XV. *On the Anatomy and Physiology of* Cordylophora*, *a contribution to our knowledge of the Tubularian Zoophytes. By* George James Allman, *M.D., M.R.I.A., Professor of Botany in the University of Dublin, and Examiner in Zoology and Botany in the Queen's University in Ireland. Communicated by Professor* Edward Forbes, *F.R.S.*

Received May 31,—Read June 16, 1853.

Though the attention of several physiologists has been directed to the Tubularian Zoophytes, and though the elucidation of many points of interest in their structure and in the physiological phenomena presented by them has been the result, yet in numerous most important particulars our knowledge of the *Tubulariadæ* is still very imperfect, notwithstanding the great value which a more thorough acquaintance with these simple organisms must possess in its bearing upon some of the leading questions in physiology.

It was with the view of filling up some of the deficiencies which still exist in our knowledge of the lower zoophytes, that the following researches were undertaken; and *Cordylophora lacustris*, affording as it does a fine typical example of tubularian structure, and being easily kept alive for months, was deemed peculiarly favourable for prolonged and careful observation; the results, moreover, which have been obtained from the investigation of this zoophyte, have been in many instances confirmed and extended by corresponding inquiries, instituted at the same time into the structure of allied genera.

It is certain that considerable confusion as well as much cumbrous circumlocution might be avoided, by giving greater precision and completeness to the terminology employed in the description of structure among zoophytes. With this view, I propose in the first place to employ the word *polype* in its most restricted sense.

* The genus *Cordylophora* may be characterized as follows:—

Fam. Tubulariadæ.

Genus Cordylophora, Allman.

Char. Gen.—*Polypi* tentaculis numerosis sparsis teretibus. *Capsulæ genitales* subsessiles in ramulis ultimis pone polypos affixæ. *Polyparium* pergamentaceum, ramosum, stolone fistuloso repente fixum. *Embryo* liber, subcylindricus, universè ciliatus.

Nomen.—Κορδύλη clava et φορέω fero.

Species unica, *C. lacustris.*

Habitat.—In aquis dulcibus quietis, corpora varia submersa obducens, et locos obscuros amans.

This word is used ambiguously by writers, being often employed to designate the entire composite fabric, the aggregate result of gemmation; while at other times it is intended to indicate each of those peculiar organisms which, almost always furnished with a mouth and tentacula, are developed upon various points of a common living basis, and are eminently characteristic of zoophytic form. In the following paper I shall use the term *polype* strictly in the latter signification; and for the entire mass, whether consisting of a single polype, as in *Hydra*, or of many united into a more or less definite assemblage, it will be sufficiently convenient to employ merely the term *zoophyte**.

Besides the more definite limits within which it is thus necessary to confine the term polype, the requirements of precise description demand the use of a few additional terms. To the common living basis by which the several polypes in a composite zoophyte are connected with one another, I propose to give the name of *cœnosarc*†, and every composite zoophyte will thus consist of a variable number of polypes, developing themselves from certain more or less definite points of a common cœnosarc. The term *polypary* has been used with just as little precision as *polype*, being sometimes employed to express this common connecting basis, and at other times being applied exclusively to the solid protective structures, whether forming for the zoophyte an external covering or constituting an internal axis; the ambiguity which thus results will be got rid of by using the word cœnosarc as here defined, and restricting the term polypary to the solid protective structures of the zoophyte. All the hydroid zoophytes can be proved to consist essentially of two distinct membranes; to the external of these membranes I shall give the name of *ectoderm*‡, and to the internal that of *endoderm*§.

ORGANS FOR THE PRESERVATION OF THE INDIVIDUAL.

1. *Ectoderm and Polypary.*

(*a.*) *Ectoderm.*—The ectoderm (Plates XXV. and XXVI. figs. 3, 4, 9*a*, *a*, *a*) is a well-defined membrane; it is composed of cells, and forms the external layer of the polypes and cœnosarc. Multitudes of *thread-cells* are developed in the substance of the ectoderm. The thread-cells, when in a quiescent state (fig. 5), present the appearance of minute ovate capsules, slightly curved at one end, and with a transparent cylinder occupying about two-thirds of the axis. Under the influence of excitement, one extremity of

* In the following paper the term *zoophyte* is thus used in its restricted application, by which it is confined to the true polype-bearing *Radiata*, and no more convenient or expressive word can be employed for the purpose. If we except the changes which modern research has rendered necessary in removing from the zoophytes of the older authors, the Sponges, Corallines and *Polyzoa*, this term was used long ago in almost exactly the same sense by PALLAS, and by ELLIS and SOLANDER, and some of our best living zoologists are now employing it with similar limitations.

† κοινὸς, σάρξ.

‡ ἐκτὸς, δέρμα.

§ ἔνδον, δέρμα.

the capsule becomes suddenly prolonged into a conical projection, surrounded near its apex by a circle of very minute curved spicula, the capsule at the same instant appearing empty (fig. 6). This phenomenon seems to consist in the sudden eversion through one end of the capsule of a delicate sac which had previously lain invaginated within it, and is generally immediately followed by the projection of a long and fine filament from the free end of the everted sac. The structure of these thread-cells, and the phenomena consequent on excitement, closely resemble what we find in the "hastigerous organs" of *Hydra*. The greater minuteness however of the thread-cells in *Cordylophora* renders it much more difficult to obtain a satisfactory examination of their structure. The thread-cells are developed in the interior of mother-cells (fig. 7), which are themselves secondary cells formed within the ectodermal cells; but I was not able to determine how far their development devolves exclusively upon certain cells of the ectoderm specially devoted to this office. The ectoderm of the tentacula differs slightly from that of the rest of the zoophyte, in the fact of the thread-cells being for the most part collected into groups, which present the appearance of little wart-like excrescences resembling the disposition of the corresponding organs in the tentacula of *Hydra*. At the extremity of the tentacula numerous thread-cells are crowded together, but there is no approach to the capitate terminations which are so striking in *Syncoryne*, and which, among other characters, zoologically distinguish that genus from *Cordylophora*.

(*b*.) *Polypary*.—The polypary (fig. 3 *b*, *b*) is a cylindrical tube investing the stems and branches of the zoophyte, and terminating just behind a short fleshy neck which immediately supports the polypes. On the younger branches it forms a thin, and almost colourless pergamentaceous investment; but in older parts of the zoophyte it is of a yellowish-brown colour, and composed of numerous layers. At the origin of the branches from the main stem, the polypary presents a number of annular corrugations. The cavity of the polypary appears by no means accurately filled by the cœnosarc, and we almost always find a considerable interval between the ectoderm of the cœnosarc and the walls of the polypary; this interval is crossed transversely by numerous processes of the ectoderm (fig. 3 *c*, *c*). It seems, however, almost certain that a very delicate living membrane is in actual contact throughout with the inner surface of the polypary, at least in all its younger portions; and the space which appears to exist between the polypary and the cœnosarc is then nothing but a large *lacuna* of the ectoderm, crossed by fleshy processes, which keep up a communication between its opposite walls. I have distinctly demonstrated the presence of such a membrane in *Syncoryne*, where I have traced the formation of the space in question from a simple lacuna of the ectoderm, though I have not succeeded in so decidedly making out these points in *Cordylophora*. No trace of organization can be detected in the polypary, which in all respects resembles a mere secretion deposited in layers from the ectoderm. Where the polypary terminates anteriorly, an exceedingly delicate transparent pellicle may be traced in continuity with it over the neck and clavate body of the polype, at least as far as the roots of the posterior tentacula.

