On a Free-swimming Hydroid, Pelagohydra mirabilis, n. gen. et sp.

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With Plates 1 and 2.

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1. INTRODUCTION.

The remarkable organism which forms the subject of the present memoir was picked up by myself on the sandy beach at Sumner, a small watering-place near Christchurch, on the east coast of the South Island of New Zealand. One evening in October last (1901), while walking on the shore, I saw lying at my feet a small gelatinous object which had evidently just been thrown up by the tide. On placing it in a glass of sea water I soon saw that it was still alive, and that it exhibited very unusual features, differing widely from any pelagic organism with which I was acquainted. After studying it for some time with the aid of a pocket lens I took it up to my laboratory at Christchurch, and continued my examination of the living animal the same night. Being unwilling to risk the attempt to keep it alive until the next morning, I then killed it by the addition of osmic acid to the sea water, and preserved it in alcohol. It was unfortunate that the lateness of the hour prevented me from making a more exhaustive examination of the living organism, as more light might have been thereby thrown upon its movements and habits; but it seemed best to try and make sure of having it well preserved for minute investigation subsequently, and in this I was fairly successful. The action of the osmic acid was, as might have been expected in the case of so large an organism, very unequal, some of the more superficial parts being much blackened, while the interior was apparently not affected at all, and consequently turned out to be not in so good a condition for minute histological investigation as I could have wished. Had I suspected how complicated and remarkable the structure of the interior really was I might have thought it best to cut the organism in half in order to allow the osmic acid to penetrate, but as it was it did not seem to me desirable in any way to mutilate the unique specimen at that early stage of the investigation.

It was very soon obvious that the organism was an enormous free-swimming hydroid, from the greater part of the surface of which numerous little medusoids were being budded off in groups. Being about to pay a visit to England, however, I postponed the greater part of the investigation until after my arrival, when I resumed the work in the zoological laboratory of the Owens College. It affords me very great pleasure to express my thanks to Professor Hickson and his staff for the kind hospitality which I received at their hands, and for the valuable assistance rendered to me during the progress of my research.

2. Notes on the Living Animal.

The free-swimming hydroid person of Pelagohydra mirabilis (fig. 1) is apparently a pelagic organism. The conditions under which it was found, its subsequent behaviour when observed in sea water, and its peculiar organisation, all point to this conclusion. When placed in a glass of sea water in front of a candle (it was too dark to examine it by daylight) it floated near the surface with the narrow proboscis-like portion of the body, bearing the mouth at its extremity, hanging downwards from the much larger balloon-like structure, which I propose to call the "float." The latter, though near the surface, was totally submerged. Subsequently, when placed in a tin can for removal to the laboratory and kept in the dark, the animal sank to the bottom, though still alive. Probably, therefore, it has the power of rising and sinking in the water like other pelagic organisms, and it may be that it always sinks to some depth beneath the surface when it is dark. The general colour of the organism was a very pale bluish tint, and it was of course translucent. The proboscis, however, was pale pink, intensified round the margin of the mouth. The manubria of the medusoids were also pink. During life the hydroid exhibited some slight power of changing its shape, the float being at one time oval (slightly elongated vertically) and at another contracted into a sphere, while the proboscis exhibited considerable power both of contraction, under which condition it became slightly trumpet-shaped at the end, and of flexion. When both elongated, as shown in fig. 1, the float was nearly an inch in greater diameter and the proboscis rather more than half as long as the float.

The long, slender, tentacular processes of the float occasionally exhibited spasmodic movements of flexion, like gigantic flagella, many of them simultaneously, or nearly so; and from this I am led to conclude that the animal has the power of rowing itself through the water by means of these organs.

Whether the medusoids naturally separate from the hydroid I cannot say from direct observation. They exhibited slight twitching movements of contraction, however, while still attached to the parent, and the structure of the larger ones leaves no doubt that they ultimately become free-swimming. Moreover many of them became detached when the organism was killed.

3. The Hydroid.

(*a*) External Characters.—The body of the hydroid is, as compared with the ordinary hydroid type—such as we see, for example, in Tubularia,—greatly modified in form and structure, and the modification is such as to bring about the necessary adaptation to the changed conditions of life. The usual stalk is entirely wanting, nor is there the slightest indication of its having ever existed. The aboral portion of the body is enormously swollen out, and quite evenly rounded off at the upper pole, forming the nearly spherical "float." To the lower pole of the float is attached the cylindrical "proboscis," bearing the mouth at its extremity. The line of junction between the float and the proboscis is well marked even externally, and corresponds to an even more pronounced internal demarcation between the two.

The float carries numerous long tentacles, which are scattered without any definite arrangement at approximately equal distances from one another all over its surface. These tentacles are cylindrical and bluntly rounded at the extremity, never distinctly knobbed. When fully extended they may be about as long as the float itself. For the most part they are, as usual amongst the Hydrozoa, unbranched, but two or three were observed each with a single branch (figs. 3, 5, *B.T.*), this condition being probably abnormal.

The proboscis is differentiated transversely into two portions (fig. 2). The upper part bears no tentacles, and exhibits an appearance of circular and longitudinal striation, The lower part, next to the mouth, bears numerous tentacles of greatly varying size; these are arranged, not quite regularly, in transverse rows or whorls, and decrease in size from the uppermost whorl, which contains the largest, towards the mouth, around the margin of which the tentacles are very minute. There is altogether a good deal of irregularity about the size and shape of these tentacles, and here again one of them was found to be branched (fig. 2, *B.T.*), but a better idea of their form and arrangement will be gained from the illustration than from any description which I can give.

Scattered all over the surface of the float, between the bases of the tentacles (figs. 4, etc.), are numerous little branching processes, which we may term "stolons." They branch quite irregularly, their branches remaining short and keeping close to the surface of the hydroid. On these stolons are borne groups of very small medusoids in various stages of development, from minute buds to fully formed bells apparently just ready to separate.

(*b*) Internal Anatomy.—The most striking feature of the internal anatomy is the presence of two large cavities, completely separated from one another by a thin horizontal septum, as shown in fig. 5. This septum lies at the level of the junction between the proboscis and the float, and is slightly arched upwards. A preliminary examination reveals the fact that the lower and very much smaller chamber is the main gastral cavity, while the upper one is apparently excavated in the enormously developed mesoglœa between the ectoderm and endoderm of the roof of the gastral cavity: this second and much larger chamber I propose to call the "cavity of the float." Its real origin will be discussed presently. It is not a simple cavity, but is subdivided by what I propose to term the "supporting membranes." On the inner surface of the wall of the float there is a network of canals, which give it a honeycombed appearance. These canals are lined by endoderm, and are in reality continuations of the gastral cavity, into which they open at their lower extremities. I shall speak of them as the "endodermal canals."

The Gastral Cavity.—The main gastral cavity, then, occupies only the interior of the proboscis, but is continued upwards into the float in the form of endodermal canals. The lining membrane of the main gastral cavity is thrown into numerous very prominent longitudinal folds, forming ridges which project inwards (figs. 5—9, *L.G.R.*), and whose edges, in the contracted specimen, are very sinuous (fig. 6). At a short distance below the septum the gastral cavity widens out somewhat, and the ridges almost die away. At the junction of the septum with the outer wall of the gastral cavity a prominent annular fold projects into the latter (figs. 7, 8, *A.F.*).

