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On the Sexual Cells and the Early Stages in the Development of Millepora plicata

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VIII. *On the Sexual Cells and the Early Stages in the Development of* Millepora plicata.

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[Plates 38, 39.]

Upon the edge of the fringing coral reefs which run along the southern shore of Talisse Island (N. Celebes), I found considerable quantities of a large handsome *Millepora* growing vigorously. The form seems to correspond very closely with the *M. plicata* of Milne Edwards (8)*, the most striking feature of which is that it is "plissé près des bords et donnant naissance à quelques lobes verticaux qui se détachent à angle droit de chaque surface des feuilles en forme de crêtes."

I broke off several pieces of these and preserved them either in absolute alcohol alone or in alcohol after treatment with corrosive sublimate.

I never saw the zooids properly expanded, either when they were living in their natural position on the reefs or in my aquaria.

Upon making a rough examination, by means of the very imperfect methods at my command in my little hut in the tropics, I found that the species is hermaphrodite, both ova and spermoblasts being present in the cœnosarcal canals. This result was sent as a short note to the Royal Society in December, 1885 (10).

Our knowledge of the soft parts of the genus *Millepora* is due to the investigations of L. Agassiz (1) and to the excellent Memoir of Moseley (13), but neither of these authors, nor Nelson and Duncan (14) were fortunate enough to discover the sexual organs.

On my return from the tropics I commenced a series of observations in the University Museum at Oxford, and continued them in the Morphological Laboratory at Cambridge, upon the origin of the sexual cells in this species and the early stages of its development. Unfortunately, my work was much delayed by finding that several of the specimens were sterile, so that I have been occupied nearly twelve months in making my series complete, in establishing my results, and confirming my conclusions. It is my intention at some future date to publish an account of my observations upon

* The numbers in parentheses refer to the Literature List at end of paper.

the general anatomy of the hard and soft parts of this species of *Millepora*. In this communication I intend to confine myself to a consideration of the male and female sexual cells and their maturation, the impregnation of the ovum, and the early stages in the development.

The Sexual Cells.—Both male and female sexual cells arise in the *ectoderm* of the cœnosarcal canals, which anastomose between the dactylozooids and the gastrozooids. They commence as undifferentiated small cells (Plate 38, fig. 3, *s.c.*) lying on the mesoglœa between or beneath the ectoderm cells, and may readily be distinguished by their homogeneous structure and the readiness with which they stain in Borax carmine. The young ova, distinguished from the young spermospores by their small clear nucleus, become spindle-shaped at an earlier period, and may be seen to penetrate the mesoglœa to take up a position in the endoderm (fig. 3 $s.c^1$.).

The young male sexual cells or spermospores generally attain to a greater size than the young ova before they penetrate the mesoglœa, and are distinguished by their large nuclei containing a coarse protoplasmic meshwork (fig. 6 *sp.*).

As soon as the young spermospore has taken up its position in the endoderm the nucleus increases considerably in size (fig. 7 *sp.*). The protoplasmic meshwork next splits up into a number of hook or rod-shaped pieces (fig. 8), and these divide again into a large number of very small particles (fig. 9). At this period these small nuclei fragments occupy the whole spermospore, which is surrounded by a thin structureless membrane.

The spermospores now migrate, probably in an amœboid manner, along the canals to the zooids. In most cases they choose the dactylozooids, but in one or two instances I have found them in the gastrozooids. At first they are to be found in the basal endoderm (fig. 1 *sp.*), but subsequently they pass into the cavity of the zooid. At about this period the surrounding membrane of the spermospore disappears, and a swarm of young spermoblast occupy the cavity of the zooid. The outlines of these are difficult to see when they are *en masse*, but their structure can be well seen where a few are scattered about at the edge of a torn section. Again entering the endoderm, they push out the mesoglœa into a number of diverticula between the tentacles, in which they remain until they are mature. These diverticula or sporosacs (fig. 12) vary considerably in number. Sometimes there are as many as four or five, but more usually only one or two. I have been unable to find any trace of the formation of a sporosac before the advent of the spermoblasts. It seems as if the spermoblasts were the active agents in the formation of the sporosacs, that, in other words, the spermoblasts do not migrate to any locality or structure already prepared for them, but choose for themselves a locality or localities which can readily be pushed out into the form of sporosacs. It is difficult to say very definitely whether the spermoblasts themselves actually perforate the mesoglœa to take up a position in the ectoderm, but I believe they do not. The wall of the sporosac seems to me to be always continuous with the mesoglœa of the body wall. There is nothing present in the sporosac at all comparable with a spadix, nor is there any other evidence of the sporosac being a degenerate medusiform gonophore.

The Ova.—The young ova, having penetrated the mesoglœa of the canals in the germinal region, increase in size rapidly (figs. 3 and 4). As they increase in size they become stalked, the stalk remaining attached to the mesoglœa. This stalk of the ovum is not a separate structure but simply a pseudopodium modified for the purpose of retaining the ovum in position. It might be compared with the stalk of an Infusorian. A structure probably similar to this has already been described in the ova of *Myriothela* by ALLMAN (3).