It is certain that the cavity of the polypary increases in diameter, up to a certain point, with the growth of the animal, a fact which we can reconcile with the account just given of its formation, only by attributing to it a capacity of distension subsequently to its original deposition.

2. *The Endoderm and its Cavity.*

The endoderm (fig. 3, *d*, *d*) constitutes a very distinctly cellular layer; it is in contact throughout with the ectoderm, but is nevertheless distinguishable from it by a very decided boundary, and can only be considered as directly continuous with it at the mouths of the polypes. It forms the walls of an uninterrupted cavity, which, extending through the axis of the entire zoophyte, opens externally at the polype-mouths. This cavity may be divided into four distinct regions, namely, the *post-buccal cavity*, the *stomach*, the *tentacular canals*, and the *canal of the cœnosarc*, a division which, though in some degree arbitrary, will be found very useful in description.

(*a.*) *Post-buccal cavity.*—The post-buccal cavity (fig. 3 *f*) is situated immediately behind the mouth (fig. 3 *e*), which is a simple unarmed orifice placed at the extremity of a conical projection, into which the body of the polype is continued anteriorly. The post-buccal cavity lies in the axis of this projection; its walls are formed of elongated cells, with their long diameter perpendicular to the surface, and its interior is quite destitute of rugæ. It is usually in the form of a narrow tube, and is capable of complete obliteration by the temporary approximation of its walls; it is sometimes, however, dilated into a globular space, and sometimes spread out by a kind of semi-eversion into a nearly flat disc, which I have seen employed by the animal as an organ of adhesion.

(*b.*) *Stomach.*—The stomach (fig. 3 *g*) occupies the whole of the interior of the clavate body of the polype; as the endoderm passes backward from the post-buccal cavity to constitute the walls of the stomach, we find it forming a peculiar tissue composed of elongated cells, whose rounded ends project in prominent masses into the cavity of the stomach, where they constitute large irregular rugæ. The tissue of these rugæ is very remarkable; the cells composing it (fig. 4 *b*) are mother-cells, giving origin in their interior to several free secondary cells with distinct nuclei. In some of these secondary cells the contents are colourless and transparent, and the nuclei are then very evident (fig. 4 *c*); others contain a brown granular matter, by which the nucleus is more or less obscured (fig. 4 *d*); while others may occasionally be found filled with a brood of young cells (fig. 8). Lying apparently free in the mother-cells may also be generally seen, besides the free secondary cells, some rather irregular masses of a deep brown granular substance (fig. 4 *e*). I have found in *Hydra* a structure in all its essential characters entirely similar to this, and we cannot refuse to recognise in it an example of true glandular structure. The secondary cells are obviously true secreting cells, destined by their own rupture and that of the mother-cells to discharge their contents into the cavity of the stomach; while the free granular masses in the interior of the mother-cells were most probably originally contained in secondary cells, of whose secreting action they are the product, and which at a subsequent period had disappeared.

(*c*.) *Tentacular canals.*—The tentacula are hollow processes from the sides of the polypes, and their cavities are simple continuations of that of the stomach. This view is certainly opposed to the appearances presented on a superficial examination, and is at variance with the accounts given by other observers of the structure of the tentacula in the marine *Hydroida*; very careful and repeated observations, however, have convinced me of its truth. It must be admitted, that at first sight, the tentacula, even under well-managed microscopical examination, have exactly the appearance of tubes whose cavity is interrupted at regular intervals by completely formed transverse septa; I have, however, satisfied myself that in *Cordylophora,* and probably also in all the other *Hydroida,* the tube of the tentacula is perfectly continuous. The tentacula consist in reality, like all other parts of the animal, of an external or ectodermic layer (fig. 9 *a*, *a*), which is a simple continuation of the general ectoderm of the body, and of an internal or endodermic layer (fig. 9 *b*, *b*), which is in the same way a continuation of the endoderm of the stomach. The tentacular ectoderm has been already described. The endoderm consists of rather large cells with very delicate walls; it constitutes a thick lining of the tube, and nearly fills up the entire cavity; and indeed this cavity, by a temporary approximation of its walls, appears capable of occasional obliteration. The cells of the tentacular endoderm are glandular, and may be generally seen to contain the peculiar brown granules characteristic of the general endodermic secretion. The appearance of transverse septa is probably due to the occurrence at regular intervals, of interruptions in the continuity of the endodermic layer.

Though the tentacula of *Hydra* present no appearance of the transverse septa, their structure is nevertheless essentially the same as that of the tentacula of *Cordylophora,* the only difference being in the fact that the endoderm forms a thinner stratum in *Hydra,* and thus encroaches less on the cavity of the tube, and does not present the successive interruptions which in *Cordylophora* give rise to the fallacious appearance of transverse septa.

(*d*.) *Canal of the Cœnosarc.*—The cavity of the stomach is continuous posteriorly with the canal of the cœnosarc, fig. 3 *h*. The rounded masses of cells constituting the large rugæ into which the endoderm of the stomach is thrown, cannot be traced further back than the posterior extremity of the clavate body of the polype, and from this point, which may be conveniently though somewhat arbitrarily assumed as the posterior termination of the stomach, the canal of the cœnosarc commences, and thence extends as a continuous tube through all the ramifications of the cœnosarc. In that portion of the canal which immediately succeeds to the stomach, and which is here much contracted, the endoderm resembles in all respects that of the stomach, except in the absence of distinct rugæ; but as the cœnosarc passes backwards under cover of the polypary, the cells lose their elongated form, the endoderm becomes thinner and the canal proportionately wider. Throughout all the rest of the cœnosarc the endoderm is formed of a compact tissue destitute of rugæ, but whose component cells continue to retain their glandular character (fig. 10).