The Endodermal Canals.—Above the fold just mentioned, around the margin of the septum, which is otherwise imperforate, lie the openings of the endodermal canals (figs. 7, 8, *Op. End.*). From the network which these canals form on the inner surface of the wall of the float (figs. 5, 6, *End. C.*) short branches are given off outwards, which run into the stolons; but the canals themselves have apparently no communication with the tentacles (fig. 8).

The Septum.—The septum which separates the main gastral cavity from the cavity of the float is a thin but firm membrane. As already stated, it is somewhat arched upwards. Its two surfaces are both smooth, but to the upper one are attached some of the supporting membranes in the chamber of the float (figs. 5—8). It is, as already stated, imperforate, except for the openings of the endodermal canals, and in this respect differs from either of the two "diaphragms" in the gigantic Branchiocerianthus imperator, which in some respects certainly resembles our hydroid.[1]

The Cavity of the Float.—The cavity of the float is very spacious, but it is subdivided by numerous very thin,

[1] *Vide* Miyajima, 'Journ. Coll. Sci. Imp. University of Tokio,' vol. xiii, p. 235, etc.

transparent, membranous sheets, which radiate outwards from a more solid mass of tissue formed by their union nearly in the middle of the chamber, and which have their edges attached to the inner surface of the wall of the float and to the upper surface of the septum. These remarkable structures I have called the "supporting membranes." The inner surface of the wall of the chamber exhibits a honeycombed appearance, being marked out into roundly polygonal areas by the projecting endodermal canals. In the centre of each depressed area between the endodermal canals a knob-like projection may frequently be seen; this is caused by the tissue which fills the cavity of the tentacle projecting inwards into the chamber of the float like a plug (figs. 6, 8, *Ten. Pl.*). These structures we may call the "tentacle plugs."

The Tentacles.—All the tentacles are filled with a highly vacuolated tissue, composed of sheets or strands of delicate membrane. In the case of the tentacles of the float this tissue may, as just stated, project as a plug into the float cavity. In the proboscis the mesoglœa in the wall of the gastral cavity is, in the neighbourhood of the tentacle bases, much thickened and highly vacuolated, giving rise to cavities of considerable size, and this vacuolated tissue is continued into the tentacles (figs. 8, 9). The exact nature and origin of the tissue which thus fills the interior of all the tentacles are, however, by no means easy to determine, and the question will be best dealt with under the next heading.

(*c*) Histology.—Pelagohydra exhibits, for a hydroid, a remarkable amount of histological differentiation. For purposes of description it will be most convenient to subdivide this part of our subject according to the different regions of the body, rather than to attempt to follow out each layer completely before passing on to the next. Indeed, as we shall see later, in some parts of the body the delimitation of the layers is by no means always obvious—at any rate, in the case of the endoderm.

As already indicated, the histological preservation of the internal tissues is not all that could be desired, and it is greatly to be hoped that an opportunity may arise of working out this subject more in detail with the aid of material specially treated for the purpose. It is also highly desirable that a detailed comparison should be made of the histological structure of Corymorpha, Monocaulus, and Branchiocerianthus, which are evidently related to Pelagohydra, and, like it, of exceptional size.

Wall of the Proboscis.—The ectoderm is a thick layer densely charged with small, darkly staining nuclei and thread-cells irregularly scattered throughout its substance (figs. 9, 10, *Ect.*).

In section it exhibits numerous fine radial lines running in at right angles from its outer surface, and perhaps indicating the boundaries of a single layer of large prismatic cells. On its inner aspect, immediately contiguous to the mesoglœa, is a well-developed layer of longitudinal muscle-fibres. In transverse sections (fig. 10) we see that this layer, consisting of an approximately single row of fibres, is thrown into longitudinal folds, the mesoglœa being produced outwards in plate-like ridges between the folds. This arrangement, so well known in the mesenteries of the Actinians, no doubt serves to increase the extent of the muscular tissue.

The ectoderm decreases in thickness from below upwards, and the folding of the muscular layer is especially conspicuous just above the region of the tentacles, and dies away as it approaches the upper limit of the proboscis. Between the bases of the proboscis tentacles the ectoderm is extremely thick, but thins out greatly over the tentacles themselves.

The endodermal lining of the proboscis wall is enormously thick, and throughout the greater part of its extent is thrown into prominent longitudinal folds or ridges in the manner already described (figs. 5—9). The structure of these ridges (figs. 9—11) is very peculiar. The mesoglœal supporting lamella which divides the endoderm from the ectoderm is not continued into them, and is indeed sharply marked off by another layer of muscle-fibres, which we may consider to be endodermal in origin. These fibres are arranged in a circular manner at right angles to those of the ectoderm (fig. 10), and the extent of the muscular layer is increased by horizontal folds, similar to the vertical folds of the ectodermal layer. These horizontal folds are, of course, recognisable only in vertical sections, while the vertical folds of the ectodermal musculature are conspicuous in transverse section (fig. 10).

The free surfaces of the gastral ridges bounding the gastral cavity are covered with an epithelium of a very peculiar type (figs. 9—11). It consists of long, slender, columnar cells arranged at right angles to the surface. They have a finely granular cytoplasm and distinct nuclei, and appear in the sections to be collected into small groups, like bundles of cigars, from the inner ends of which delicate wavy fibres run obliquely towards the central plane of the ridge, and thence inwards side by side till they meet the mesoglœal supporting lamella, where they probably give rise to the circular musculature.[1] The grouping of the epithelial cells into bundles is, I think, probably a post-mortem condition due to contraction in alcohol. I imagine that the cells are normally arranged so that each is continued inwards into a separate fibre. We may probably regard the endoderm of the gastral ridges as glandular-muscular in function, for no doubt it secretes the digestive fluid. There are no thread-cells in the gastral ridges, nor, indeed, have I seen them in any part of the endoderm. On approaching the annular endodermal fold which marks the upper limit of the proboscis the gastral ridges gradually die away, and their epithelium gives place to that which lines the gastral face of the septum on the one hand, and the endodermal canals on the other (fig. 8).

The mesoglœal supporting lamella of the proboscis wall may be regarded as being bounded on the outside by the

[1] Compare the structure of the endodermal villi with their muscle-fibres in Myriothela (Hardy, 'Quart. Journ. Micr. Sci.,' vol. xxxii, p. 505).

ectodermal, and on the inside by the endodermal layer of muscle-fibres respectively. It is continued into the folds of the muscular layers, and also into the annular fold of endoderm. It has the usual clear gelatinous appearance,[1] and though everywhere more or less distinct, attains its maximum development in the neighbourhood of the tentacle bases, where it appears to become immensely thickened, and at the same time broken up by large vacuoles into a network of irregular sheets (figs. 8, 9). It may possibly be invaded in this region by cells migrating from the endoderm, as will be described later in the case of the supporting membranes of the float; but this point I have not been able to determine.

