A CONTRIBUTION TO OUR KNOWLEDGE OF SPLACHNIDIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 220

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(WITH PLATES XIV–XVIII)

Introduction

Splachnidium rugosum Grev. is a monotypic genus of more than ordinary interest because investigators have placed it in one group or another according as some particular feature seemed more worthy of emphasis. The earliest mention of this plant was by LINNAEUS (9) as *Ulva rugosa;* a few years later SUHR (18) described it as *Dumontia rugosa;* and in 1830 GREVILLE (3) founded the genus *Splachnidium*, retaining the specific name already given.

Most authors have placed it with the Fucaceae, but in 1892 MITCHELL and WHITTING (10) published an account which was incorporated in 1895 by MURRAY (11) in his book. This account includes the morphology of both vegetative and reproductive tissues. As a result of their investigations, these authors felt justified in establishing a new family, making the following statement (p. 9): "The sum of the characters of *Splachnidium* so expressly excludes it from any existing natural order that there is no other course open to us than to establish one for its reception under the name of Splachnidiaceae." KJELLMAN'S account (6) restored it to the Fucaceae; and in 1904 OLTMANNS (13) placed it with the Ectocarpaceae under the subgroup Encoelieae.

The material for this investigation was secured by Professor CHARLES J. CHAMBERLAIN at Glen Cairn, near Cape Town, South Africa, on February 28, 1912. A second collection was made at the same place on August 30, 1914, by Miss EDITH STEPHENS of South African College, Cape Town, and sent to Professor CHAMBERLAIN. The work was undertaken with the hope of determining (1) the nature of the contents of the reproductive sacs, whether zoospores or gametes; and (2) the origin of the so-called "apical cell," a strikingly characteristic feature of *Splachnidium*. The material proved inadequate for the study of reproduction, but furnished a good series for the development and fate of the "apical cell." No mitosis was observed, and hence no chromosome count was possible. It is hoped that some one in the region where *Splachnidium* grows may be interested enough to investigate material secured at the exact time when cell division occurs, probably at night, or to observe the behavior of the living bodies after discharge from the reproductive sac.

Origin of the initial row

The first feature which tends to set the initial cells apart from adjacent border tissue is the taking on of a heavy coat of mucilage (fig. 1). In this and subsequent early stages the heavy mucilage coat is the only character which distinguishes the initial from young vegetative hairs abundant in the apical region (figs. 2–5). A second feature marking this unique structure is the beginning of resorption of cross-walls and loss of original definite nuclear structure (figs. 4, 6, 13, 15). Gradually a complete linear row of cells, reaching entirely through the thallus, is differentiated from the surrounding tissue as an initial row (figs. 5, 7, 8, 13, 15).

Sometimes there is no evident differentiation of tissue at an early stage, but portions of old apical hairs may assume the heavy mucilage coat (figs. 9–11), and there follows an involving of the entire linear row of which the hair is a terminal portion. Part of the old hair may be cast off, eventually leaving only the lower portion (fig. 11).

By the time an entire linear row is so differentiated, the characteristic filiform appendage, which has been described (**10**) as "growing between the cells of the thallus toward the center of the branch," begins to be evident (figs. 15, 16). Pressure of abutting tissue has narrowed the basal portion into a tail-like process as resorption of old walls and cell contents has gone on, whereas freedom from pressure above has allowed expansion into a pear-shaped oval. At this stage all of the original contents left in the filiform portion consist of granular patches of cytoplasm, and in the oval portion there is a similar granular substance with the addition of darkly staining bodies; there is no trace left of nuclear structure.

As active growth continues on each side of the initial row, rapid division occurs in the external layers of the thallus, whereas the inner cells, lying on the border of the central cavity, are pulled apart, not dividing to keep pace with the active outer tissue. This separation leaves the filiform basal process swinging loose, as it were, in the central cavity (figs. 17–20). The entire structure lies at the base of a slight depression, the result of arrested growth of the initial row followed by activity of abutting tissue.

Such, then, is the history of the initial row. *It is the result of more or less disintegration of an entire linear row of the thallus*, with perhaps the addition of portions of a terminal hair. *The exact amount of tissue originally involved*, whether including a terminal hair in part or in entirety, *determines the length and size of the mature structure*. For a long time the writer was puzzled by the great variation in length displayed by these bodies, and the explanation was apparent only when their origin was completely worked out.