The canal of the cœnosarc is filled with a fluid containing globular and irregular corpuscles of various sizes; these corpuscles may be observed to exhibit a kind of circulatory movement, which however is very irregular; they may be sometimes seen running from below upwards and again turning round in order to take a retrograde course; the motion of each corpuscle is generally confined to a small circuit, frequently not exceeding the diameter of the canal; sometimes many of the corpuscles stop altogether and allow others to pass them, while sometimes no motion whatever can be observed in any of the contents. The corpuscles while moving in their linear paths have besides a peculiar vibratile or tremulous motion in themselves, and this motion may generally be witnessed while the corpuscles are otherwise entirely at rest. The motion of the corpuscles may be traced all through the stems and branches, and even into the stomach. The cause of this phenomenon is very obscure; the existence of vibratile cilia on the walls of the canal might be adduced as an explanation, but these organs have never been made the subject of direct observation, notwithstanding the most careful attempts to demonstrate them; it appears to me that the true cause is to be found in currents produced by the active vital processes going on in the secreting cells of the endoderm, processes which we can hardly imagine to take place without causing local changes in the chemical constitution of the fluids in immediate contact with the cells, and a consequent disturbance of the stability of these fluids.

3. *Muscular System.*

Under this head may be described the only specialized motor apparatus which these animals present. It consists of numerous longitudinal fibres, which are in close contact with the inner surface of the ectoderm. These fibres (fig. 3 *i*, *i*, fig. 4 *f*, fig. 9 *c*) may be seen in all the naked portion of the cœnosarc, and in the body of the polype, and may be thence easily traced into the tentacula, in which they can be followed to the remote extremities of these organs, but they disappear where the cœnosarc passes under cover of the polypary. There can be little doubt that we are correct in considering them as the representatives of a muscular system, and in attributing to them the chief share in effecting the various changes of form which the polypes are perpetually presenting. Similar fibres may be witnessed in *Coryne*, *Syncoryne*, and other marine *Tubulariadæ*, in some of which they are even more distinct than in *Cordylophora*. In none could I detect the least trace of transverse striæ.

ORGANS FOR THE PRESERVATION OF THE SPECIES—EMBRYOLOGY.

The researches of modern naturalists, especially of Ehrenberg, Loven, Van Beneden, Sars, and Dujardin, have thrown much light on the embryology of the inferior zoophytes, and their observations have brought to our knowledge many remarkable and unexpected facts, though physiologists are by no means of one mind as to the true signification of several of the facts with which we have thus become acquainted.

During the later summer and autumn months *Cordylophora lacustris* may be seen with numerous oval capsules borne upon the ultimate or polypiferous ramuli, fig. 2. Each ramulus generally carries one, two, or three of these capsules, which are situated alternately on either side of the ramulus at some distance behind the body of the polype, and where the branch is still covered by the polypary, the more advanced capsules being always nearer to the main stems. They are nearly sessile on the supporting branches, and when fully developed are somewhat larger than the club-shaped bodies of the polypes. They are surrounded externally by a delicate continuation of the polypary, and as they approach towards maturity are found to contain within them either ova or spermatozoa.

The structure and development of these capsules and their contents are exceedingly interesting. The capsule on its first appearance presents itself as a small tubercle, consisting of a simple hernia-like protrusion, or diverticulum of the cœnosarc (fig. 11 *a*), enveloped by a delicate production of the polypary (fig. 11 *b*), and as the cavity of the diverticulum continues to communicate with the common canal of the branch, the contents of the latter pass freely into its interior. As the tubercle increases in size, we perceive that the external investment from the polypary immediately surrounds a sac of distinctly cellular structure, having the diverticulum from the cœnosarc projecting into it below, and having a remarkable system of branched tubes developed on its internal surface (figs. 12, 13, 14). These tubes spring from the sides of the diverticulum with whose cavity their own communicates; they occasionally inosculate with one another, and passing upwards in close connection with the walls of the cellular sac, extend to the summit of the sac where their branches terminate in cæca; they are lined with a layer of cells, which contain secondary cells and brown granules, and which thus resemble the general endoderm of the zoophyte. Thread-cells occur in the walls of the cellular sac, which is plainly referable to the ectodermal system. Between the cellular sac and the diverticulum is a considerable interval, which is filled with a granular fluid.

We next find that in those capsules which are to contain ova a number of spherical dark grey or bluish bodies (fig. 14 *f*) have become apparent in the midst of the granular fluid: these are *ova*; in most of them we may perceive the germinal vesicle in the form of a minute clear point, but the germinal spot is not apparent. The germinal vesicle soon disappears, and when the ova are now examined, the phenomenon of yelk-cleavage may be distinctly perceived in them, fig. 16. In the mean time a delicate structureless pellicle (fig. 13 *e*) has been formed on the external surface of the cellular sac; it is evidently a mere secretion from the surface of the sac, resembling the secretion of the polypary from the cœnosarc. Soon after the commencement of segmentation of the vitellus, the cellular sac with its system of ramified tubes disappears, and the cluster of ova is now distinctly exposed (fig. 15) lying upon the diverticulum from the cœnosarc, and immediately enclosed by the delicate structureless sac formed by the pellicle which had been secreted on the outside of the cellular sac, while the whole is included within the external pergamentaceous investment from the polypary. The ova vary in number; in many capsules I have counted ten, twelve, or even more, while some few contained only two or three.

The mulberry-like condition of the ova at length disappears, and these bodies now begin to elongate themselves, and when viewed by transmitted light, present a transparent margin (fig. 17). As development advances the ova become more and more elongated, and they soon exhibit a slow but evident motion in the interior of the containing sac (fig. 18). They are now in the condition of free embryos, only waiting for the rupture of the enclosing structures to escape into the surrounding medium and enjoy an independent existence. We accordingly soon find that these structures no longer confine them, and the embryos may now be seen escaping from the torn summit of the capsule in the form of infusorial animalcules clothed with short cilia, and swimming freely through the surrounding water (fig. 19).

The embryos on their escape from the capsule are usually of an elongated oval figure (figs. 19, 20), but very contractile, and capable of undergoing considerable change of form; they frequently assume a pyriform shape (fig. 21), but they never appear compressed, and the comparison with a *Planaria*, to which DALYELL and others have likened the embryos of *Campanularia*, will not here strictly apply. They are included in a distinct ectoderm, and contain in their interior a cavity which is separated from the ectoderm by a cellular interval representing the endoderm of the adult zoophyte, but in which the brown granules have not yet shown themselves. No mouth is yet evident, and the ectoderm seems in this early stage destitute of thread-cells.

After the embryo has continued for some time in the condition now described, the period of its final fixation approaches; the cilia disappear; one extremity becomes expanded into a kind of disc, by which it soon attaches itself to some fixed object; the mouth has now become apparent, and thread-cells are developed in the ectoderm (fig. 22); the embryo increases in length and thickness, and from the free extremity, which has begun to assume a clavate form, a single series of tentacula soon shoot forth (fig. 23); these are about four in number, and are situated a little behind the anterior end; the portion of the body which lies before them becomes the post-buccal cavity of the adult; the gastric cavity has become prolonged through the young stem; a delicate polypary has begun to invest it; and its walls begin to be coloured by the characteristic secretion of the endoderm; other tentacula soon shoot forth behind those first formed, and the little *Cordylophora* resembles in all respects, except in size, a full-grown stem with a solitary polype. Its solitary condition however is not long retained; prolongations have already been sent out from its base; these attach themselves to the body on which it grows, and constitute the system of prostrate adherent tubes, while *gemmæ* are soon formed from these tubes and from the free stem, and convert the young single-polyped zoophyte into the adult many-polyped *Cordylophora**.