Tentacles of the Proboscis.—The larger tentacles of the proboscis are identical in structure with those of the float, shown in transverse section in fig. 15. The outer wall of the tentacle is formed by a single layer of short columnar cells; it is highly vacuolated, and abundantly charged with thread-cells in all stages of development; on its inner face is a well-developed single layer of longitudinal muscle-fibres. A more or less distinct layer of mesoglœa comes next, crossed in places by slender strands (of protoplasm?) extending inwards from the ectoderm, while the axis of the tentacle is occupied by an irregular network of sheets continuous with the vacuolated mesoglœa of the proboscis wall. Here and there over the surfaces of these thin and apparently structureless sheets are scattered very well-defined bodies, which may be either small isolated cells with small nuclei, or, as I am inclined to think, themselves large nuclei with conspicuous nucleoli. These bodies are flattened against, or perhaps in the thickness of, the septa which separate the enormous vacuoles from one another. When seen en face they are nearly round, and about 0·0125 mm. in diameter. Their protoplasm stains fairly deeply, especially that of the small enclosed body, and is scarcely at all granular. It is note-

[1] It seems probable that the fibrillated character of the mesoglœa described by Allman and Miyajima (loc. cit.) in Branchiocerianthus may be due to the ectodermal and endodermal muscle-fibres attached to it.

worthy that two of these large nuclei may be found lying close together, side by side, on the same side of one septum, which seems to indicate that each cavity in the axial tissue is not simply the enlarged vacuole of a single cell. Though abundant in the tentacles themselves, the large nuclei are, so far as my experience goes, not to be found in the vacuolated mesoglœa with which the axial tissue of the tentacle becomes continuous in the proboscis wall.

Owing partly to the specimen being somewhat injured in the neighbourhood of the mouth (possibly by being washed about by the tide on the sand, with mouth downwards), I have been unable to make a satisfactory investigation of the minute structure of the smallest tentacles. It is evident, however, that these conform much more closely to the ordinary Tubularian type than do the large ones. This may be chiefly owing to their smaller diameter, which enables the membranous septa to stretch right across transversely and more or less parallel with one another, so as to divide the interior into approximately a single row of chambers, surrounded by a very thick layer of mesoglœa inside the ectoderm. Thus it would seem that the axis of the smallest tentacles is occupied by a single row of large vacuolated endoderm cells as usual. Whether even in the smallest tentacles these axial cells retain their connection with the endodermal lining of the gastral cavity is extremely doubtful. In the case of the large tentacles there is no trace of any connection remaining between the axial tissue and the endoderm of the gastral cavity,[1] and the origin of this tissue must remain doubtful. It has probably been originally derived from the endoderm, but it has become so modified in structure and so completely disconnected that perhaps only embryological research can decide the question.

W a l l o f t h e F l o a t.—The wall of the float forms but a comparatively thin shell, enclosing the central cavity with its remarkable system of supporting membranes. The histological characters of the ectoderm (fig. 12, *Ect.*) are very

[1] Compare Miyajima's remarks on *Branchiocerianthus*, loc. cit.

similar to those of the corresponding layer in the wall of the proboscis. It is, however, less distinctly muscular. In the immediate neighbourhood of the tentacles it retains the characters which it exhibits in the tentacles themselves, being comparatively thin, and having the muscle-fibres arranged radially in continuation with the longitudinal muscular layer of the tentacle. Elsewhere the ectoderm is thick and very densely crowded with thread-cells.

The Endodermal Canals.—The lining epithelium of the endodermal canals, directly continuous with that of the gastral cavity proper, is differentiated into two very distinct portions, differing greatly in histological character. The canals are somewhat flattened against the wall of the float; their own outer walls form part of the thickness of the latter (fig. 12), and are lined by a layer of large epithelial cells with rounded club-shaped ends projecting into the lumen. These cells have very large vacuoles and small round nuclei, and their very darkly staining granular contents are collected together in or near their swollen club-shaped ends (fig. 12, *End. O.*). They also contain darkly staining spherical globules of various sizes. The epithelium forming the inner walls of the endodermal canals, on the other hand, consists of a single layer of smaller cells, approximately cubical in shape, with small nuclei and only a small quantity of faintly staining, finely granular cytoplasm (fig. 12, *End. I.*).

The Supporting Membranes of the Float.—The thin transparent sheets of membrane which subdivide the cavity of the float (figs. 5—8, 12, *Sup. Mem.*) appear to have a very remarkable structure and origin. Each sheet consists of a thin structureless layer of mesoglœa (fig. 13, *Mes.*), thickening at the angles where the sheets meet one another. Spread out on each surface of this mesoglœal sheet is a still thinner layer of finely granulated, frothy-looking protoplasm, containing rounded nuclei irregularly scattered through it (fig. 14). No cell boundaries can be distinguished in my preparations, but the protoplasm appears to form a vacuolated syncytium. It may occasionally be collected or drawn together into a thick rounded blob or drop, containing many nuclei (fig. 13), but this condition appears to be of rare occurrence. Probably the nuclei multiply by division, as indicated in fig. 14, at *x*. This peculiar tissue appears to originate, in part at any rate, from the inner walls of the endodermal canals.[1] The mesoglœal portion of these walls may be very thick, and occasionally little groups of cells (fig. 12, *End. Bud*) may be seen growing into it from the endodermal lining of the canal. These cells have very finely granular contents and small nuclei. Irregular cavities (fig. 12, *D. F. C.*) are apparently developed between them, and gradually enlarge until the nuclei become widely separated, while the mesoglœa is reduced to thin sheets separating adjacent cavities from one another, and the protoplasm of the endoderm cells becomes spread out over these sheets in the form of a granular syncytium.

Sometimes, where a comparatively thin layer of mesoglœa lies behind the endoderm of the inner wall of an endodermal canal, threads of finely granular protoplasm may be seen stretching at right angles through the mesoglœa from the one surface (covered by the finely granular syncytium) to the other (covered by the endodermal cells of the canal wall).

Thus it appears that the supporting membranes of the float originate in a peculiar manner from the endoderm. It is not certain, however, that they do not receive cells from the external ectoderm also, for thread-cells in various stages of development may sometimes be observed in places where the mesoglœa is thick, beneath the external ectoderm and doubtless derived from the latter. This inward migration of the cnidoblasts can hardly be looked upon as normal, but if they are able to migrate inwards it seems equally possibly that other ectoderm cells may do the same, and possible eventually take part in the formation of the supporting membranes.

[1] Professor Ray Lankester has pointed out to me that a somewhat similar method of tissue formation has been observed in the "laminar tissue" of Amphioxus (vide Pouchet, "On the Laminar Tissue of Amphioxus," 'Quart. Journ. Micr. Sci.,' vol. xx, n. s., p. 421, pl. xxix).

The Septum.—The histological structure of the septum which divides the main gastral cavity from the cavity of the float is practically identical with that of the inner walls of the endodermal canals, with which it is directly continuous. On its lower face it is covered by a layer of lightly staining cells with small nuclei and finely granular contents, and this is separated by a moderately thick layer of mesoglœa from the finely granular syncytium which covers its upper surface. Some of the supporting membranes of the float are attached to its upper surface, and probably originate from the septum in the same way as those already described originate from the inner walls of the endodermal canals.

