular contents. Their caudal prolongations, moreover, do not seem to run into one another to such an extent as to give rise to the botrylliform condition which characterizes this tissue in other parts of the animal.

The endoderm of the arm (fig. 13, b) is formed externally by a tissue of large, clear, polygonal cells containing some minute granules, which are chiefly accumulated on the walls of the cells, while internally there is an irregular disconnected layer of small round cells filled with brown corpuscles. The increase of the endoderm in volume has nearly obliterated the axile canal of the arm.

The arm is very contractile, and, when in different states of contraction, the cells of the ectoderm may often be seen forming irregular projections of various length and thickness. These vary from time to time in shape and size, and look so exactly like pseudopodial processes that without careful observation they might easily be mistaken for them. They are, however, mainly the result of the contraction of the arm. When the arm is shortened by the action of its contractile elements, the hyaline lamella is thrown into irregular corrugations, and these are communicated to the superjacent cellular ectoderm. In macerated sections of the arm the cellular ectoderm will become disintegrated and broken down, and then the exposed hyaline lamella will often show nearly an exact repetition of the pseudopodia-like projections. I am, however, inclined to think that, after the contraction of the fibrillated layer has thus crumpled the hyaline lamella and overlying ectoderm, the protoplasm of the latter exerts a certain contractility which exaggerates the prominence of its projections, and thus to a certain extent brings them within the category of pseudopodia.

In the ectoderm of the body of the actinula we find not only the deep clavate tissue, but the more superficial layer of cells well developed. Here, during certain states of contraction, pseudopodia-like projections are also formed; and I believe that these are referable to the same cause here as in the ectoderm of the tentacles.

The proximal extremity of the actinula body is capable, as already said, of acting as a sucker of attachment; and here the ectoderm has acquired a considerable increase of thickness (Plate 56. fig. 15). The increased thickness is mainly owing to the great development of the clavate tissue at this spot. This tissue forms here a hemispherical cap over the *cul-de-sac* of the gastric cavity, and the elements composing it are scarcely at all united to one another into ramified groups. Its peculiar development here is probably connected with a special irritability with which this part of the walls would appear to be endowed. Over this cap the superficial ectodermal layer is continued, forming a zone of small, spherical, membranous cells with minutely granular contents. In the uninjured state a fine longitudinal striation may be witnessed in this part of the actinula (Plate 58. fig. 6, b); it is caused by the appearance of the terminal mass of clavate tissue as seen through the overlying layer*.

The endoderm of the stem-like proximal portion of the actinula (Plate 56. fig. 15) closely resembles that of the transitory arms. It is composed of an external layer of large, clear, polygonal cells, with an internal one of small round cells filled with brown corpuscles.

GENERAL REMARKS.

I believe we are justified in regarding the claspers as true zooids rather than as mere organs; and if so *Myriothela* may be compared with *Hydractinia* in the extent to which the polymorphism of the zooids is carried. We have here hydranths, blastostyles,

^{*} A very similar appearance may be seen in the actinula of *Tubularia*, and I have now little hesitation in referring it to a similar cause.

gonophores, and claspers, all different forms of zooids, each endowed with its own special function in the physiological division of labour, and all associated into a compound colony which forms the proper zoological Individual, the logical element of the species*. In *Hydractinia* we have hydranths, blastostyles, gonophores, and "spiral zooids" similarly associated. In *Hydractinia*, however, there is a common cœnosarcal basis which gives origin to many hydranths, as well as to the blastostyles with their gonophores, and to the spiral zooids; while in *Myriothela* the hydranth is solitary, and the blastostyles and claspers are budded off from this.

It will be seen that the account here given of the development of Myriothela offers no support to the view that the generative elements originate in certain cells of the ectoderm—a view which has been defended by Kleinenberg, who, in his excellent memoir on the structure and development of Hydra, maintains that both ova and spermatozoa have their origin in what he calls the "interstitial tissue" of the ectoderm. Neither does it support the view more recently put forward by Ed. van Beneden in his valuable memoir on the origin of the testis and ovary. According to the Belgian zoologist the ova in Hydractinia always originate in the endoderm, while the spermatozoa just as constantly have their origin in the ectoderm. To this observation M. Ed. van Beneden attributes great significance; for by adopting the highly probable hypothesis enunciated many years ago by Huxley, that the ectoderm represents the outer layer of the blastoderm in the higher animals and the endoderm the inner layer, he generalizes the results of his observations on Hydractinia, and maintains that throughout the animal kingdom the female generative system is a product of the inner leaf of the blastoderm, and the male of the outer leaf.

From the observations on *Myriothela*, however, recorded above, it would seem to follow that both ova and spermatozoa originate in a special chamber which has become excavated in the substance of the endoderm, and that the ectoderm has nothing to do with either.

I believe this to be the legitimate conclusion to be drawn from the appearances presented. At the same time I admit that other observers may put a different interpretation on these appearances; for it may be asserted that the material which is to become developed either into spermatozoa or into ova is in one or both cases a product of the ectoderm, and that it has subsequently to its origin migrated into the endoderm; while in proof of this the orifice which exists in the roof of the endodermal chamber will probably be adduced and maintained to be the channel through which the generative elements have gained access to this chamber.

Knowing the memoir of M. E. VAN BENEDEN, in which he maintains that the spermatic

ÉDUARD VAN BENEDEN, "De la Distinction Originelle du Testicule et de l'Ovaire," Bull. de l'Acad. Roy. de Belgique, 2º série, tome xxxvii. no. 5, Mai 1874.