But besides the ovigerous capsules, a second kind (fig. 24) is developed on certain branches. These differ neither in situation nor in visible organization from the capsules destined to contain ova; their component sacs, internal diverticulum, and ramified canals entirely correspond with those of the ovigerous capsules; but instead of containing ova, they are filled with a turbid fluid, in the midst of which innumerable minute corpuscles may be seen to exhibit a peculiar vibratory movement occasionally visible under slight pressure through the transparent walls, and the same motion is continued in these corpuscles after they are liberated from the containing capsule and spread over the field of the microscope.

That these capsules represent a male system with spermatozoa, there cannot be the least doubt. When liberated from the capsule, the moving bodies show themselves under two different forms; they are either oval corpuscles with an excessively delicate caudal filament (fig. 24 *c*), or they are minute spherical cells (fig. 24 *b*) with a similar caudal filament (by whose undulations the cells are moved about through the surrounding fluid), and enclosing a nucleus-like corpuscle, with which the filament appears to be connected. The former would seem to be the spermatozoa in their free and fully developed condition, while the latter appear to be "vesicles of evolution," in which the body of the spermatozoon is still confined, the tail alone being disengaged. It still remains difficult to explain the mode in which the spermatozoa gain access to the ova. In some cases I have succeeded, under slight pressure, in forcing out the contents through a minute orifice which made its appearance in the summit of the capsule, but this orifice, notwithstanding its definite position, was probably the result of rupture, and I could not detect anything corresponding to it in the ovigerous capsules. It would perhaps be more in accordance with analogy to suppose that the spermatozoa make their way into the cavity of the diverticulum, that they are thus conveyed into that of the cœnosarc, and ultimately reach the ova through the diverticulum of the ovigerous capsules. The male and female capsules appear to be always borne on different stems.

* See an interesting paper by the Rev. THOMAS HINCKS, entitled 'Further Notes on British Zoophytes, with Descriptions of New Species,' published in the Annals and Magazine of Natural History, March 1853.

GENERAL CONSIDERATIONS.

From the description now given, it is manifest that *Cordylophora* (and there is little doubt that we are justified in extending the generalization to all the hydroid zoophytes) consists essentially of two distinct membranes, enclosing a cavity which opens externally by one or more orifices (polype-mouths), and which is prolonged into the interior of a variable number of filiform processes (tentacula)*. The two membranes appear to be essentially secreting structures, but the products of their respective secretory action strikingly differ from one another; for while the cells of the endoderm give origin to secondary cells which secrete a coloured granular substance, which may be fairly assumed as representing the biliary secretion of higher animals, the ectodermal cells give origin to cells of a very remarkable kind, whose characteristic secretion is a peculiar filament, whose import and office are as yet but very imperfectly understood.

In none of these zoophytes can any approach to a specialized circulatory system be discovered; the function of circulation appearing to be represented merely by a gradual transmission of the fluids from cell to cell, depending wholly on the permeability of tissue. A respiratory system is equally without any special representative. Whatever aërating influence the surrounding water exerts must be received through the entire surface of the zoophyte, though doubtless most powerfully through the portion not covered by the polypary. The muscular system has begun to be specialized, but no trace of a nervous system can yet be detected.

The existence of an extensive system of *lacunæ*, as described by Dujardin†, in some marine *Tubulariadæ*, and by Ecker‡ in *Hydra*, where this anatomist describes them as constituting a network of ramified canals, has not been confirmed by my own researches.

The true signification of the reproductive capsules of the hydroid zoophytes is a matter of considerable interest. On this subject much additional light will be thrown by comparing the embryological phenomena of *Cordylophora* with those which are known to occur in the allied genera of the sea. In the marine *Tubulariadæ*, two distinct kinds of bodies are developed besides the ordinary terminal polypes. Of these one consists in medusa-like bodies, which are generally developed at the bases of the tentacula§, and which after a time have been seen to detach themselves from the supporting polype and swim freely away. The other kind of bodies met with in these polypes are peculiar sacs, occupying a similar position to that of the medusoid

* The composition of the hydroid zoophytes out of two distinct membranes has been already pointed out by Huxley (Philosophical Transactions, 1849, Part II.), who has shown that the organs of the *Medusæ* are in the same way essentially composed of two distinct membranes. A very important affinity of structure is thus established between the hydroid zoophytes and the *Medusæ*.

† Ann. Sci. Nat. 3me sér. tome iv. 1845.

‡ Ann. des Sc. Nat. 3me sér. tome 10, 1848.

§ In *Eudendrium* the medusoid bodies are situated at a short distance behind the terminal polypes, and in *Perigonymus*, Sars, they are borne upon every part of the stems and branches.

bodies, but never detaching themselves from the parent, and always after a time filled with ova or spermatozoa*.

In *Campanularia* bodies of highly developed medusan conformation are produced, generally in considerable numbers, in external capsules situated on parts of the polypary always at a distance from the terminal polypes. When arrived at a certain degree of maturity, they escape from the capsule and swim freely through the surrounding water. In the capsules of *Campanularia* another kind of body has been also observed, in which the medusan structure is less complete, and these, after disengaging themselves from the cavity of the capsule, continue attached to its mouth, never becoming entirely free; while a third kind of bodies, corresponding with the fixed sacs of the *Tubulariadæ*, is also borne in the capsules of *Campanularia*†.

In some instances the free medusoid bodies of the *Tubulariadæ* have been found to contain ova, as has been observed by WAGNER‡ in a tubularian polype from the Adriatic, apparently referable to *Hydractinia*, VAN BENEDEN, by LOVEN§ in a *Syncoryne*, and by DUJARDIN|| in another species of *Syncoryne*, whose medusoid was seen to produce ova in the thickness of the stomach-walls. The less perfectly developed medusoids which remain attached to the mouth of the capsule in *Campanularia* have also been observed to contain ova as noted by LOVEN¶; while the previous observation of LISTER**, who saw multitudes of moving bodies escaping from these medusoids, is possibly also an instance of a similar phenomenon, though the form of the moving bodies as described by LISTER leaves a doubt of their being truly embryos; they are probably spermatozoa, and then LISTER's medusoids would be males; a view supported by SHULTZ's†† recent observation, that these attached medusoids of *Campanularia* sometimes contain spermatozoa instead of ova.