Tentacles of the Float.—The tentacles of the float are histologically identical with the large tentacles of the proboscis, as will be seen by comparison of fig. 15 with the description already given. The peculiar manner in which the axial tissue seems to project into the cavity of the float in the form of a cushion or plug has already been referred to. In the projecting plug, however, when best developed, the network of tissue is made up chiefly of a finely granular frothy syncytium, with very little mesoglœa and small nuclei. In the tentacle itself the granular material is hardly recognisable, the septa (fig. 15, *S.M.T.*) are very thin, and the nuclei (fig. 15, *Nu.*) much larger and of a different character, like those in the proboscis tentacles. Thus the "plug" seems to be to some extent transitional in character between the true axial tissue of the tentacle and the very much coarser reticulation formed by the supporting membranes in the interior of the float. It is not always recognisable as a distinct structure, however, and even where best developed it passes gradually into the axial tentacular tissue beyond, while its apparent histological differences may be in part due to the want of penetration of the osmic acid with which the specimen was hardened.

The endodermal canals come very close to the bases of the tentacles, and we may be pretty certain that the axes of the latter are endodermal in origin, though, as in the case of the proboscis tentacles, embryological research may be required before we can say exactly how they arise.

The Stolons.—The stolons are simply branching hollow outgrowths of the wall of the float in the neighbourhood of the endodermal canals, which are prolonged into them to their extremities (figs. 8, 12, *St.*). The ectoderm (fig. 12, *Ect.*) is composed of the usual large clear cells, rectangular in longitudinal section, with small nuclei pressed against their dividing walls. At its base lies a feebly developed layer of longitudinal muscle-fibres. Thread-cells are almost entirely wanting. The mesoglœa is thick, and traversed by slender threads crossing from ectoderm to endoderm. The endoderm (fig. 12, *End.*) is simply a continuation of the endoderm which lines the outer walls of the endodermal canals, and, like the latter, is composed of large cells, often with rounded extremities projecting into the central lumen, with enormous vacuoles and darkly staining contents massed together either in the rounded end or elsewhere. They have small nuclei, and in addition contain darkly staining spherical globules of various sizes.

The Thread-cells.—The thread-cells (figs. 16, 17) are of large size. The actual nematocysts or capsules are approximately ovoid in shape, but truncated at the somewhat narrower outer ends, and measure, when fully developed, about 0·0128 mm. in longer diameter. Each one is more or less enclosed in a delicate cnidoblast (fig. 17, *cnb.*). When fully developed the thread-cells lie in the outer parts of the large ectoderm cells just beneath the surface, and the cnidoblast is prolonged inwards to the base of the cell in the form of a long thread—the cnidopod[1] (figs. 16, 17, *Cnp.*). The cnidopod is remarkably distinct and tough, so much so that when the ectoderm of a tentacle has been abraded, so that the large ectoderm cells have disappeared, the cnidopods may still remain projecting from the surface like hairs, with or without the thread-cells still attached to their extremities.

[1] Compare Allman, 'Challenger Reports,' "Hydroida," Part 2, p. xv, for the use of this term.

I have seen no thread-cells with the threads everted, and have not been able to make out any details with regard to the thread itself. No barbs were visible in my preparations. Smaller thread-cells, in various stages of development, lie in the deeper parts of the ectoderm.

4. The Medusoid.

(*a*) Structure.—Although no free-swimming medusæ have as yet been observed, there can be little doubt that they normally separate from the parent hydroid. As already pointed out, they exhibit movements of contraction while still attached, and separate very readily in the process of killing and preserving. Moreover none of the medusæ, which were found attached to the hydroid in large numbers, were sexually mature, and the largest were only about 1 mm. in longer diameter of the bell.

In the largest examples the bell is considerably deeper than wide, and nearly square, though with rounded angles, in cross-section (figs. 22—24). The mouth of the bell is still very narrow (fig. 23), probably expanding considerably later on. It is surrounded by the velum, around which the margin of the bell has grown out into four arms or lobes, arranged in the form of a cross, per-radially, corresponding to the angles of the bell. Each of these arms bears five tentacles arranged in a very peculiar manner—a pair of larger ones, a pair of smaller ones, and a very small odd one; the largest being furthest from the mouth, the odd nearest to the mouth, and the remaining pair intermediate in position, as shown in fig. 23. All the tentacles are short, even in the living animal, and they are only very slightly if at all swollen at their extremities. It is possible that the number of tentacles increases as the medusa grows older, but their peculiar and definite arrangement seems to indicate that the full complement is already present. The tentacles are filled with solid endoderm formed in the usual manner, while the arms or lobes upon which they are borne are characterised by an enormous thickening of the ectoderm, containing numerous thread-cells.

At the aboral apex of the bell is a depression, where the exumbrellar ectoderm dips in to meet an outward extension of the endodermal lining of the gastral cavity. This marks the spot where the young medusa is attached to the stolon (fig. 22, *Z.*).

The manubrium (figs. 22, 25, *Man.*) is large, but does not project beyond the mouth of the bell. Its surface is smooth, and there are no outgrowths at its extremity.

The subumbrellar cavity is, in the middle, somewhat octagonal in transverse section (fig. 25), being produced into four shallow per-radial angles where the ectoderm is attached to the radial canals, and four deeper interradial angles where it is attached to the endodermal lamella. Immediately beneath the subumbrellar ectoderm cells is a layer of transverse ("circular") muscular fibres, and the entire epithelium with its musculature is thrown into transverse folds, as shown in figs. 22—24. Towards the mouth of the bell the cross-section of the subumbrellar cavity becomes square, the interradial angles alone remaining.

The gastral cavity immediately above the manubrium is cruciate in transverse section, the four arms of the cross being produced outwards into the radial canals, and the endoderm being greatly thickened between them to form four ridges. In the manubrium itself the gastral cavity is squarish or irregular in section, with a variable number of longitudinal endodermal ridges.

The four radial canals present no features of special interest, nor does the thin endodermal lamella by which they remain connected. Near the margin of the bell they open into the circular canal (fig. 22, *c. can.*), enlarged per-radially in the tentacle-bearing arms and then produced to form the solid axes of the tentacles.

No gonads are yet recognisable, but the ectoderm of the manubrium exhibits a thickening all round about the middle of its length, which probably indicates the position in which they will subsequently appear.

There appear to be no sense-organs, and I have not satisfied myself as to the existence of a nerve-ring. In life there is a pink spot on the outside of the base of each tentacle group, and the manubrium also is more or less pink in colour.

(*b*) Development.—The medusæ are developed as hollow outgrowths or "buds" from the branching stolons already described, and each stolon may bear as many as half a dozen at the same time in various stages of development. As soon as one medusoid approaches maturity another bud (fig. 20 A) appears on the stolon close to its point of attachment, ready to replace the first when it falls off.