^{*} The terms Zooid and Individual are used here with the significations originally proposed by HUXLEY. The former is the "Individual of the fifth order, Person" of HAECKEL, the latter the "Individual of the sixth order, Stock or Cormus" of HAECKEL.

mass originates as a cellular bud from the inner surface of the ectodermal layer of the gonophore, and that this pushes itself into the endoderm and becomes afterwards cut off from its attachment to the ectoderm, I paid great attention to the gonophores of Myriothela from the earliest moment when they became recognizable, but entirely failed to detect any process resembling that described by the Belgian zoologist as taking place in Hydractinia. In the very earliest stages of the gonophore which I could find the gonogenetic cavity had been already formed and filled with the primitive generative matter, and I failed to meet with any thing which would lead me to believe that this had its origin in the ectoderm. It is true that in Myriothela a difficulty occurs in the observation which we do not meet with in Hydractinia; for while the complete separation of the sexes on different colonies in Hydractinia will enable us at all times to say, no matter how young may be the gonophore under examination, whether this be male or female, in Myriothela we have no certain sign by which to decide as to the sex of the gonophore in its youngest stages, gonophores of both sexes being here borne on the same blastostyle. It is scarcely possible, however, that among the many cases of extremely young gonophores which I examined there were not both male and female examples; and in no case did I find any thing which would lead me to believe that the origin of the generative elements in one was different from what it was in another.

The facts here noted have thus led me to maintain that both male and female elements have their origin in the endoderm. Still, considering the difficulty of the observations, and the fact that the appearances lie possibly open to another interpretation, I do not desire to insist on the impossibility of the generative elements being in one or both sexes primarily introduced from the ectoderm into the endoderm; and I am willing to wait for the confirmation which may be expected from further investigations.

As is well known, all the fixed hydroids pass through a free locomotive stage before finally attaching themselves. I have elsewhere* pointed out that this free stage shows itself under one or other of two forms, namely, that of a planula (as in the great majority of hydroids, *Campanula*, *Sertularia*, *Coryne*, &c.) and that of an actinula (as in *Tubularia*).

The free hydroid planula is a closed sac in whose walls an endoderm and an ectoderm are differentiated, not by a process of invagination, but by one of dilamination, and in which an oral orifice is afterwards formed by a perforation of its walls, the planula thus becoming the *gastrula* of HAECKEL. The external surface of the planula is almost always clothed with vibratile cilia.

The actinula represents a form more highly organized than either the planula or the gastrula; for not only is a mouth always present in it, but locomotion is effected not by vibratile cilia, but by means of external appendages in the form of tentacles or arms, which may be either transitory or permanent.

It must not, however, be supposed that the planula stage does not exist in hydroids whose free phase is that of an actinula. It is, on the contrary, as truly a phase of their development as it is of that of the others: but the planula stage is then, if we

^{*} Gymnoblastic Hydroids, p. 85.

except Hydra, entirely passed within the gonophore, and the planula in such cases is never ciliated or locomotive.

In *Tubularia* the planula is a non-ciliated compressed sac, developed directly out of the plasma mass which occupies the cavity of the gonophore; while still retained within the gonophore it develops tentacles by outgrowths from its sides, elongates itself, becomes perforated by a mouth, and then escapes as a free locomotive actinula destined to undergo further changes of shape before attaining the final form of the hydroid trophosome.

Just in the same way Myriothela passes through the non-ciliated planula stage before it attains the form of the free actinula. In one important point, however, the actinula of Myriothela differs from that of Tubularia, namely, in the possession of embryonic transitory organs which take the form of long contractile arms, by which locomotion is aided, and which entirely disappear during the subsequent course of the development.

In *Hydra*, too, which never presents a permanently fixed trophosome, we find a true planula stage, the planula being here, as in the actinula-forming hydroids, destitute of cilia. It acquires a mouth by perforation, and develops itself by continuous growth and the emission of tentacles into the form of the adult without passing through any intermediate actinula stage.

Properly speaking, *Hydra* represents a permanent actinula. *Hydra* (if we except the somewhat obscure form described by Greeff under the name of *Protohydra*) may thus be assumed as the lowest known hydroid, and, in accordance with the Descent Theory, would be the remotest ancestral form yet discovered of the Cœlenterata.

In all cases, however, it must be borne in mind that the planula is nothing more than the blastodermic sac after the two leaves of the blastoderm have become differentiated. In some few cases it never clothes itself with cilia, and then it almost always remains, as long as it continues a planula, included within the gonophore; while in the great majority of cases it develops cilia over its surface, and becomes free and locomotive.

KLEINENBERG, finding that in the adult Hydra the entire cellular ectoderm is composed of the caudate cells with an interstitial network of simple cells interposed between their proximal attenuated ends, while their wide distal ends form the outer surface of the animal, concludes that there is here no external epithelium or epidermis. Hydra would thus present an apparent anomaly, inasmuch as one of the most universal features in ontogenesis—the development of an epidermal layer from the outer germ-lamella (ectoderm)—would seem to be absent.

This anomaly, however, is brought into agreement with the established facts of development by Kleinenberg, whose observations have led him to maintain that the so-called egg-shell of Hydra is really a transformed epidermis, but, being needed only as a protective investment for the embryo, is a transitory structure destined to be cast off in the later periods of development.

Though this may be a correct view of the state of things in *Hydra*, it is certain that in *Myriothela* we have a perfectly distinct and well-developed layer which lies external

to the claviform tissue, and forms the outer surface of the body. To this layer we must attribute the significance of a true epidermis. It appears, however, to be absent from the stems of the transitory arms of the actinula after these have attained their full growth. In their early stages, while yet they are invaginated processes of the body walls, and even for some time after their complete evagination, it is present as elsewhere; but during the growth of the actinula it is gradually absorbed, and then allows the claviform tissue to come to the surface. In the capitulum of the arm, however, it never disappears, being here needed as a protective envelope for the specially and more highly developed sensitive structures of this part.

It is thus obvious that *Myriothela* offers no exception to the ontogenetic law, which derives both the central nervous system and the epidermis from the outer layer of the blastoderm.