Now in *Cordylophora* I have never witnessed the production of medusoids, but I think nevertheless that it will be easily seen that the reproductive capsules of this genus have essentially the same organization as the medusoids of the marine genera. These capsules in an advanced stage exhibit but little of a medusoid conformation, but at an earlier period of their development, as we have just seen, they present us with an organized sac having a hollow central and fleshy column projecting into it below, and furnished with a system of branched canals which are developed on its walls, and communicate at their origin with the cavity of the central column. In this structure we can have no hesitation in recognising a true medusoid type; the organized cellular sac is homologous with the disc of the Medusa, the central fleshy column will represent the peduncle or proboscidiform stomach, while the system of branched tubes will correspond to the gastro-vascular canals‡‡. It is true that neither

* See KROHN in MÜLLER's Archiv. † Vide *infra*, p. 378. ‡ WAGNER in the Isis, 1833. Heft iii.

§ LOVEN in WIEGMANN's Archiv, 1837.

|| DUJARDIN in Ann. des Sci. Nat. 3me sér. tom. iv. 1843. ¶ LOVEN, *l. c.*

** LISTER in Philosophical Transactions, 1844. †† SHULTZ in MULLER's Archiv, 1851.

‡‡ The ramified tubes of the reproductive capsules must, I think, be also assumed as homologous with the tentacles of the terminal polypes. The tentacles of a hydroid polype will thus find their homologues in the gastrovascular canals of a medusa.

disc nor stomach presents any obvious opening in the capsules of the polype, but this is merely a particular and non-essential modification of structure adapted to the function which more especially devolves on them, and it must be recollected that being in direct communication with the common cavity of the parent stem, they are in no need of the admission of nutritive matter from without. Neither does the ramified condition of the tubes, nor the absence of the marginal canal, invalidate the view here taken, for we know that the gastro-vascular canals in certain true Medusæ are ramified, while the closed condition of the disc brings with it the absence of the marginal canal*.

There is a difficulty in the determination of the exact part of the reproductive capsules, which is immediately concerned in the production of the ova or spermatozoa. As soon as ever these bodies become apparent, they are seen to occupy the entire space between the diverticulum and the walls of the inner vesicle. The observation already mentioned, as made by DUJARDIN on a *Syncoryne*, in whose free medusoid the ova were produced in the substance of the stomach-walls, would render it probable that in *Cordylophora* also they had their origin in the part homologous, namely, the central diverticulum, and that from this they became liberated at a very early age to undergo subsequent development in the cavity of the capsule; and this view is further supported by what I have myself observed in the fixed egg-bearing organs of *Sertularia argentea*, to be presently referred to.

With the reproductive capsules of *Cordylophora* we may now compare the fixed ovigerous sacs of the marine genera. It will be seen that these also possess a true medusoid structure, though this is perhaps not quite so easily made out in every case as in *Cordylophora*. In the marine *Tubulariadæ*, the sacs in question consist of a closed vesicle composed of cells, and surrounded externally by a delicate structureless capsule; into its bottom projects a large, hollow, cylindrical and contractile organ, whose cavity is in connection with that of the supporting polype, and round which the ova are developed. Now this central organ corresponds exactly to the central diverticulum in the reproductive capsules of *Cordylophora*, and plainly represents the proboscidiform stomach of a Medusa, while the cellular sac is homologous with the disc. It is true there is nothing here which evidently represents the gastro-vascular canals of the Medusæ and the ramified tubes in the capsules of *Cordylophora*, but there is yet quite sufficient essential resemblance to justify us in referring the reproductive capsules of the marine *Tubulariadæ* to the type of medusoid structure, to which we have just seen that those of *Cordylophora* admit of a close comparison.

In the *Campanulariæ*, besides the bodies of obvious medusoid structure which have been noticed by so many observers to escape from the capsule and then swim freely away, and those of less completely developed, though still obvious medusoid structure which remain attached at the mouth of the capsule, others are commonly seen in the

* The medusoids of the marine *Tubulariadæ* are, during the early stages of their development, contained in a delicate external sac which afterwards disappears. This is the homologue of the external investment of the reproductive capsules of *Cordylophora* and the marine *Tubulariadæ*.

interior of the capsule clustering round the central axis, and described by various naturalists as eggs. In these so-called eggs, however, there may be detected a medusoid structure quite as manifest as in the ovigerous sacs of the marine *Tubulariadæ*; each of them is in fact a fixed Medusa developing within it true ova which possess the germinal vesicle and germinal spot, and present the phenomenon of yelk-cleavage, and after a time escape as locomotive ciliated embryos. It is probable however that in some cases the production of spermatozoa instead of ova is the true office of these bodies.

In *Sertularia argentea* I have found the axis developed in the interior of the capsule into a body of very obvious medusoid conformation. In this body the medusoid structure has experienced an advance over that of the reproductive sacs of the *Tubulariadæ*; both mouth and disc are open, and four unbranched gastro-vascular canals are present, but it is permanently fixed, no marginal tentacula are developed, nor could I observe the least motion of the disc corresponding to the systole and diastole of the medusoids of the *Tubulariadæ* and the *Campanulariæ*. It is supported on a short stem, which springs from the bottom of the capsule, and is directly continuous with its stomach. In this stem the ova originate and appear to escape from it into the stomach of the medusoid, to be discharged from the mouth into an external delicate vesicle, where they are retained during subsequent stages of their development.

If the views now taken be correct, the reproductive capsules of *Cordylophora*, and those of the marine *Tubulariadæ*, as well as the parts immediately concerned in the sexual reproduction of the *Sertulariadæ*, must be regarded as distinct zooids*, presenting a more or less degraded type of medusoid structure†.

On investigations into the embryology of the lower polypes, an important influence was exercised by EHRENBERG's determination of the signification of the ovigerous capsules of *Campanularia* and *Coryne*. The existence of these capsules was, as is well known, supposed by the celebrated Berlin micrographist‡ to indicate a distinction of sex in the polypes of a zoophyte, the ordinary terminal polypes being considered by him as non-sexual, while the ovigerous capsules were maintained to be female polypes. This view was ardently adopted by LOVEN§, who, observing

* The introduction of the term *zooid* into the language of zoology is of very recent date. This term is intended to indicate each of the distinct organisms which, with various degrees of independence, express when taken together the total result of the development of a single *ovum*. It is a valuable addition to our terminology, enabling us to avoid the ambiguous sense which attaches itself to the word *individual* when this word is used in its biological signification as the logical element of a *species*. See HUXLEY, observations on Salpa, &c., in Philosophical Transactions, 1851, and Lecture on Animal Individuality, Ann. Nat. Hist. June 1852. See also CARPENTER, Princ. Gen. and Comp. Physiol. p. 906.

† Our knowledge of the egg-bearing and spermatozoa-bearing bodies of *Hydra* is not yet sufficiently accurate to enable us to decide with certainty how far the reproductive organization of this animal should be included in the same type with that of *Cordylophora* and the marine hydroid zoophytes. I believe that indications of a medusoid type may be here also witnessed, but further observations are necessary for the complete elucidation of this point.

‡ Corallenthiere des Rothen Meeres.