I am not certain at what period, but certainly some time before maturation, the ovum changes its position in the canal by amœboid movement (fig. 5). The ovum throws out pseudopodia, withdraws its stalk, and wanders away to a more favourable locality, where it again settles down as an oval stalked ovum.

Maturation takes place while the ovum is at rest.

The germinal vesicle, which in immature ova is very distinct, becomes obscured (Plate 39, fig. 14, D) and eventually disappears (fig. 14, E). A spindle-shaped structure with longitudinal striæ next appears in the middle of the ovum (fig. 14, F), and this gives off the first polar globule. In the next stage the spindle-shaped structure is much longer but more indistinct (fig. 14, G); this gives off the second polar globule, and the spindle is dispersed. During the formation of the second spindle, and subsequently, the substance of the ovum becomes clouded and heterogeneous, as if some considerable disturbance of the protoplasm was going on.

After the dispersion of the second spindle, impregnation takes places. It is very probable that at this stage the ovum withdraws its stalk again, and wanders in the lumina of the canals in search of the spermatozoa, for I have never found one with a stalk. The heads of the spermatozoa enter the ovum, leaving their tails on the surface. When the head of the spermatozoon is within the ovum it appears as a dark corpuscle which stains deeply, surrounded by a clear transparent space. As many as three or four spermatozoa may thus enter the ovum, but whether they all take part in impregnation, or are all but one of them discharged again, I cannot tell (fig. 14, J and K).

After impregnation the ovum again becomes clear and homogeneous, and the nucleus reappears (fig. 14, L). It would be difficult to distinguish an ovum at this stage from an ovum just before maturation, were it not for the presence of remains of the polar globule. The nucleus, soon after its reappearance, is seen to be filled with a number of small spherical bodies like nucleoli (fig. 14, M). The wall of the nucleus next disappears, and these spherical bodies, together with a number of very small fragments, are seen scattered about in the region of the ovum formerly occupied by the nucleus (fig. 14, N). Later, they migrate towards the centre of the ovum, where they form an equatorial zone of two or three rows (fig. 14, O, P and Q). This zone divides into two clusters of fragments which, travelling first to the two poles (fig. 14, R), eventually are scattered over the whole ovum (fig. 14, S).

At this stage, but not before, it is possible to discern in favourably stained specimens certain faint shadings in the substance of the young embryo, which indicate that each fragment is surrounded by its own proper protoplasm. The fragments have grown to such a size as to enable us to call them nuclei, and the young embryo has reached a stage which corresponds with the morula stage of other embryos.

At this period in the development the stalk is withdrawn, and the embryo generally wanders into the neighbouring gastrozooid, where it either fixes itself again to the basal mesoglœa or lies unattached in the basal endoderm (fig. 2). The nuclei next arrange themselves circumferentially so as to form a solid blastosphere.

At this period I believe most of the embryos are set free, probably as ciliated larvæ, being discharged into the sea by the mouth of the gastrozooid.

Were they discharged as the spermatozoa are from a sporosac on the body wall, I must have found at least one example in many hundred preparations; but not only have I found no female sporosacs, but also not one single embryo in a gastrozooid in any other position than in the basal endoderm.

Sometimes the embryos seem to remain a long time in their position in the basal endoderm of the gastrozooid. In one example I found three or four embryos nearly twice as large as the mature ovum. In one of them there was a slight invagination of the nuclei at one point, accompanied by a proliferation of the nuclei there (fig. 14, W). Later stages in the development are unknown to me.

The Origin of the Sexual Cells.—My investigations upon the sexual cells support the views of the HERTWIGS (9) and WEISMANN (15), that the sexual cells of the Hydromedusæ originate consistently in the ectoderm. I am inclined to agree with the suggestion of WEISMANN (15) that in the ancestral forms of the Hydromedusæ all the sexual cells originated in the ectoderm, and were ripened in and eventually discharged from that tissue, without entering into any other.

The reason for the wandering of the sexual cells in *Millepora* from the ectoderm to the endoderm must be sought for in the presence of a hard, inflexible, calcareous exoskeleton.

The corallum or cœnenchym (MOSELEY) of the *Millepora* is undoubtedly a product of the ectoderm of the cœnosarcal canals, and it seems most probable that the proper growth and nutrition of the young sexual cells would be seriously interfered with by contact with such a substance, were they to remain in the ectoderm.

Consequently we find that at an early stage they perforate the mesoglœa to take up a position in the endoderm. Whether this is a sufficient and the only cause of the migration of the sexual cells it is impossible to say.

I am inclined to believe that the possibility of better nourishment in the endoderm should be taken into consideration. Professor WEISMANN (15) maintains that in the Tubularian Hydroids there is no difference in the nourishing powers of the ectoderm and the endoderm. It is true, as he points out, that these cells do not feed in an amœboid fashion upon unprepared food, but are only nourished by the fluid or chyme prepared by the action of the endoderm cells.

But surely there must be more of this fluid in the tissue which prepares it than in the tissues to which it is distributed. There must be more surplus chyme in the endoderm, which has to supply the whole organism, than in the ectoderm, which has to seize and appropriate only what is brought to it.