The structure described in the foregoing is found in connection with any activity of the plant, as growth at the main apex, or production of lateral branches, or inception of conceptacles.

The conceptacle

In the formation of the conceptacle, the cavity in which the initial row lies becomes deepened as more and more of the abutting border tissue is involved. *Rapid radial division of these border cells contributes new tissue to the conceptacle at the same rate and in the same way as ordinary thallus tissue is developed.* In the early stages of the conceptacle, except for the initial row, there is no essential difference between adjacent tissue of the thallus and that of the actual cavity of the conceptacle (fig. 19). Presently, however, the lining cells of the conceptacle become elongated, and subsequently, by transverse division at the basal end, develop into septate hairs (figs. 20, 21). This behavior is exactly as noted by the writer in a recent investigation of *Fucus* (14) as the stage in the history of the conceptacle known as the "hair pit."

Some of the hairs, as in *Fucus*, are shed later and the lining cells put forth new papillate growths which elongate into sacs (fig. 22) which are ultimately filled with spherical bodies (fig. 24), variously described as zoospores (**10, 11**) and gametes. AGARDH (**1**), HARVEY (**4**), HOOKER (**5**), and LAING (**8**) all describe *Splachnidium* as dioecious, although no one of these authors reports having actually observed antheridia. LAING speaks of oogonia "obscurely pedicelled," developed from the lining of the conceptacle, each oogonium giving rise "to a large number of oospheres, thus differing from all other Fucaceae that have hitherto been described. Each oosphere is very small, compared with the oospheres of other Fucaceae." In another paragraph he states that "as antheridia have never been observed it is just possible that these hairs [apical hairs] may be antheridial in function." The writer's feeling is that the reproductive sacs contain isogamous gametes. However that may be, the conceptacles, at the time the reproductive bodies are ready for discharge, still contain the "initial" as a conspicuous feature (fig. 23).

Discussion

MURRAY (**11, 12**) and also MITCHELL and WHITTING (**10**) speak of the "modified cell" of *Splachnidium* as homologous with the "initial" of *Fucus;* and yet these same authors make this "unique cell" one of the reasons for separating *Splachnidium* from other families. The similarity holds true only in so far as the conceptacle is concerned, where, as previously shown by the writer (**14**), the conceptacle in each genus is the result of arrested development and partial breaking down of a portion of the external layer of the thallus followed by great activity of abutting tissue. The initial row is in no way comparable to the true apical cell of *Fucus*, segments of which are the basis of all tissue of the thallus.

The fact that the initial row of Splachnidium occurs wherever there is great activity is additional evidence for the simple origin of the conceptacle. Splachnidium is a particularly favorable plant for study along this line, since the same structure accompanies ordinary vegetative growth as well as reproductive activity.

In establishing a new family MITCHELL and WHITTING (10) summarize their reasons in the following statement (p. 8):

While, then, the characteristics of *Splachnidium rugosum* are such that it can be placed in no existing natural order of the Phaeophyceae, its nearest allies appear to be the Fucaceae on the one hand and the Laminariaceae on the other. In its vegetative structure, in the nature of its thallus, and in the existence of conceptacles, *Splachnidium* bears a resemblance to the Fucaceae; it differs from them, however, in its mode of growth, the former increasing by means of an apical meristem, while the growth of the latter is due to division of an apical cell. In the presence of an apical meristem *Splachnidium* approaches the Laminariaceae, but at the same time there is no plant in this order which has a cell corresponding to the remarkable cell found at the apex of the main axis and lateral branches of *Splachnidium*. In its reproduction it is allied to the Laminariaceae, and the production of sporangia within conceptacles might seem to point to a narrower limitation of the fertile sorus of plants of this order, recalling the difference between perithecium and apothecium in the fungi.