§ WIEGMANN's Archiv, 1837.

some of the free medusoids of a *Syncoryne* to be filled with ova, supposed these medusoids to possess the same signification as that which EHRENBERG had attributed to the fixed capsules. STEENSTRUP, adopting with some slight modification the same view, has found in it one of the most striking of the facts which he has so skilfully collated in his essay on "The Alternations of Generations;" while VAN BENEDEN*, in two elaborate memoirs full of beautiful and accurate observations, has strenuously opposed it, maintaining that the ovigerous fixed capsules are merely organs, "ovisacs," while the free medusoids are larvæ destined to undergo a series of transformations during a process of development into the form of the parent zoophyte. M. VAN BENEDEN, however, though he has had the medusoids long under his eyes, has never witnessed an actual development into the form of the parent polype, and the changes which he has figured as occurring in them do not appear to show any tendency to such a transformation. I have had the medusoids of a *Syncoryne* for more than a fortnight under constant inspection without perceiving the slightest change towards the form of the adult polype; at the end of this period they perished.

DUJARDIN† opposes the views both of EHRENBERG and VAN BENEDEN, and taking the medusoids for true *Medusæ*, and viewing them even as distinct genera of *Acalepha*, he generalizes the observed instances of their production, and maintains that the claviform polypes are universally only inferior phases of the development of the *Acalepha*; while he considers the bodies produced in the fixed sacs only as "*bulbillæ*," by which he understands gemmæ, which become detached at an early stage, and are then capable of an independent development. The strong resemblance however between true *Medusæ* and the medusoids produced by a process of gemmation from polypes does not afford sufficient grounds for maintaining that all *Medusæ* are only advanced stages of tubularian zoophytes and of *Campanulariæ*, or that all these zoophytes are only earlier phases in the development of *Medusæ*; and M. DUJARDIN's generalization, from which would result the complete abolition of the *Campanulariæ* and tubularian zoophytes as distinct groups of the animal kingdom, is certainly destitute of sufficient foundation, while the bodies contained in the fixed sacs are undoubtedly not *gemmæ* but *ova*, as their structure and the whole history of their development must render evident. I cannot think, then, that either VAN BENEDEN or DUJARDIN has succeeded in overthrowing the theory of EHRENBERG.

The conclusion to which the facts sought to be demonstrated in the present paper would seem to lead, is that in the tubularian zoophytes there exist three kinds of zooids, all produced by a process of gemmation from an original stolon, which is itself the immediate product of a true ovum. These are,—1. the ordinary terminal

* Mém. sur les Campanulaires, and Recherches sur l'Embryogenie des Tubulaires, Nouv. Mém. de l'Acad. Roy. de Bruxelles, t. vii.

† DUJARDIN, Sur le Développement des Méduses et des Polypes Hydraires, Ann. des Sci. Nat. 3me sér. t. iv. 1845.

zooids, on which devolves more especially the function of the reception, digestion, and elaboration of the nutrient material; 2. the fixed reproductive zooids, in which every function is rendered subordinate to the production and development of the ova or spermatozoa, and in which a medusoid structure is more or less disguised; and 3. the free medusiform zooids, in which a complete medusoid structure is obvious. The office of these last is less exactly determined than that of either of the others; sexual reproduction is probably, as in the fixed reproductive zooids, their characteristic function; for as we have already seen, they have in several instances been found to contain ova; yet in the greater number of cases no ova have been detected in them, and observations are still wanting to enable us to decide whether at one period or another of their existence a true generative office is not, under favourable circumstances, always performed by them. It is certain that the other functions are not here so completely subordinated to reproduction as in the fixed sacs, for since the medusoid has become entirely detached from the parent, a more elaborate organization is necessary to enable it to maintain an independent existence. Uniting the functions of reproduction with extensive locomotive powers, it is probably destined to carry the ova to a distance from the parent stock, and thus provide for the dispersion of the species, for the motion of the ciliated embryo is too slow to be of any use in this respect. In the *Campanulariæ*, besides these three forms of zoöids there exists a fourth, in which the medusoid structure is also obvious, though not so completely developed as in the free medusoids; the bodies belonging to this group remain permanently fixed at the mouth of the capsule; their function is that of true sexual generation, and after giving birth to ova or spermatozoa they wither away. The ovigerous sacs of degraded medusoid structure concealed in the interior of the capsules of *Campanularia* are quite different from these, and belong to the second kind of zooid enumerated above. In *Sertularia* and its immediate allies no locomotive zooids have as yet been found, and the generative zooids of *Sertularia argentea* already described admit of comparison rather with the fixed medusoids attached to the mouth of the capsule in *Campanularia*, than with the ovigerous sacs of the *Tubulariadæ*.

It would seem then that EHRENBERG struck upon the true determination of the ovigerous sacs in *Coryne* when he called them "female polypes," though he erred when, supposing the "ovarian vesicles" of *Campanularia* to be the homologues of the ovigerous sacs of *Coryne*, he called these vesicles also by the same name; the true homologues of the reproductive sacs of the *Tubulariadæ* being, not the external capsules of the *Campanulariæ*, but fixed bodies with a disguised medusoid structure contained in the interior of these capsules*.

The present state of our knowledge of the Tubularian and Sertularian polypes would seem to justify the generalization, that for the production of ova in these

* KROHN has already pointed out that the capsules in *Campanularia* have a signification different from that of the ovigerous sacs of *Coryne*, *l. c.*

polypes a more or less perfectly developed medusoid organization is required, this organization being demonstrable not only in the free medusoids themselves, which are occasionally observed to give origin to ova, but in those reproductive capsules and imperfectly developed medusoids which remain permanently adherent to the parent.

Description of the Plates.

PLATE XXV.

Fig. 1. *Cordylophora lacustris*, attached to a dead valve of *Anodon cygneus*. Natural size.

Fig. 2. A branch magnified with the polypes in various states of expansion, and with the reproductive capsules more or less developed.

Fig. 3. Longitudinal section of polype to show the details of its structure.

- *a*. Ectoderm.
- *b*. Polypary.
- *c*. Processes from the ectoderm attached to inner surface of the polypary.
- *d*. Endoderm.
- *e*. Mouth.
- *f*. Post-buccal cavity.
- *g*. Stomach.
- *h*. Common canal of the cœnosarc.
- *i*. Muscles.

PLATE XXVI.

Fig. 4. Portion of the walls of the stomach more highly magnified.

- *a*. Ectoderm, its cells containing thread-cells.
- *b*. Endoderm composed of elongated cells, with true secreting cells in their interior.
- *c*. Secreting cells with evident nucleus.
- *d*. Secreting cells with the nucleus obscured by the opake contents.
- *e*. Granular mass.
- *f*. Muscles.

Fig. 5. Thread-cells previous to the exsertion of the filament.

Fig. 6. Thread-cells after the exsertion of the filament.

Fig. 7. A group of cells liberated under pressure from the ectoderm. Some contain a single thread-cell, others a nucleus-like body, probably an undeveloped thread-cell. They appear to have been originally contained as secondary cells within the proper cells of the ectoderm.