That the rapid absorption of a large amount of nutritive material is of the utmost importance we see from many examples, but none more striking than that of *Hydra*, which, according to KLEINENBERG (11), throws out a considerable number of pseudopodia to increase its absorbing surface.

Perhaps it is premature, however, to say definitely that the endoderm does afford more nourishment for the sexual cells than the ectoderm; but as it seems to me to be quite possible, if not highly probable, that it does, we cannot dismiss this as an impossible cause of the migration of the sexual cells until we have some definite grounds for saying it is not.

The Ova.—The pseudopodia and the peculiar stalk of the ova of *Millepora* are not altogether unknown in other types. Thus, the ova of *Hydra* (11) and *Halisarca* (17) possess pseudopodia, and, according to WEISMANN, the ova of some Tubularian Hydroids wander in the colony in an amœboid manner.

The stalk of the ovum of *Millepora*, to which a similar structure exists in *Myriothela* (3), simply serves to keep the ovum in its proper position in the canal. It seems to be sometimes completely withdrawn when the ovum migrates, and to be re-formed when the ovum comes to rest. It is, in fact, simply a pseudopodium modified to keep the ovum in its position in the endoderm.

The Maturation and Impregnation of the Ovum do not offer any striking peculiarities. The formation of the nuclear spindles was difficult to observe, as my specimens were not specially prepared for this kind of minute histological investigation; but from what I was able to observe in well-stained specimens, with a high power, I should think that the history of the formation of the nuclear spindles does not differ materially from what has been described by other authors in other ova.

That the two polar globules are not always seen at the same point is not peculiar to *Millepora* (*cf.* CARNOY (6), vol. 2).

The absence of any true segmentation in the ovum of *Millepora* is a very striking phenomenon, because it is not associated with the presence of a considerable amount of yolk.

The ova are only ·01 mm. in diameter, and contain none of the yolk spherules or granules which are so commonly present in the ova of other Hydroids.

The ova of some other Hydroids are known to develop without segmenting. Thus, in *Myriothela*, KOROTNEFF (12) says, "Nach der Befruchtung kommen in dem Entoplasma Zellen vor (wahrscheinlich nach der Art der freien Zellenbildung) die sich theilen und deren Abkömmlinge sich gegen die Peripherie des Eies bewegen und in das feinkörnige Ectoplasma übergehen und da ein Blastoderm rund um das Ei bilden."

In this case, however, the egg contains a considerable amount of yolk, and the formation of the blastoderm is probably comparable to that of certain Crustacea (*Eupagurus Prideauxii*) and Insects (*Tetranychus telarius*) (4).

The peculiarity of the ovum of *Millepora* is that it is a small egg with little or no yolk, in which complete division of the nucleus into numerous nuclei takes place, without any apparent division of the ovum itself.

In this respect it is unique, and the question arises whether we must believe that the ovum of the Millepore is an ovum which formerly possessed a large quantity of yolk and has subsequently lost it, or whether the segmentation of the ovum has been lost from other causes.

In the first place, it does not seem to me to be a necessary conclusion that, because the ovum exhibits phenomena which can be paralleled only by telolecithal or centrolecithal ova, that therefore the ovum must have contained in bygone times a considerable amount of yolk.

In the second place, the loss of segmentation may have been caused by the migration of the egg after the early stages of development have commenced.

And thirdly, the evidence before us indicates that the Millepore ovum never passed through a stage with much yolk.

These three points must be considered a little more in detail. The complete segmentation of an ovum must be considered to be rather of the nature of a repetition of phyletic history, than a necessary process in the formation of an embryo.

It is impossible to imagine *à priori* any definite use which the complete segmentation of the ovum can be in the building up of animal tissues.

Every ovum upon fertilisation, or even before, must possess a tendency to pass through all the stages in the phyletic history of the animal. If it did not possess this tendency, we should have lost all traces of an animal's history in its ontogeny. There would be no gill slits in Mammalian embryos, no pineal gland in Vertebrates. The science of Embryology would be of little value to us.

We know that this tendency may be overcome, by the fact that many stages in ancestral history, many organs and structures undoubtedly possessed by ancestors, disappear. But what causes govern the obscuration or disappearance of these organs, structures, and stages, we do not, in most cases, know with any degree of certainty.

Turning now to the stages represented in the various phases of segmentation and the morula.

Most ova with but little yolk completely segment; the tendency to repeat ancestral types is not interfered with. Most ova with a large amount of food-yolk do not segment; the tendency to repeat ancestral types is interfered with. The natural conclusion to come to is, that in such cases this tendency to repeat ancestral types is interfered with by the food-yolk; that the delay, which would be occasioned by the complete separation of considerable amounts of yolk, is of such disadvantage to the animal that the tendency to repeat ancestral types is overcome and lost. But this is not necessarily the only cause which can bring about this result.

It is very probable that limited space, or a migration of the young embryo, would bring about the same result; because, in the first place, an unsegmented ovum would occupy less space than a segmented one, and in the second place, an unsegmented ovum would move with much greater facility and less friction.