One of the most remarkable features in *Myriothela* consists in the presence of the bodies to which I have here given the name of claspers. These, as we have seen, are tentacle-like zooids endowed with great contractility; and no sooner is the plasma mass, which is to become developed into the actinula, set free from the gonophore which had hitherto confined it, than one or more claspers direct themselves towards it, and fixing themselves to it by their sucker-like ends, hold it tenaciously during certain subsequent periods of its development. The manner in which the claspers thus seize upon the liberated plasmodium forcibly reminds us of the way in which the Fallopian tubes are supposed to seize the mammalian ovum at the moment of its liberation from the Graafian follicle.

There is something very surprising in the selective faculty thus apparently exercised by the claspers; for it is, as a rule, to the liberated plasma mass alone that they become attached, while no reason whatever can be assigned why they should not seize upon some of the neighbouring parts which are just as easily within their reach. Once or twice I have seen a clasper fixed to some other part of the hydroid; but this occurrence is so rare that it cannot in any way be regarded as a manifestation of its normal function.

We have at present no data which will enable us to arrive at an absolute conclusion as to the object gained by the seizure of the plasmodium by the claspers. It is not improbable, however, that it is connected with fecundation. We must remember that in *Myriothela* we have the very exceptional condition of one and the same blastostyle carrying both the male and the female gonophores, and, further, that the spermatozoa of this hydroid are remarkable for their extreme minuteness; they are smaller, indeed, than in any other hydroid with which I am acquainted. Now I have never seen the spermatozoa escape spontaneously as in other hydroids from the gonophore; and when one of the *Myriothela* gonophores containing mature active spermatozoa is subjected to slight pressure, it is not through any breach of continuity in the thick external walls of the gonophore that the spermatozoa are ejected, but through the walls of the spadix, which appear to be easily ruptured. In this way they pass directly into the gastric cavity of the blastostyle, and through this may be easily conducted to the base of a clasper, and

thence carried through its narrow axial channel to its summit, where this has become attached to the plasmodium just liberated from the female gonophore. When once arrived there the spermatozoa may make their way through the terminal tissue of the clasper, and be thus brought into immediate relation with the plasmodium, whose investing membrane is at this time exceedingly thin and weak, a process which will be obviously facilitated by the exceptional minuteness of the spermatozoa.

We should further bear in mind that it is not until after the seizure of the plasmodium by the claspers that we have any evidence of the phenomenon of segmentation—a fact which renders it highly probable that the act of fecundation also takes place subsequently to the seizure. Spermatozoa, if searched for in the cavity of the clasper, would probably be found there; but, short of their detection in this situation, we have a combination of facts about as strong as could be desired, all tending to the conclusion that the function of the claspers is that here suggested, and offering a case in many respects parallel with that of the hectocotyle in the Cephalopoda, or with certain phenomena of fertilization among the Algæ.

EXPLANATION OF THE PLATES.

PLATE 55.

- Fig. 1. Myriothela phrygia. A group, natural size, attached to a stone; some of the individuals contracted, others extended.
- Fig. 2. Magnified view of an individual extended.
 - a, a, a, a. Blastostyles; b, b, b, b. Gonophores; c, c, c, c. Claspers; d. Basal portion of the hydranth invested with its perisarc; e, e. Processes of attachment.
- Fig. 3. Magnified view of an individual contracted.

PLATE 56.

- Fig. 1. Transverse section of the hydranth at some distance behind the mouth. Magnified.
 - a. Endoderm; b. Villi-like processes of endoderm projecting into gastric cavity; c. Ectoderm; d, d, d. Tentacles.
- Fig. 2. Portion of transverse section of hydranth, still more magnified.
 - a. Endoderm; b. Villi-like processes from the free surface of endoderm; c, c. Small spherical cells loaded with coloured granules, and terminating the villi; d. Thin stratum of homogeneous protoplasm extending over the free surface of the endoderm; e, e, e, e. Pseudopodial processes emitted from the protoplasmic stratum, along with which fine vibratile cilia are also seen extending into the gastric cavity; f. Base of a tentacle; g. External layer of cellular ectoderm; h. Internal layer of same (clavate tissue); i. Hyaline lamella.

- Fig. 3. Longitudinal section through summit of tentacle, much magnified.
 - a. Rod-like tissue; b. Pedunculated capsules.
- Fig. 4. Thread-cells.
 - a. Oviform thread-cell in its quiescent state; a'. Same, with the filament ejected; b. Fusiform thread-cell in its quiescent state; b'. Same, with the filament ejected.
- Fig. 5. Cells of ectoderm of tentacle liberated at the commencement of putrescent histolysis. In each of the two larger cells may be seen a thread-cell.
- Fig. 6. A portion of the hyaline lamella with its attached clavate tissue, from the body of the hydranth.
 - a. Clavate tissue; b. Fibrillated layer of the hyaline lamella; c. Delicate structureless layer of the same lamella.
- Fig. 7. Some of the rods of the bacillar tissue of tentacle, greatly magnified.
- Fig. 8. One of the pedunculated sacs, with its contents, from the tentacle isolated.
- Fig. 9. The capsule, with its contained cord liberated from the pedunculated sac.
- Fig. 10. The capsule after the ejection of the cord, which is still attached by one end to its summit.
- Fig. 11. Distal extremity of a clasper.
 - a. Endoderm; b. Hyaline lamella; c. Clavate tissue; d. External layer of ectoderm; e. Extension of ectoderm with its clavate tissue greatly developed over the distal end of the clasper.
- Fig. 12. Isolated cells of the clavate tissue from the distal extremity of a clasper.
- Fig. 13. Distal extremity of one of the transitory arms of the actinula.
 - a. Modified claviform tissue, which here forms the whole thickness of the ectoderm; b. Endoderm with axial cavity; c. Capitulum.
- Fig. 14. Pedunculated sac from the capitulum of one of the transitory arms of the actinula.
 - a. The pedunculated sac with its contents still undisturbed; b. The capsule liberated from the sac and with its spiral cord ejected.
- Fig. 15. Distal extremity of actinula, showing the peculiar development of the clavate tissue at the extreme end (a), which acts as a sucker of adhesion.