Fig. 8. Cells liberated by pressure from the endoderm of the stomach. They are filled with smaller cells, which contain coloured granules, and seem to have been originally contained within the proper cells of the endoderm.

a. Nuclei of contained cells distinct.

b. Nuclei concealed by the coloured granules.

Fig. 9. Portion of a tentacle near its root, to show its structure.

a. Ectoderm with thread-cells.

b. Endoderm, its cells containing coloured granules.

c. Muscular fibres.

Fig. 10. Cells containing secondary cells with granular contents from the endoderm, when covered by the polypary.

*** In figs. 11–14 the same letters are used to indicate corresponding portions of structure, viz. *a*. Diverticulum from the cœnosarc. *b*. External investment of the reproductive capsule continued from the polypary. *c*. Cellular sac. *d*. Ramified canals. *e*. Structureless sac secreted on the outside of the cellular sac.

Fig. 11. Reproductive capsule—very early stage.

Fig. 12. The same—more advanced stage; the cellular sac and ramified canals are now visible.

Fig. 13. Ideal longitudinal section of a reproductive capsule of about the same period as fig. 12; showing the relation of the ramified canals to the diverticulum and cellular sac, and the presence of a delicate structureless sac which has been secreted on the outside of the cellular sac.

Fig. 14. Reproductive capsule in a more advanced stage; the ova are now visible in its interior.

Fig. 15. Reproductive capsule still further advanced; the cellular sac and ramified canals have disappeared, and the ova are now seen lying upon the extremity of the diverticulum, and immediately included within the structureless sac which had been formed upon the outside of the cellular sac.

Fig. 16. A more magnified view of an ovum from fig. 15; the germinal vesicle has disappeared, and the segmentation of the vitellus has converted the ovum into a mulberry-like mass.

Fig. 17. A capsule still further advanced; the mulberry-like condition has disappeared, and the ova have begun to elongate themselves.

Fig. 18. A capsule in a still more advanced stage; the ova have become still more elongated, and they now present a swarming motion in the interior of the capsule.

Fig. 19. Termination of the intra-capsular life of the embryo; the enclosing sacs have become ruptured, and the embryos are escaping in the form of free ciliated infusoria.

Fig. 20. Embryo just after its escape from the capsule, more highly magnified; it presents an internal closed cavity with ectoderm and endoderm.

Fig. 21. The same, showing the pyriform figure which it frequently assumes.

Fig. 22. Embryo subsequently to its locomotive stage; the cilia have disappeared, and it has become permanently fixed by one extremity.

Fig. 23. Further progress in the development of the young polype; the tentacula have begun to bud forth, and the stem is already surrounded by a delicate polypary.

Fig. 24. Male capsule with its contents.

a. Capsule with the contents escaping under slight pressure.

b. Caudate cells liberated from the capsule.

c. Spermatozoa.

Fig. 2.

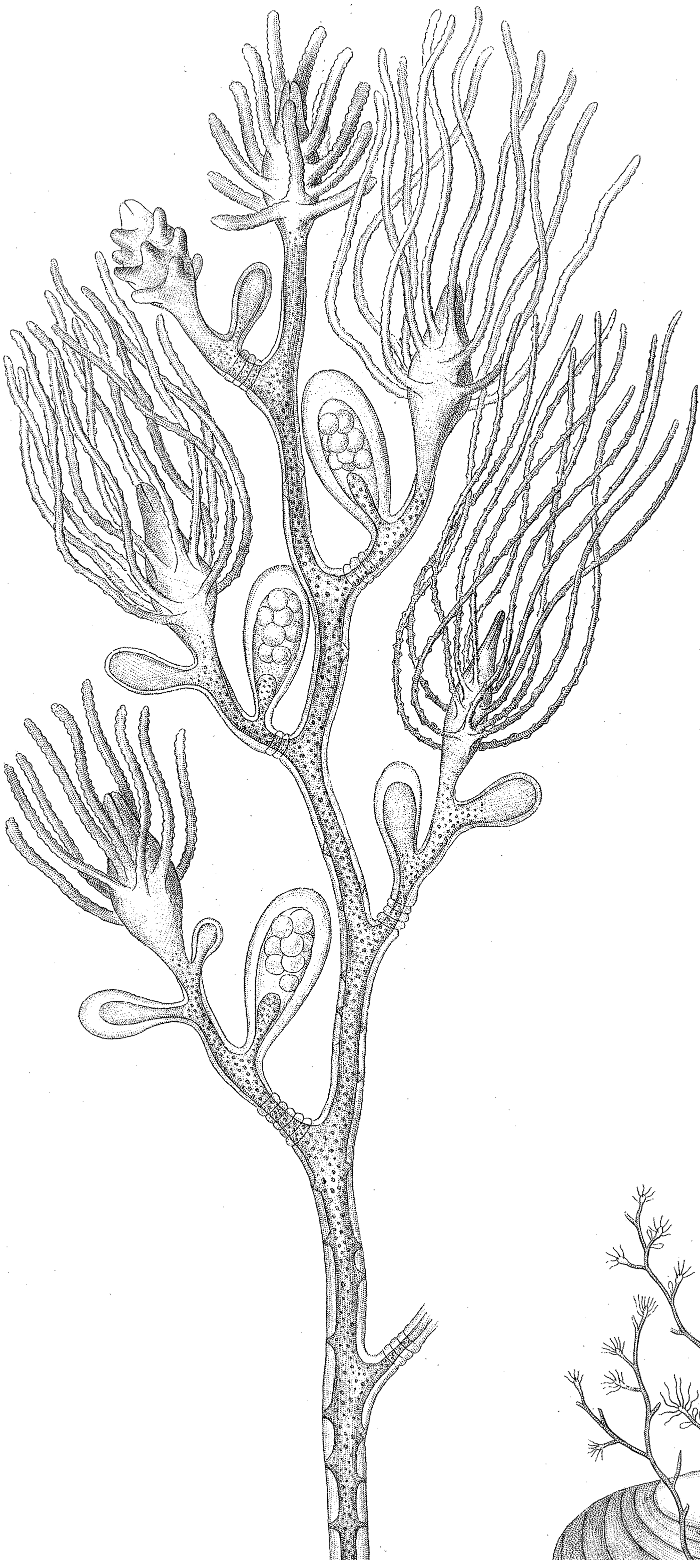


Fig. 3.