Now most ova do not move immediately after they are fertilised, and consequently they usually occupy a place either within or without the body of the mother, which is of sufficient size for the accommodation of the embryo when it is older and larger; consequently, in nearly every case, the ovum segments when it is not charged with yolk.

Even the ovum of Mammals, which we have good reason to believe formerly contained much yolk, segments. The tendency of the ovum to repeat ancestral types being no longer checked by the yolk nor by any other cause.

In *Millepora* we have an example of an ovum which is not only matured and fertilised in a confined space—the cœnosarcal canals—lined by solid carbonate of lime, but also has to migrate to the gastrozooids after the early stages of development have commenced.

These facts are, I think, quite sufficient to account for the absence of segmentation.

But what evidence have we that the ovum of *Millepora* never did contain a large amount of food yolk?

In the first place, had the ovum of *Millepora* ever been much larger than it is at present, it must have possessed either ampullæ or larger canals. Not a trace of these is to be found in *M. plicata*, the only species of which the sexual cells have been examined.*

Had these ever been developed it is most probable they would have been retained, and the ovum, having more space for its development in the early stages, would have segmented, as the ovum does in Mammalia.

But it is difficult to frame any reason to explain why the ovum of a Hydroid having once acquired yolk should lose it again, such as we can put forward in the case of the Mammalian ovum.

Lastly, I believe that the general anatomy of *Millepora* indicates that this Hydroid is of a very old type, and has come down to us from pre-eocene times almost unchanged.

The curious phenomena which have been described, in connection with the fragmentation of the germinal vesicle after impregnation, are so important and so strange

* It is possible that the ampullæ described by QUELCH (16) in *M. Murrayi* may have been produced by parasitic growth, or that, if they are true ampullæ, the species may be a more modified one than *M. plicata*, and possess ova with food-yolk, but this cannot be determined until the soft parts of *M. Murrayi* have been examined.

that I dare not offer any explanation of them before trying other methods of treatment.

It is possible that the processes of nuclear division are accelerated by the absence of yolk and segmentation.

The Development of the Spermatozoa.—The view that the ovum does not segment on account of its migrations is supported by the history of the development of the spermatozoa.

In most animals the division of the nucleus of the spermospore is accompanied by its segmentation into a sperm morula or spermosphere (*cf.* BLOMFIELD (5) and GILSON (6)).

In *Millepora* the division of the spermospore into a sperm morula does not take place, the spermoblasts being formed by the rupture of the spermosphere at a very late period. It is highly probable that this is due to the same cause as the similar phenomena in the development of the ovum, and this cause is the wandering or migration that takes place through narrow channels before they reach their ultimate position in the zooids.

The Zoological position of Millepora.—The very prevalent idea that *Millepora* and *Hydractinia* are related to one another, must now be abandoned. The skeleton formed by the former is calcareous, by the latter chitinous, the zooids of *Millepora* are very different in character from the zooids of *Hydractinia*, and lastly the phenomena of sexual reproduction in the two genera are totally different. Indeed, beyond the facts that they are both Hydrozoa with dimorphic zooids and a certain similarity of growth, there are no points of relationship between them.

I am inclined to believe that the Milleporidæ, together with the Stylasteridæ, belong to a separate stock altogether from the Hydromedusæ, a stock which never possessed *medusæ* or *medusiform gonophores*. To this point I purpose to return in a subsequent Memoir.

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EXPLANATION OF PLATES 38 AND 39.

The following lettering is used throughout :—

A. Albuminous sheath of the embryo in fig. 14, W.
emb. Embryo in the basal endoderm of the gastrozooid.
End. Endoderm of the zooids.
Ect. Ectoderm of the zooids.
end. Endoderm of the canals.
ect. Ectoderm of the canals.
fr. Fragments of the nucleus.
gr. Germinal vesicle.
M. Mouth of the gastrozooid.
m. Mesoglœa.
N. Large nematocyst.
n. Small nematocysts of the tentacles.
Nu. Nuclei of the embryos.
ov. Ova.
p. Pedicle or stalk of the ovum.
p.g. Polar globule.
S.c. Sexual cells lying in the ectoderm.
S.c.[1] Sexual cells perforating the mesoglœa.
sp. Spermospore.
sp.b. Spermoblast.
spi. Spindle.
spz. Spermatozoon.
S.s. Sporosac.
t. Tentacle.
z. Zoanthancellæ.

PLATE 38.

Fig. 1. Longitudinal section through a partially retracted dactylozooid of *M. plicata*, showing a nearly mature spermospore in the basal endoderm. × 200 diam.

Fig. 2. Longitudinal section through a partially retracted gastrozooid, showing two young embryos lying in the basal endoderm. × 200 diam.

Fig. 3. Longitudinal section through a portion of a cœnosarcal canal in the germinal region, showing the young sexual cells (*sc.sc.*) lying in the ectoderm, and one (*sc.*[1]) penetrating the mesoglœa to take up a position in the endoderm.