PLATE 57.

- Fig. 1. Very early stage in the development of the gonophore.
 - a. Offset from the endoderm of the blastostyle which has pushed itself into the ectederm; b. Gonogenetic chamber filled with a granular plasma; c. Diverticulum from the cavity of the blastostyle; d. Ectoderm of the blastostyle as yet scarcely raised above the general surface.
- Fig. 2. More advanced stage (female); the gonophore has formed a very decided projection from the external surface of the blastostyle, and the gonogenetic chamber has begun to show a differentiation in its contents.

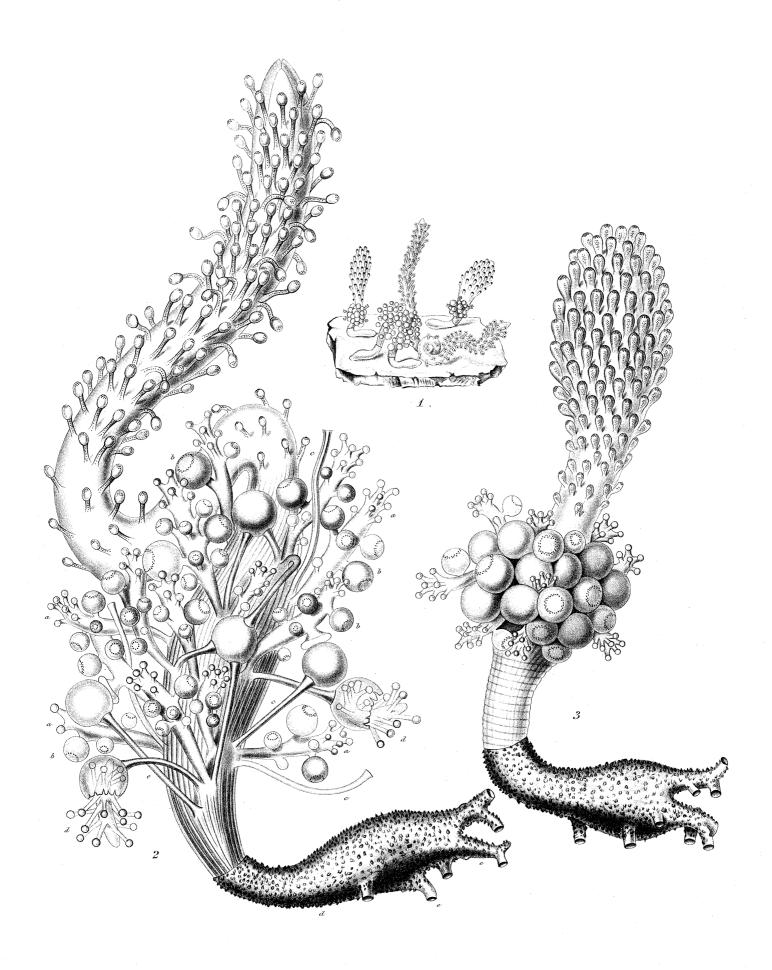
- b. Gonogenetic chamber, in which the contents have become accumulated on the walls and show imbedded nucleus-like bodies; c. Diverticulum from the cavity of the blastostyle; d. Orifice in the endoderm forming the roof of the gonogenetic chamber.
- Fig. 3. A still more advanced stage of the female gonophore.
 - b. Gonogenetic chamber filled with a granular plasma, in which a great number of nuclei have become developed; c. Diverticulum from the cavity of the blastostyle, which with its endodermal walls now projects as a spadix into the gonogenetic chamber; d. Very delicate structureless membrane, which separates the generative mass from the endodermal walls of the gonogenetic chamber.
- Fig. 4. Stage still further advanced. Cell-boundaries have begun to show themselves in the plasma of the gonogenetic chamber, and the nuclei have become surrounded by differentiated masses of protoplasm.
- Fig. 5. Nucleolated nuclei, isolated from the contents of the gonogenetic chamber in fig. 3.
- Fig. 6. Some of the cells forming the contents of the cavity of the gonophore in fig. 4.
- Fig. 7. More advanced stage of the female gonophore. The ovarian tissue has become looser, and now consists for the most part of detached oval masses of protoplasm each with a nucleus and nucleolus. Towards the centre, where they are in contact with the spadix, some of these have coalesced into larger masses.
 - a. Cellular lining of the cavity of the gonophore, where at the summit of the gonophore its cells become loaded with coloured granules, forming a purplish ring which surrounds the orifice.
- Fig. 8. Some of the nucleated oval masses of fig. 7 removed from the gonophore, and seen to have become united to one another by protoplasmic prolongations.
- Fig. 9. A group of the same bodies. Between several of them the union has become closer.
- Fig. 10. Gonophore still further advanced than fig. 7. Nearly all the free oval bodies have coalesced into a small number of large protoplasm masses.a. As in fig. 7.
- Fig. 11. Surface of one of the protoplasm masses of fig. 10, very much magnified, showing the presence of minute pseudopodial projections.
- Fig. 12. Portion of the walls of a mature gonophore (fig. 7), very much magnified, showing details of structure.
 - a. External zone of spherical cells; b. Zone of clavate tissue; c. The fibrillated lamella; d. Cellular lining of the gonophore cavity; e. Very thin structureless membrane directly investing the generative elements; f. Generative elements.
- Fig. 13. Structure of plasmodium formed by coalescence of the simple ova.