The youngest buds observed are represented in figs. 20 A and 18 B; each is a single hollow outgrowth of the stolon, composed of ectoderm and endoderm, but the thick mesoglœa of the stolon disappears almost if not quite completely in the bud (fig. 20). The ectoderm and endoderm also change their character, becoming much more compact and solid-looking, and staining much more darkly.

In the next stage (fig. 18 C) the endocodon is formed from the ectoderm at the apex of the bud. There is, in the section represented in the figure, some appearance of invagination, but if not at first solid the endocodon speedily becomes so.

The endocodon grows inwards, and at the same time the endoderm invaginates as if pushed before it (figs. 18, 19), forming a deep cup. The bottom of this cup is then pushed outwards again through the endocodon to form the hollow, finger-like manubrium, which makes its appearance very early (fig. 20).

Meanwhile the cells of the endocodon arrange themselves in a single layer over the outer surface of the manubrium, the inner surface of the future subumbrella, and the inner surface of the future velum (fig. 20). These layers are at first in close contact, but ultimately the subumbrellar cavity makes its appearance between them.

While these changes have been going on the original gastral cavity of the bud becomes further subdivided by the union of its inner and outer walls interradially (fig. 21) to form the solid endodermal lamella, thus defining the four radial canals and the circular canal. The ectoderm becomes greatly thickened outside the circular canal, and the tentacles begin to grow out.

Hitherto ectoderm and endoderm have everywhere remained in close contact (figs. 20, 21), but the transparent gelatinous mesoglœa now appears and forces the layers apart (fig. 25). About the same time the subumbrellar cavity is developed and the velum is ruptured in the middle (fig. 20, w.), giving rise to the mouth of the bell (fig. 23).

5. Discussion of Results, Relationships, etc.

Pelagohydra mirabilis is a remarkably interesting organism from several points of view. In the first place it forms an excellent example of adaptation to changed conditions of life, showing us how a representative of a group whose members are normally attached, in the hydroid phase, to the ends of fixed stalks may become adapted to a free-swimming pelagic existence. In the second place it exhibits remarkable structural features, especially in the complication of the gastral cavity with its endodermal canals, and the development of the float with its extraordinary supporting membranes. It also has very striking histological peculiarities, showing in this respect a degree of differentiation perhaps unequalled in any other hydroid.[1]

As a pelagic member of a typically non-pelagic group of animals we may compare it with Pelagonemertes amongst the Nemertines, Tomopteris amongst the Annelids, and Pelagothuria amongst the Holothurians, and it may

[1] The gigantic Branchiocerianthus imperator probably resembles Pelagohydra closely in histological features, but requires further investigation (vide Miyajima, 'Journ. Coll. Sci. Imp. University of Tokio,' vol. xiii, p. 235, etc.).

possibly throw some light upon the origin of that remarkable pelagic group of Hydrozoa the Siphonophora, although it will perhaps hardly bear close comparison with any known member of that order.

That it is an aberrant Tubularian hydroid there can, I think, be no doubt, and its nearest relations appear to be the enigmatical Corymorpha and its allies.[1] In the genus Corymorpha we also find that there is no true stalk, and the curious prolongation of the body by which the animal fixes itself in the sand or mud is, I believe, homologous with what I have termed the float in Pelagohydra. In Corymorpha also we have a system of endodermal canals forming a network around a spongy central mass, and communicating at one end with the main gastral cavity. Then, again, in Corymorpha curious processes are given off from the surface of the body in the neighbourhood of the endodermal canals, which may be homologous with the stolons of Pelagohydra, or possibly with the tentacles of the float. Little is known, however, of the minute anatomy and histology of Corymorpha, and a careful investigation in comparison with Pelagohydra is greatly to be desired. There are, of course, sufficiently striking differences between the two forms, but these are of a more superficial character, and mainly to be accounted for by the difference in mode of life. Instead of a float we find in Corymorpha a kind of rooting process, and the tentacles are confined to one end of the elongated body, where they are arranged in a proximal and a distal set, the latter obviously representing the tentacles of the proboscis in Pelagohydra. The position of the stolons, between the two sets of tentacles, is totally different; and the medusæ also are quite distinct, for in Steenstrupia, the medusa of Corymorpha, we find a single odd tentacle, representing one only of the four tentacle groups of the Corymorpha medusa. In both cases, however, the medusæ are markedly quadriradiate, and essentially similar in internal organisation; while in Amalthæa, which appears to

[1] Allman, 'Tubularian Hydroids,' p. 386, etc.

be closely related to Corymorpha, all four tentacles are developed.

It is a very curious fact that two distinct genera of Tubularian hydroids agreeing in such striking anatomical peculiarities should have become adapted to two such different modes of life, the one swimming freely in the open ocean, and the other rooting itself in the sand at the bottom. It would indeed be difficult to find a better example of the powers of adaptation to divers conditions of life. So far as I am aware there is no other hydroid yet known which has become specially adapted to a pelagic mode of life. It is true that floating hydranths—Acaulis and Nemopsis—are known, but these have probably become detached from stalks, and are not structurally adapted to a free-swimming existence.

6. Diagnosis of New Genus and Family.

Genus Pelagohydra, n. gen.—Hydroid solitary, free-swimming; the proximal portion of the body modified to form a float, supported internally by a system of radiating membranes of endodermal origin; the distal portion forming a flexible proboscis, with the mouth at its extremity. Gastral cavity continued from the proboscis into the float in the form of endodermal canals, from which arise branching stolons. Tentacles filiform, scattered over the surface of the float and in whorls around the mouth. Medusæ developed on stolons between the tentacles of the float; quadriradiate, symmetrical, probably with gonads in the wall of the simple manubrium; tentacles in four per-radial groups of five (possibly more in the adult).

The genus may be regarded as belonging to a distinct family, for which I propose the name Pelagohydridæ, and for which the generic diagnosis may at present suffice. This family is, however, closely related to the "Corymorphinæ" of Delage and Herouard;[1] indeed, some zoologists might

[1] 'Traité de Zoologie concrète:' "Les Cœlenterés," p. 88.

prefer to modify and extend their conception of the Corymorphinæ so as to include Pelagohydra (as the authors referred to include the Hybocodonidæ and Monocaulidæ of Allman) in preference to making a new family for its reception.

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7. DESCRIPTION OF PLATES 1 & 2.

Illustrating Professor Dendy's memoir on "Pelagohydra mirabilis."

Explanation of Lettering.