Fig. 4. Two young ova lying in the endoderm of a canal and attached to the mesoglœa by a stalk (*p.*).

Fig. 5. An ovum changing its position in the canal by amœboid movements. In the last two figures the zoanthancellæ have been omitted.

Fig. 6. Section through a small portion of a canal wall, showing a young spermospore lying in the ectoderm.

Fig. 7. Section through a portion of a canal showing a young spermospore lying in the endoderm. The nucleus is large and contains a coarse protoplasmic meshwork.

Fig. 8. Section through a portion of a canal, showing a young spermospore at a later stage than in fig. 7, the protoplasmic meshwork having split up into a number of loops or rods.

Fig. 9. A spermospore at a still later stage. The fragments of the nuclear meshwork are now much smaller, more numerous, and occupy nearly the whole spore.

Fig. 10. Transverse section through a canal, showing a nearly ripe spermospore wandering in the lumen. The fragments of the nucleus are now scattered throughout the whole of the spore, but a thin spore-wall keeps the contents together. × 200.

Fig. 11. Longitudinal section through an expanded dactylozooid with a swarm of young spermoblasts occupying its cavity. × 200.

Fig. 12. Longitudinal section through another expanded dactylozooid in which the young spermoblasts are situated in four sporosacs between the tentacles.

Fig. 13. *a.* Spermoblasts of *Millepora*, as they appear when the ripest sporosacs are broken artificially.

b. Spermatozoa of *Millepora* (?) found in the canals.

[I place (?) after *Millepora* because it is impossible for me to say for certain to what animal stray spermatozoa in the canals of a Millepore may belong, but it is highly probable that the ones figured are really the spermatozoa of *Millepora*.]

PLATE 39.

Fig. 14. A series illustrating the maturation, impregnation, and early stages in the development of the ova of *Millepora*.

A.B.C. Three ova before maturation, all with a well-marked germinal vesicle. A. An ovum at rest and attached to the mesoglœa by a stalk. B. An ovum, also attached by its stalk, but which has thrown out pseudopodia. C. An ovum wandering in the canal by means of its lobose pseudopodia.

D. An ovum in which the germinal vesicle is becoming matured previous to maturation.

E. An ovum in which the germinal vesicle has completely disappeared.

F. An ovum in which the first spindle has appeared, and a projection on the surface of the ovum just opposite one end of it, which marks the position of the discharge of the first polar globule, $p.g^1$.

G. An ovum, showing the second spindle stretching across the whole length of the ovum and just giving rise to the second polar globule, $p.g.^2$

H. An ovum, showing the dispersion of the spindle after the discharge of the second polar globule.

I. An ovum, mature and ready for impregnation.

J.K. Two ova, into which the heads of the spermatozoa (*spz.*) have entered. The head of each spermatozoon appears as a dark corpuscle surrounded by a clear space.

During stages G–K the ovum, which was previously clear and homogeneous, becomes clouded and heterogeneous.

L. An ovum, showing the appearance of the nucleus after impregnation.

M. An ovum in which the nucleus contains a number of nucleolus-like bodies.

N. The fragmentation of the nucleus. The wall of the nucleus has disappeared, and the nucleolus-like bodies or fragments of the nucleus are scattered over the proximal end of the ovum.

O. The fragments are travelling towards the equatorial plane of the ovum.

P.Q. The stages in which the fragments are arranged in an equatorial zone.

R. The stage in which the fragments are situated in two polar zones.

S. The stage in which the fragments of the nucleus may be fairly called the nuclei of the embryo and the embryo a morula. Very faint shading between the nuclei indicates the limits of each cell.

T.U. The nuclei in these stages approach the circumference of the embryo. No blastocœl can be distinguished.

W. Latest stage in the development of the embryo observed : *Nu.* Circumferential nuclei. *Nu.*[2] Nuclei lying in the central mass of the embryo. *Nu.*[3] Nuclei invaginating and proliferating at one point.

A. Albuminous sheath surrounding the embryo. *p.* remains of the stalk of the embryo.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