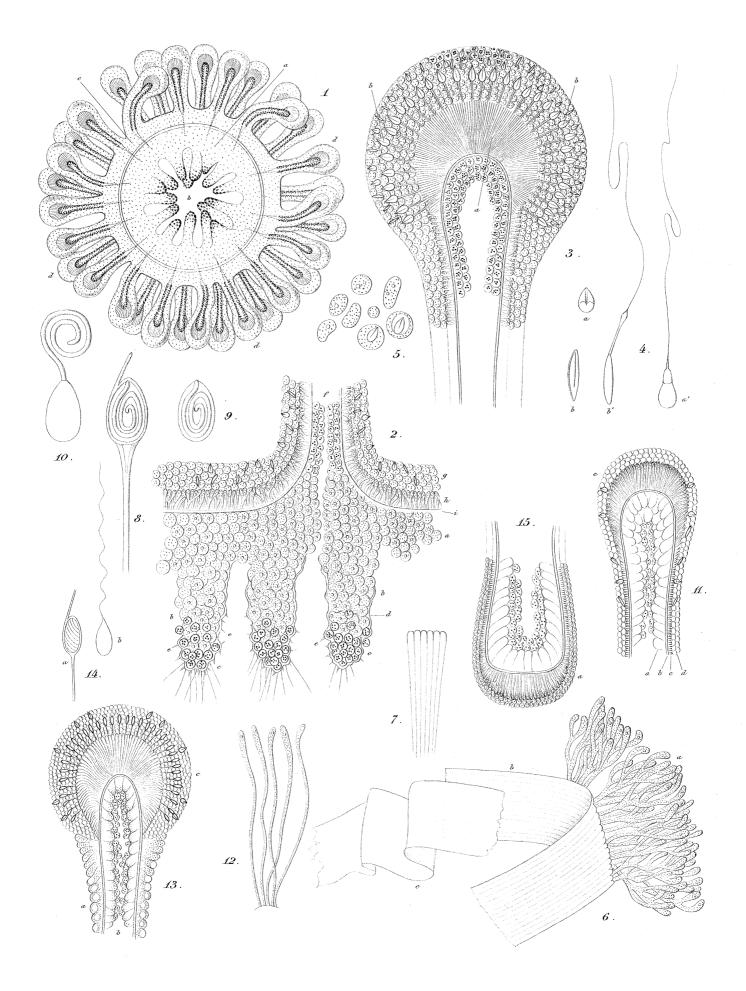
- Fig. 14. Part of a blastostyle with gonophores, plasmodia, and claspers.
 - a. Blastostyle; b, b. Claspers; c, c. Young gonophores; d. A mature gonophore, with the plasmodium escaping through its summit; e. Walls of gonophore retracted and everted after the liberation of the plasmodium; f. Plasmodium liberated from the cavity of the gonophore, but still held in in its place by the spadix, and already seized by a clasper. The plasmodia (d and f) present a lobed condition at the part turned towards the blastostyle, owing to the coalescence of their constituent plasma masses being here still incomplete; g. A plasmodium entirely withdrawn by a clasper from its original position on the summit of the gonophore peduncle.
- Fig. 15. A male gonophore filled with the generating vesicles of the spermatozoa.
- Fig. 16. Mature free spermatozoa.
- Fig. 17. Structure of the plasmodium shortly after its seizure by the claspers.

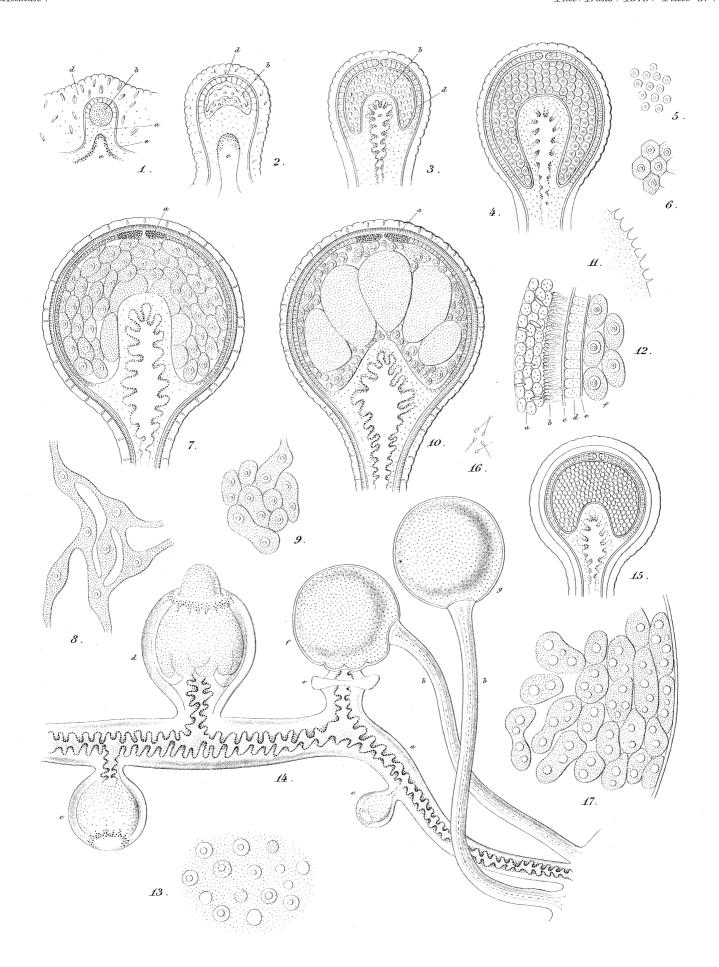
PLATE 58.