A.F. Annular fold of endoderm around the margin of the septum. *B.T.* Branched tentacles. *C.Can.* Circular canal. *Cnb.* Cnidoblast. *Cnp.* Cnidopod. *D.F.C.* Developing float cavities. *Ecn.* Endocodon of medusa bud. *Ect.* Ectoderm. *End.* Endoderm. *End.Bud.* Buds of endoderm growing into the mesoglœa from the inner walls of the endodermal canals. *End.C.* Endodermal canal. *End.I.* Endoderm of inner wall of endodermal canal. *End.L.* Endodermal lamella of medusa. *End.O.* Endoderm of outer wall of endodermal canal. *E.U.E.* Exumbrellar epithelium of medusa. *Fl.* Float. *G.C.Man.* Gastral cavity in manubrium. *L.G.R.* Longitudinal gastral ridges of endoderm. *Man.* Manubrium. *Med.* Medusæ in various stages of development. *Mes.* Mesoglœa. *M.F.Ect.* Ectodermal muscle-fibres. *M.F.End.* Endodermal muscle-fibres. *Mo.* Mouth. *Nu.* Nucleus. *Op.End.* Openings of endodermal canals into gastral cavity. *Pr.* Proboscis. *R.Can.* Radial canals. *Sep.* Septum between the main gastral cavity and the cavity of the float. *S.M.T.* Internal supporting membranes of the tentacles. *St.* Stolons. *S.U.C.* Subumbrellar cavity. *S.U.E.* Subumbrellar epithelium of the medusa. *S.U.M.* Subumbrellar muscular layer of the medusa. *Sup.Mem.* Supporting membranes of the float. *Syn.* Vacuolated syncytium covering the supporting membranes of the float. *T.C.* Thread-cells. *Ten.Fl.* Tentacles of float. *Ten.Pr.* Tentacles of proboscis. *Th.A.* Thin area of wall of float around tentacle base. *w.* The point where the ectoderm of the young medusa ruptures to form the opening in the velum. *x.* Nucleus in syncytium apparently dividing. *y.* Point of attachment of subumbrellar epithelio-muscular layer to endodermal lamella. *z.* The place where the medusa was attached to the stolon.

Figs. 1—17 inclusive refer to the hydroid stage of Pelagohydra mirabilis; Figs. 18—25 inclusive refer to the medusoid stage of the same.

Fig. 1.—The free-swimming hydroid, from a sketch of the living animal. × 2.

Fig. 2.—External view of a piece cut out of the preserved specimen, showing the arrangement of the proboscis tentacles, etc. × 7.

Fig. 3.—Three adjacent tentacles of the float, showing variation in shape, from the preserved specimen.

Fig. 4.—Portion of the surface of the float, much enlarged, showing the stolons with the developing medusæ, lying between the bases of the tentacles.

Fig. 5.—The preserved specimen after removal of a portion of the wall, showing the gastral cavity, septum, float cavity, supporting membranes of float, endodermal canals, etc. × 4.

Fig. 6.—Internal view of the piece represented in Fig. 2, showing septum, longitudinal gastral ridges, endodermal canals, etc. × 7.

Fig. 7.—Portion of the same turned so as to show the under surface of the septum, with the annular fold of endoderm and the openings of the endodermal canals into the main gastral cavity. × 7.

Fig. 8.—Diagrammatic longitudinal section through a portion of the wall, showing the relations of the internal cavities, septum, endodermal canals, supporting membranes, tentacles, stolon, medusa buds, etc.

Fig. 9.—Part of a transverse section of the wall of the proboscis, through the bases of the larger tentacles and the longitudinal gastral ridges of the endoderm. Drawn under Zeiss objective A, oc. 2, camera outlines.

Fig. 10.—Portion of a transverse section similar to and near the last, to show especially the arrangement of the muscle-fibres. Drawn under Zeiss objective D, oc. 2, camera outlines.

Fig. 11.—Portion of a transverse section of one of the longitudinal gastral ridges, showing the endodermal epithelial cells continued into muscle-fibres. Drawn under Zeiss objective F, oc. 2.

Fig. 12.—Part of a transverse section through the wall of the float, showing an endodermal canal continued outwards into a stolon, and giving rise to supporting membranes of the float by means of groups of cells budded off from its lining epithelium. Drawn under Zeiss objective C, oc. 2, camera outlines (slightly diagrammatic).

Fig. 13.—Part of a transverse section of a supporting membrane from the interior of the float, showing the mesoglœal layer covered on each side by a syncytium, here collected on one side into a rounded multinucleate mass of protoplasm. Drawn under Zeiss objective F, oc. 2, camera outlines.

Fig. 14.—Surface view of one of the supporting membranes of the float,

showing syncytium and nuclei. Drawn under Zeiss objective F, oc. 2, camera outlines.

Fig. 15.—Part of a transverse section of a tentacle from the float. Drawn under Zeiss objective D, oc. 3, camera outlines.

Fig. 16.—Part of the ectoderm layer from a section similar to the last. Drawn under Zeiss objective F, oc. 2, camera outlines.

Fig. 17.—Two thread-cells with their cnidoblasts and cnidopods, from one of the tentacles of the float. Drawn under Zeiss objective F, oc. 2.

(In Figs. 18—21 inclusive, showing stages in the development of the medusæ, the histology is, for the sake of clearness, rendered diagrammatically; the endoderm is shaded; the external ectoderm is unshaded, and the ectoderm of the endocodon and its derivatives is unshaded but has the nuclei represented by dots. All are drawn, with the aid of the camera lucida, under Zeiss objective D, oc. 2.)

Fig. 18.—Two young medusa buds seen in longitudinal section,—B before the formation of the endocodon; C with the endocodon and manubrium developing. (Owing to slight obliquity of the sections, the cavity of the stolon is not shown.)

Fig. 19.—Slightly older medusa bud in longitudinal section.

Fig. 20.—Still older medusa bud in longitudinal section, with a very young bud also springing from the same stolon at A.

Fig. 21.—Transverse section of a medusa bud a little older than the last, showing the radial canals, etc.