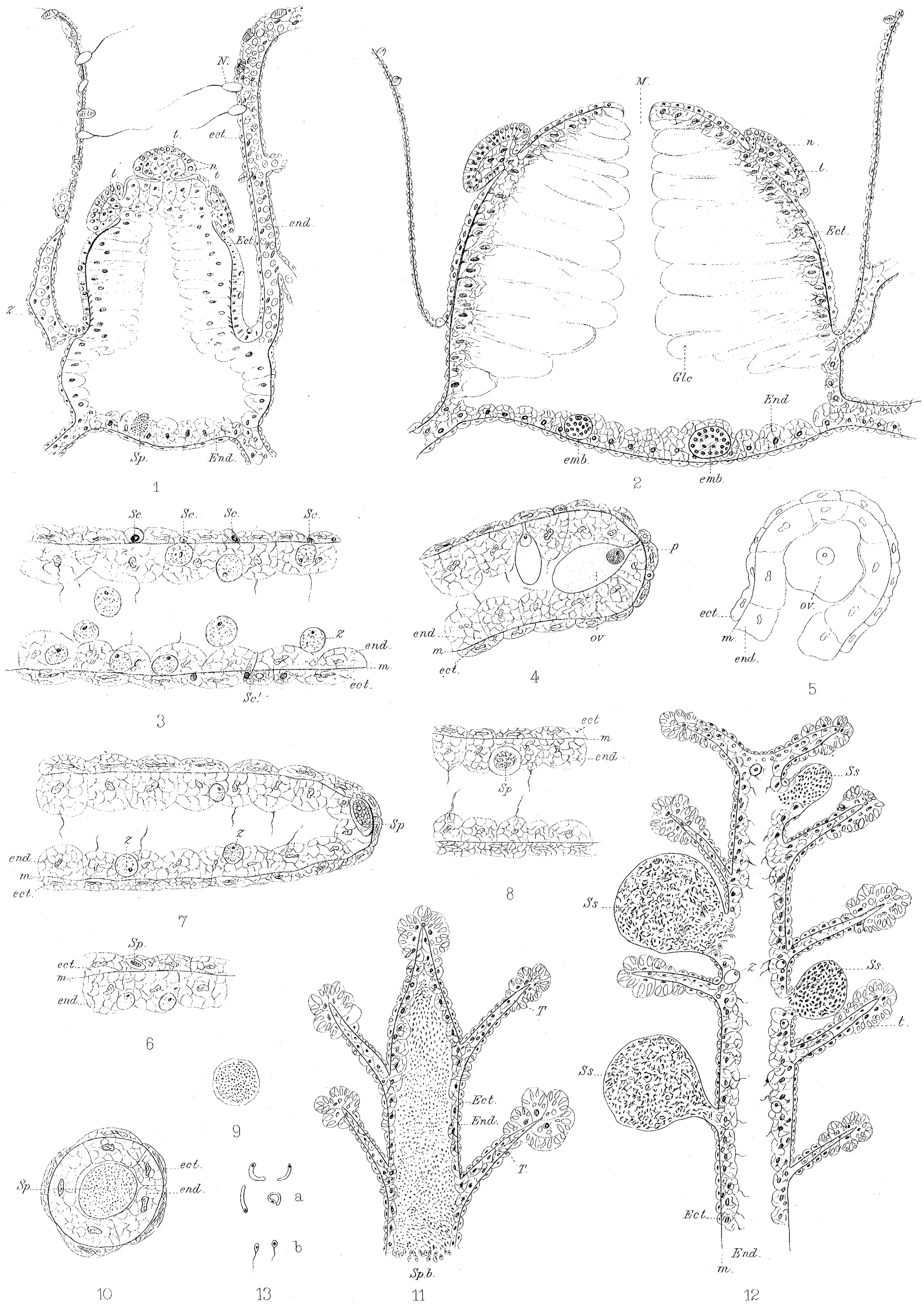

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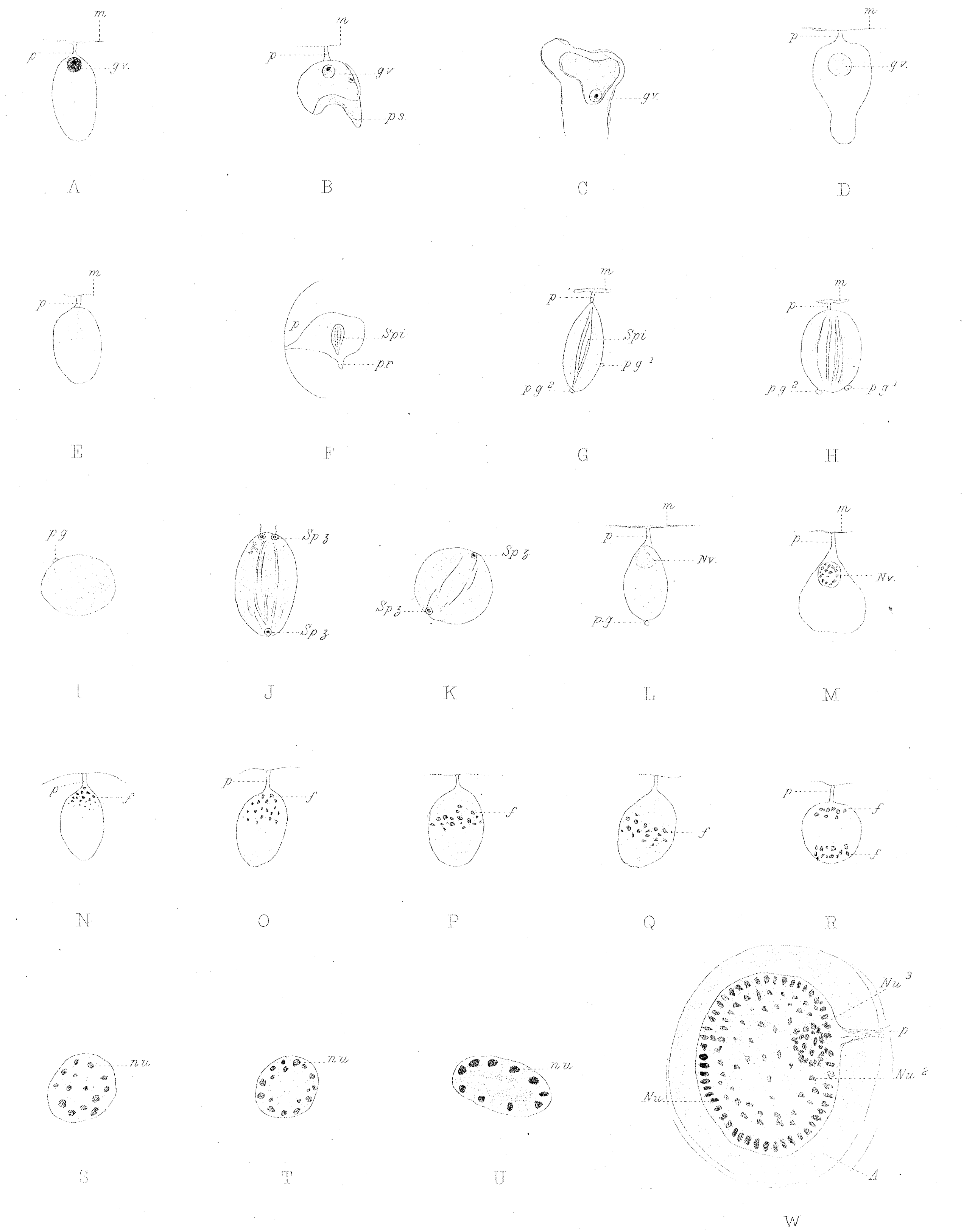