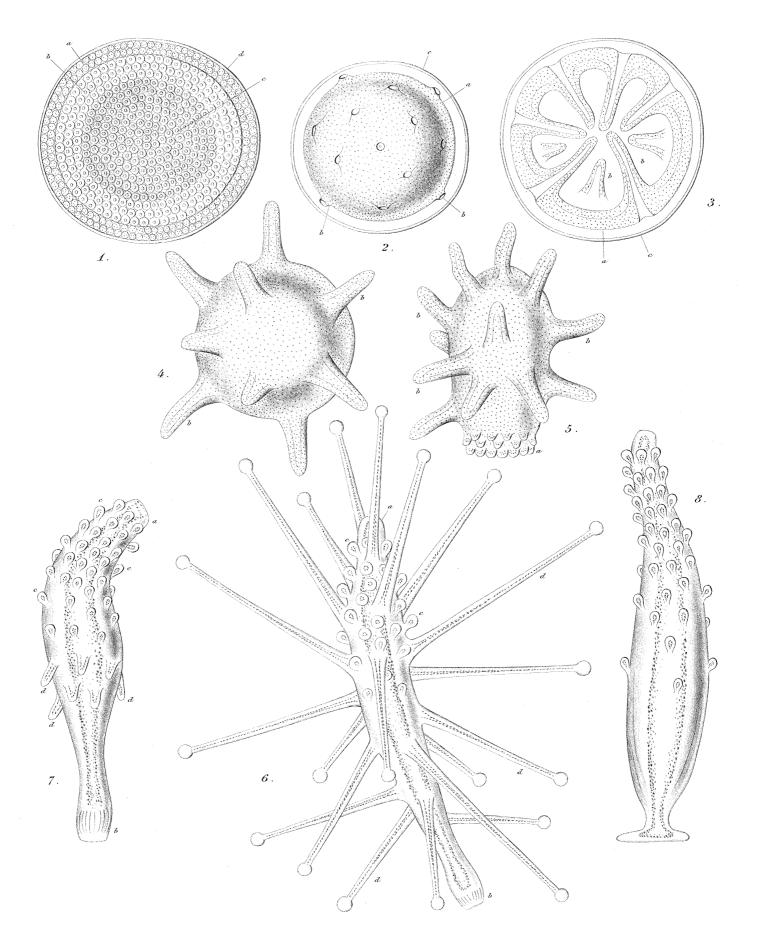
Fig. 1. Planula.

- a. Ectoderm; b. Endoderm; c. Cavity of planula; d. External structure-less capsule.
- Fig. 2. Embryo after the walls of the planula had become invaginated to form the transitory arms.
 - a. Body of the embryo; b, b. Orifices of involution; c. External structureless capsule.
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 - a. Body of the embryo; b, b. Arms formed by involution of the walls of the embryo; c. External structureless capsule.
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 - b, b. The evaginated arms.
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 - a. Commencement of permanent tentacles; b, b, b. Transitory arms.
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 - a. Distal extremity; b. Proximal extremity; c, c. Permanent tentacles; d, d, d. Long transitory arms fully developed.
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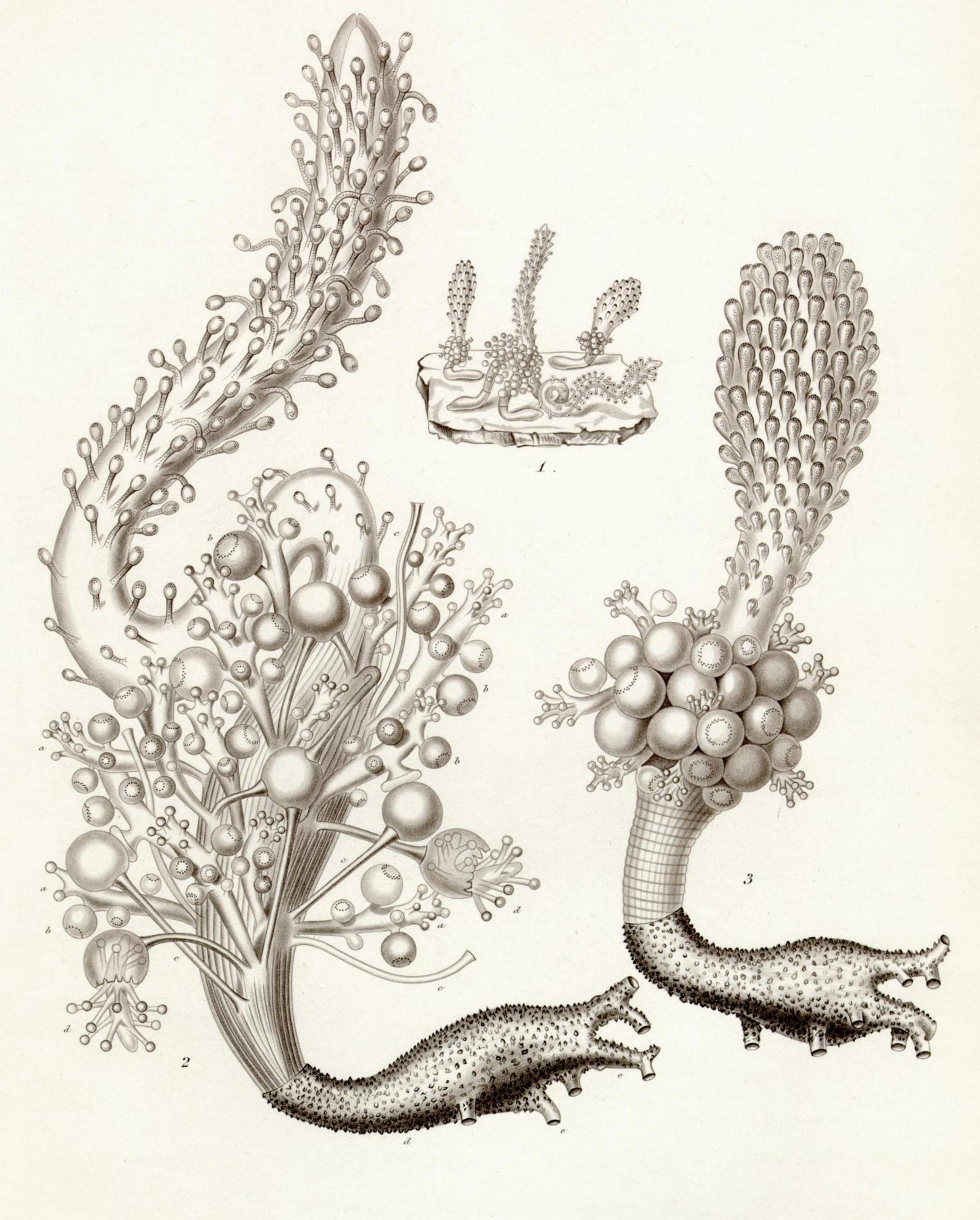