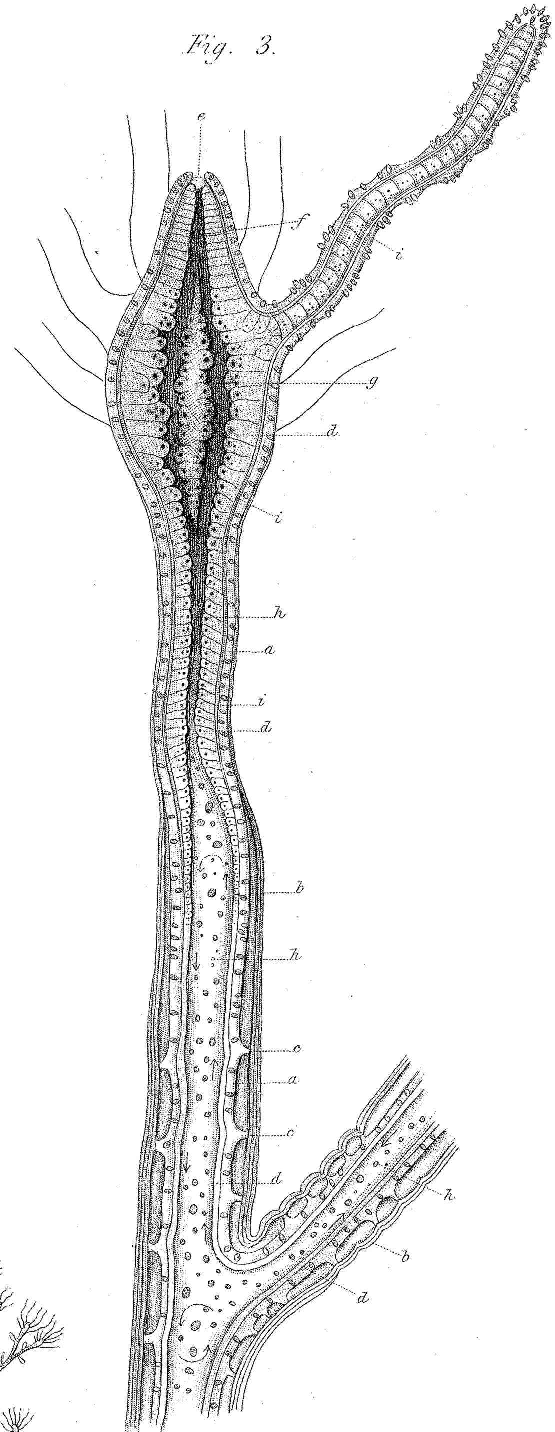
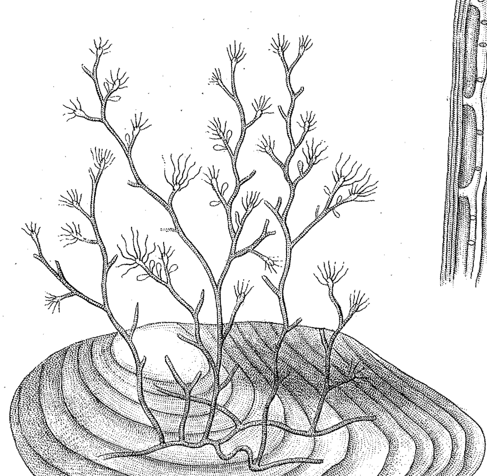
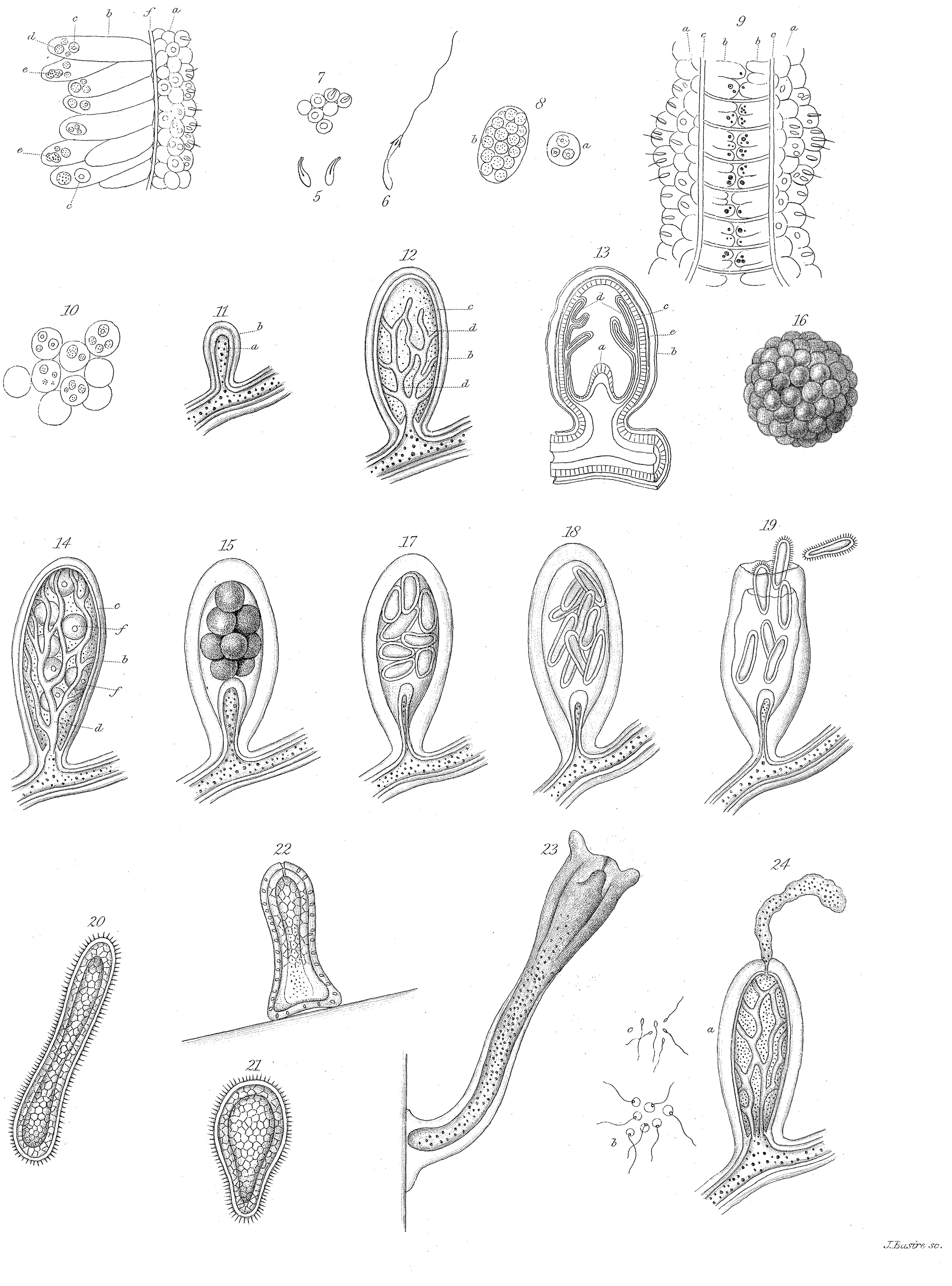


Fig. 1.



G. J. Allman, del. J. Basire, sc.



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