Fig. 14.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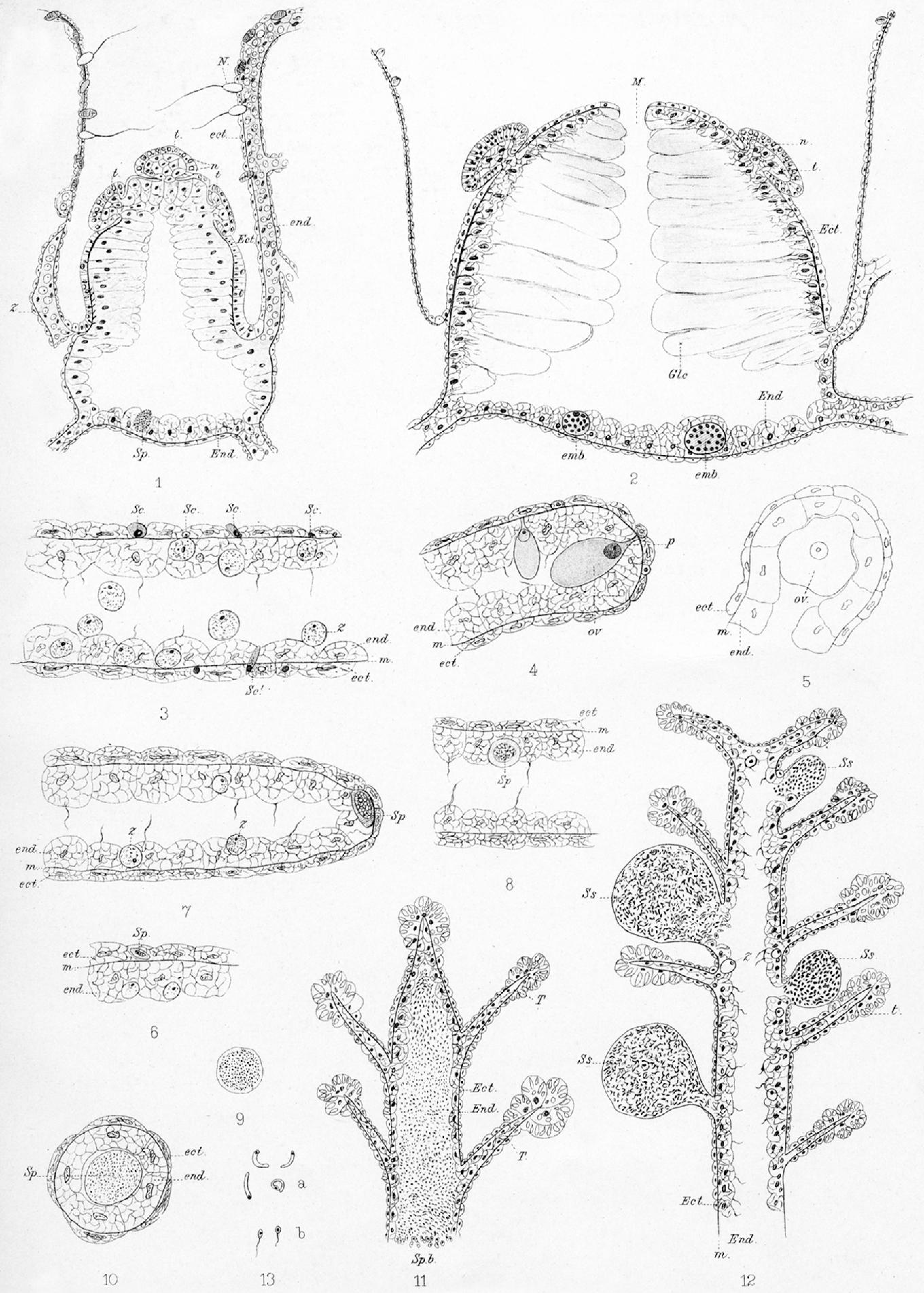

PLATE 38.