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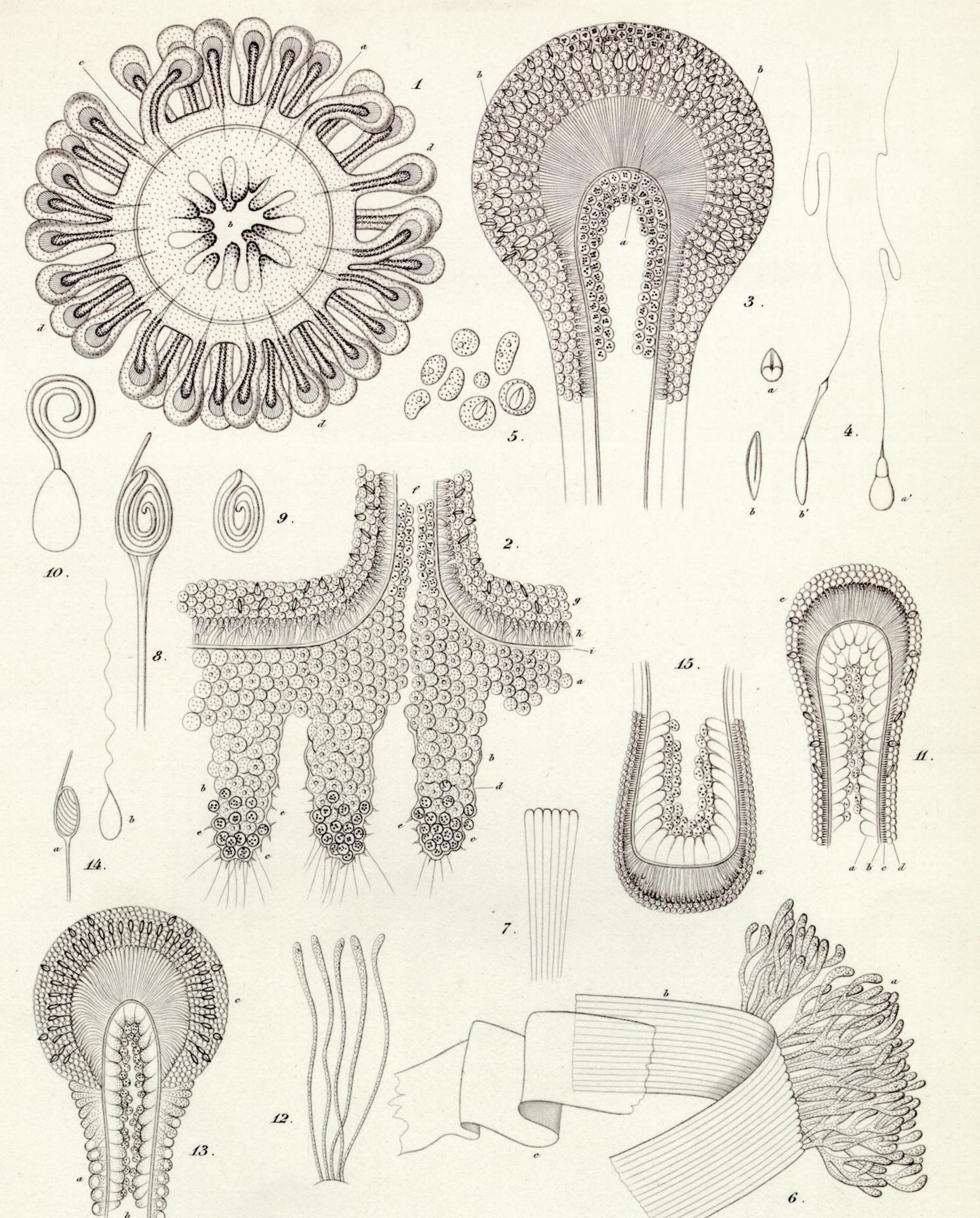