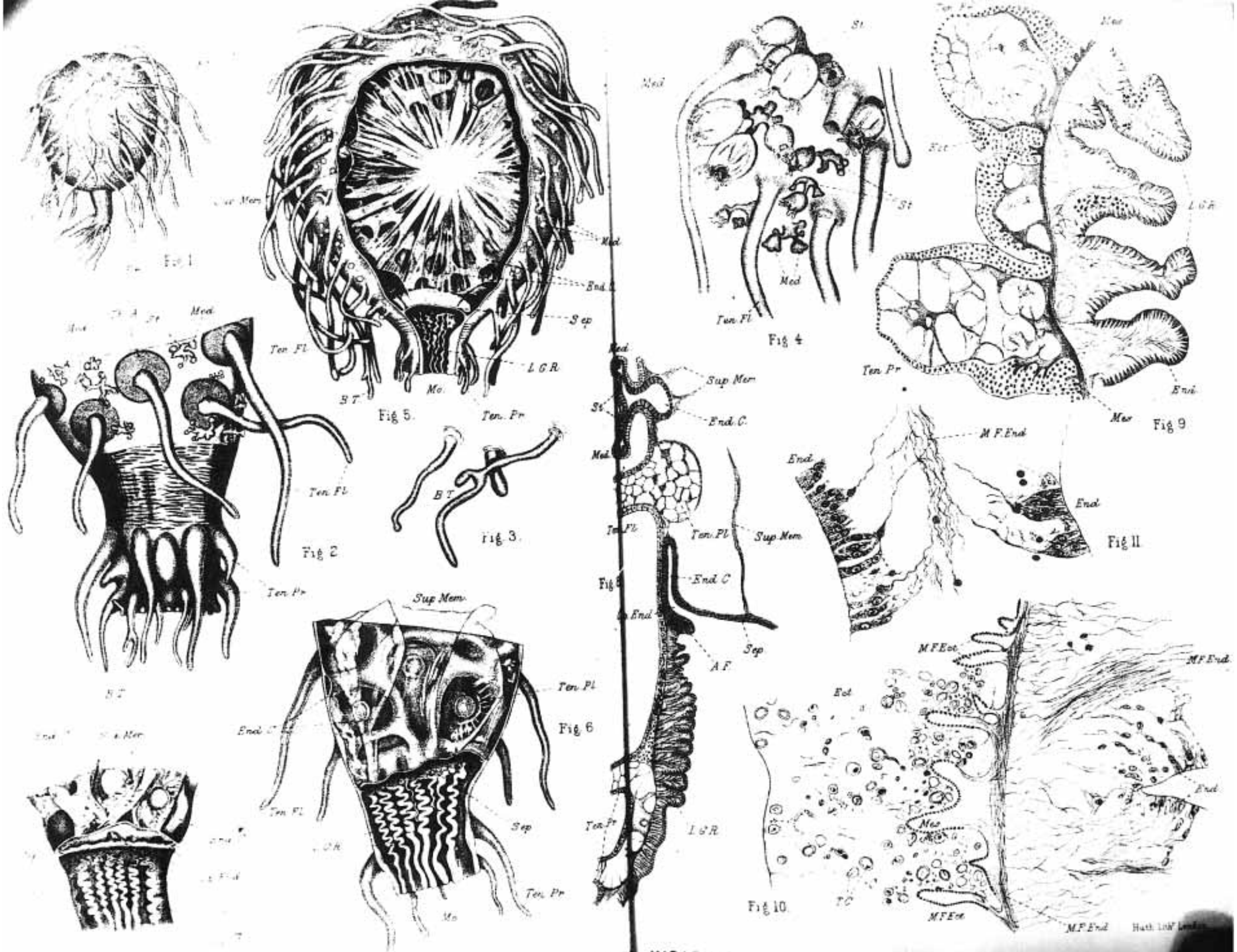
Fig. 22.—Side view of one of the oldest medusæ found. Drawn from spirit specimen under Zeiss objective A, oc. 1, as a transparent object.

Fig. 23.—Oral view of similar specimen under similar conditions. The mouth of the bell is now visible in the middle of the velum, between the four tentacle-bearing arms.

Fig. 24.—Aboral view of similar specimen under similar conditions, showing the four radial canals, subumbrellar musculature, etc.

Fig. 25.—Transverse section of a medusa of about the same age. Drawn under Zeiss objective A, oc. 3, camera outlines.

Note.—The microscopical sections were all stained with borax carmine.



PELAGOHYDRA MIRABILIS.