Fig. 1. Longitudinal section through a partially retracted dactylozooid of *M. plicata*, showing a nearly mature spermospore in the basal endoderm. ×200 diam.

Fig. 2. Longitudinal section through a partially retracted gastrozooid, showing two young embryos lying in the basal endoderm. × 200 diam.

Fig. 3. Longitudinal section through a portion of a cœnosarcal canal in the germinal region, showing the young sexual cells (*sc.sc.*) lying in the ectoderm, and one (*sc.*[1]) penetrating the mesoglœa to take up a position in the endoderm.

Fig. 4. Two young ova lying in the endoderm of a canal and attached to the mesoglœa by a stalk (*p.*).

Fig. 5. An ovum changing its position in the canal by amœboid movements. In the last two figures the zoanthancellæ have been omitted.

Fig. 6. Section through a small portion of a canal wall, showing a young spermospore lying in the ectoderm.

Fig. 7. Section through a portion of a canal showing a young spermospore lying in the endoderm. The nucleus is large and contains a coarse protoplasmic meshwork.

Fig. 8. Section through a portion of a canal, showing a young spermospore at a later stage than in fig. 7, the protoplasmic meshwork having split up into a number of loops or rods.

Fig. 9. A spermospore at a still later stage. The fragments of the nuclear meshwork are now much smaller, more numerous, and occupy nearly the whole spore.

Fig. 10. Transverse section through a canal, showing a nearly ripe spermospore wandering in the lumen. The fragments of the nucleus are now scattered throughout the whole of the spore, but a thin spore-wall keeps the contents together. × 200.

Fig. 11. Longitudinal section through an expanded dactylozooid with a swarm of young spermoblasts occupying its cavity. × 200.

Fig. 12. Longitudinal section through another expanded dactylozooid in which the young spermoblasts are situated in four sporosacs between the tentacles.

Fig. 13. *a.* Spermoblasts of *Millepora*, as they appear when the ripest sporosacs are broken artificially.

b. Spermatozoa of *Millepora* (?) found in the canals.

[I place (?) after *Millepora* because it is impossible for me to say for certain to what animal stray spermatozoa in the canals of a Millepore may belong, but it is highly probable that the ones figured are really the spermatozoa of *Millepora*.]

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Fig 14.

PLATE 39.

Fig. 14. A series illustrating the maturation, impregnation, and early stages in the development of the ova of *Millepora*.

A.B.C. Three ova before maturation, all with a well-marked germinal vesicle. A. An ovum at rest and attached to the mesoglœa by a stalk. B. An ovum, also attached by its stalk, but which has thrown out pseudopodia. C. An ovum wandering in the canal by means of its lobose pseudopodia.

D. An ovum in which the germinal vesicle is becoming matured previous to maturation.

E. An ovum in which the germinal vesicle has completely disappeared.

F. An ovum in which the first spindle has appeared, and a projection on the surface of the ovum just opposite one end of it, which marks the position of the discharge of the first polar globule, $p.g^1$.

G. An ovum, showing the second spindle stretching across the whole length of the ovum and just giving rise to the second polar globule, $p.g.^2$

H. An ovum, showing the dispersion of the spindle after the discharge of the second polar globule.

I. An ovum, mature and ready for impregnation.

J.K. Two ova, into which the heads of the spermatozoa (*spz.*) have entered. The head of each spermatozoon appears as a dark corpuscle surrounded by a clear space.

During stages G–K the ovum, which was previously clear and homogeneous, becomes clouded and heterogeneous.

L. An ovum, showing the appearance of the nucleus after impregnation.

M. An ovum in which the nucleus contains a number of nucleolus-like bodies.

N. The fragmentation of the nucleus. The wall of the nucleus has disappeared, and the nucleolus-like bodies or fragments of the nucleus are scattered over the proximal end of the ovum.

O. The fragments are travelling towards the equatorial plane of the ovum.

P.Q. The stages in which the fragments are arranged in an equatorial zone.

R. The stage in which the fragments are situated in two polar zones.

S. The stage in which the fragments of the nucleus may be fairly called the nuclei of the embryo and the embryo a morula. Very faint shading between the nuclei indicates the limits of each cell.

T.U. The nuclei in these stages approach the circumference of the embryo. No blastocœl can be distinguished.

W. Latest stage in the development of the embryo observed: *Nu.* Circumferential nuclei. *Nu.*[2] Nuclei lying in the central mass of the embryo. *Nu.*[3] Nuclei invaginating and proliferating at one point.

A. Albuminous sheath surrounding the embryo. *p.* remains of the stalk of the embryo.