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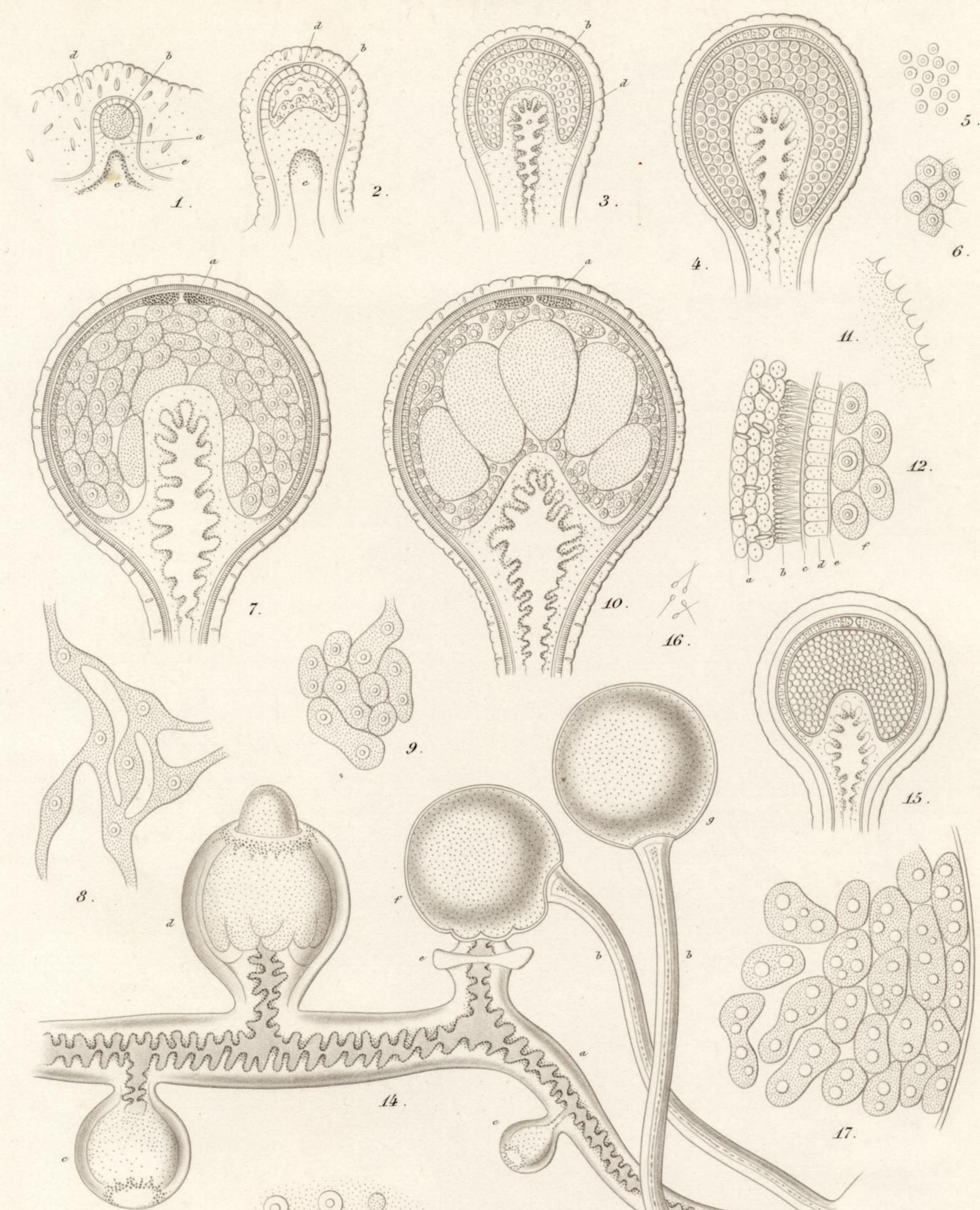


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13.

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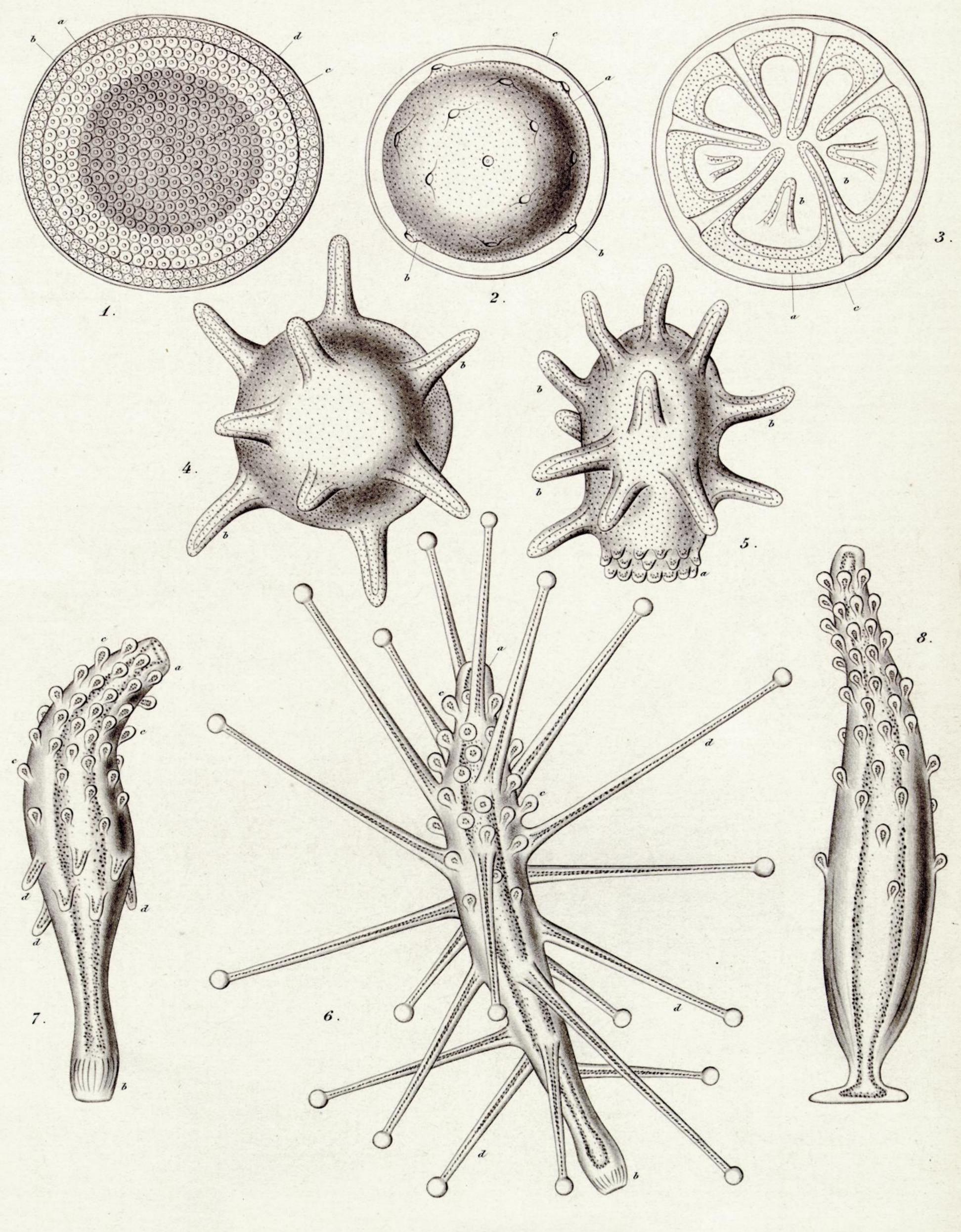


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