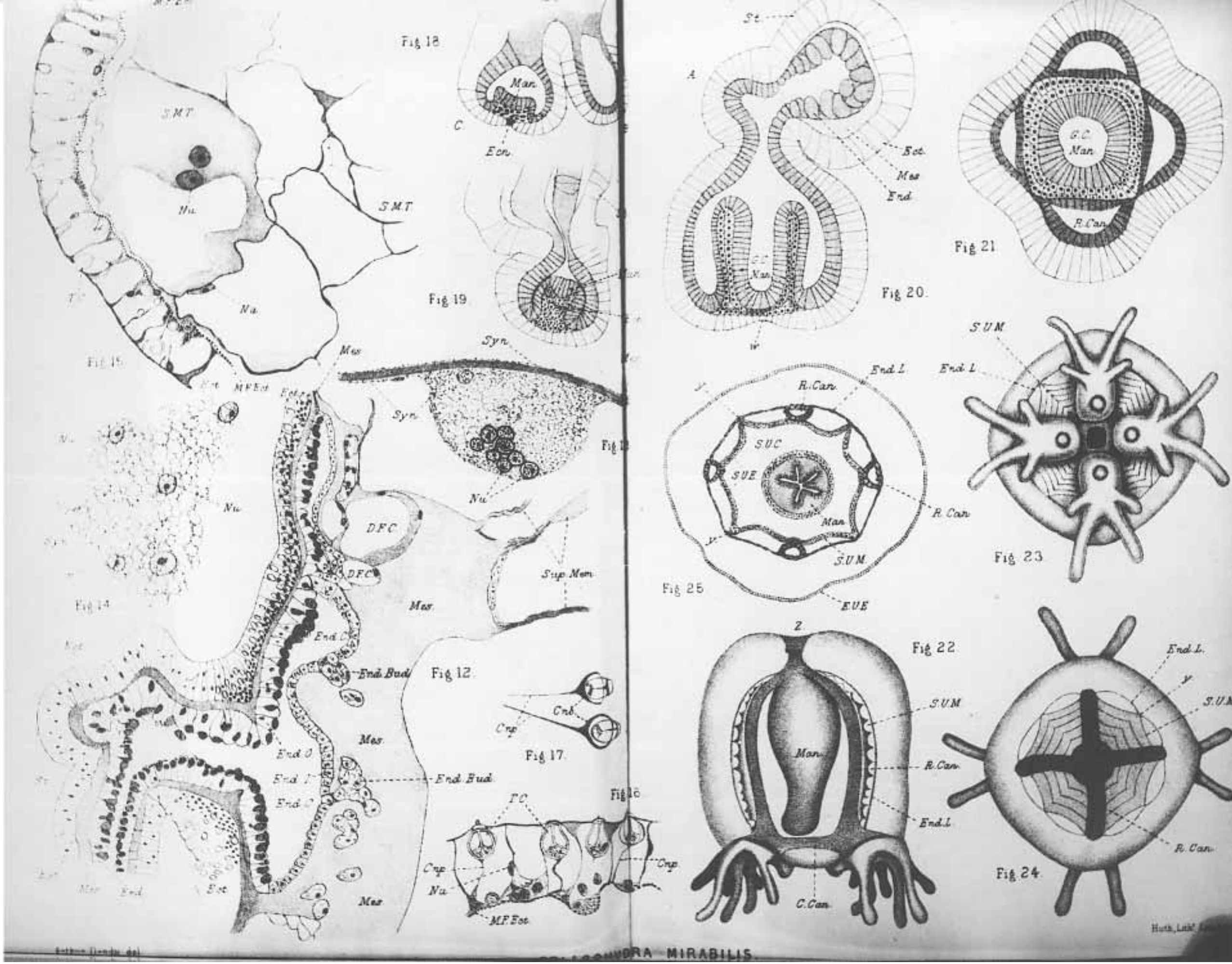


Fig 12
Fig 14
Fig 15
Fig 16
Fig 17
Fig 18
Fig 19
Fig 20
Fig 21
Fig 22
Fig 23
Fig 24
Fig 25
S.M.T.
Nu
Mes
Syn
D.F.C.
Sup. Mem.
End. Bud
End. C
End. O
End. I
Cnb.
Cnp
T.C.
M.F.Ect.
Man.
Ecn.
St.
Ect.
End
G.C.
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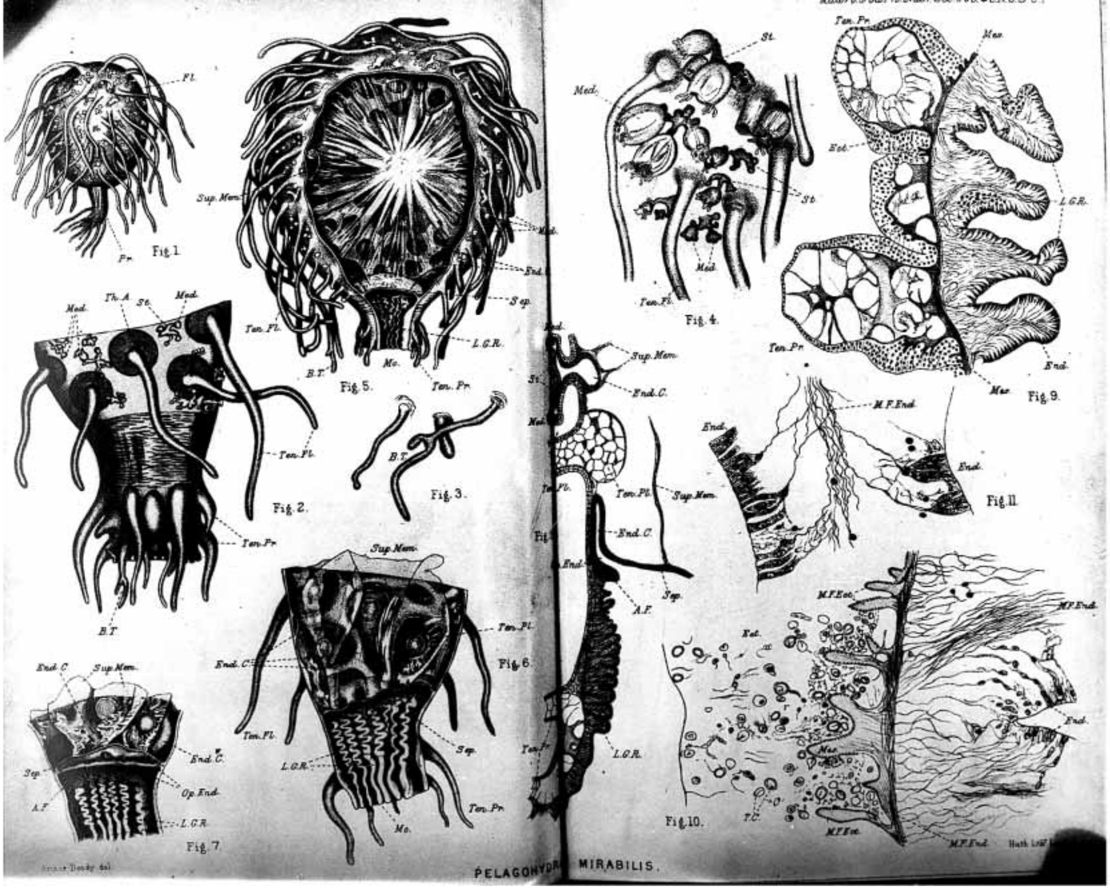

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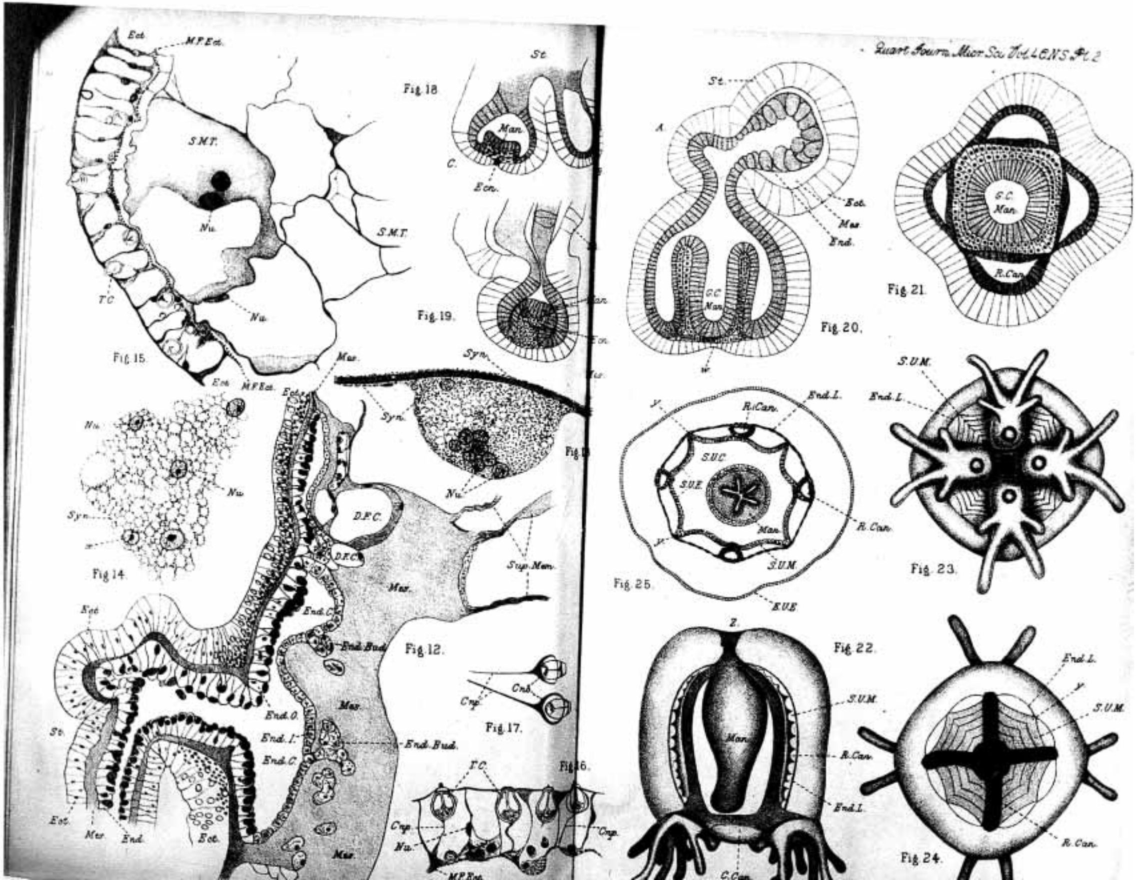
Fig. 15.
Ect.
M.P.Ect.
S.M.T.
Nu.
T.C.
Fig. 18
St.
Man.
C.
Ecn.
Fig. 19.
Syn.
Mes.
Fig. 14
Syn.
Fig. 12.
D.P.C.
Sup.Mem.
End.C.
End.Bud.
End.O.
End.I.
Fig. 17.
Cnb.
Cnp.
Fig. 16.
Fig. 20.
G.C.
Ect.
End.
Fig. 21.
R.Can.
S.U.M.
End.L.
Fig. 23.
Fig. 25.
S.U.C.
S.U.E.
E.U.E.
Fig. 22.
Z.
C.Can.
Fig. 24.