As to vegetative growth, the tissue of the thallus of *Splachnidium* bears an equal resemblance to the Fucaceae and the Laminariaceae, the only essential difference being in origin. *Splachnidium* and the Laminariaceae are products of a meristem, the former apical, the latter intercalary, according to the evidence of most authorities, and not apical as described by MITCHELL and WHITTING in the passage just quoted. The Fucaceae, too, are characterized by apical growth of the thallus, but all tissue is the actual result of segmentation of a definite apical cell. In vegetative growth, then, *Splachnidium* is intermediate between the two groups.

The presence of conceptacles certainly seems a definite connecting link with the Fucaceae; and yet some of the Laminariaceae show a tendency to approach this method of reproduction. SMITH and WHITTING (17) describe deep furrows in *Macrocystis* and *Postelsia*, which closely resemble conceptacles in form and origin. In this feature, too, *Splachnidium* is intermediate between the Fucaceae and the Laminariaceae.

MURRAY (11, 12) and MITCHELL and WHITTING (10) conclude that the reproductive sacs of *Splachnidium* are neither oogonia nor antheridia homologous with those of the Fucaceae, but are sporangia homologous with those of the Laminariaceae, because of the size of the organ, its unilocular nature, its single wall, the number of spores contained, the size of the spore, and the persistent empty case. On the basis of these features there is no reason why *Splachnidium* may not equally well be considered as having unilocular gametangia containing isogamous gametes. This would give to *Splachnidium* a primitive position among the Fucaceae, but would offer for the Phaeophyceae a link in the phylogenetic sequence comparable to the position occupied in the Chlorophyceae by such plants as *Ulothrix*.

Moreover, in the Fucaceae the oogonia and antheridia are unilocular, no permanent walls separating the gametes. Also DREW (2) has reported conjugation of isogamous gametes in *Laminaria digitata* and *L. saccharina*. "The resulting zygospore divides and gives rise to a chain of cells which may represent the $2x$ generation, and this in turn gives rise to the *Laminaria* plant, which represents the gametophyte, or x generation." His observations have as yet neither been verified nor disproved.

Recently SAUVAGEAU (15, 16) has concluded from his investigations that *Sacchorhiza* (and probably all Laminarias) presents a heterogamous sexuality with alternation of generations. The large plant is the sporophyte bearing uniform sporangia, and each sporangium develops like zoospores "which after transformation into embryospores become male gametophytes or female gametophytes of microscopic size and independent for life. The oosphere expelled from the female gametophyte, then fertilized, germinates at once and develops the plant of *Laminaria*."

In the contents of the reproductive sacs, therefore, as well as in form and origin of the conceptacles and in vegetative growth, *Splachnidium* is intermediate between the Fucaceae and the Laminariaceae. There seems to be no justification for establishing a separate family (10) with its main character "reproduction by spores contained in sporangia which are borne within conceptacles."

Further investigation will doubtless show a much more intimate connection between the Laminariaceae and Fucaceae than is at present recognized. *Splachnidium* may be placed with either group, since it has features common to both. Perhaps the presence of definite and conspicuous conceptacles, even though scattered indefinitely over the entire thallus, places it more closely with the Fucaceae. There seems no good reason for placing *Splachnidium* (13) with the Ectocarpaceae.

Summary

1. The initial row of *Splachnidium* is similar in origin and development to the "initial" of the Fucaceae, except that in *Splachnidium* it involves an entire linear row of thallus tissue; it may or may not include a terminal hair; and it accompanies vegetative as well as reproductive activity.

2. It seems unwise to place *Splachnidium* under a separate family; rather is it preferable to retain it under the Fucaceae, regarding it as a primitive member of that group for the following reasons: (*a*) it closely resembles the Fucaceae in the structure of the thallus, but has an apical meristem in place of a segmenting apical cell with consequent dichotomy; (*b*) true conceptacles are present which in origin and development are of the same general type as those of the Fucaceae, but are scattered indefinitely over the entire plant body; (*c*) the reproductive sacs may prove to contain isogamous gametes.

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LITERATURE CITED

1. AGARDH, J. G., Species, genera, et ordines Algarum. London. 1848.
2. DREW, G. H., The reproduction and early development of *Laminaria digitata* and *L. saccharina*. Ann. Botany **24**:177–190. *pls. 14, 15.* 1910.
3. GREVILLE, R. K., Algae Britannicae. Edinburgh. 1830.
4. HARVEY, W. H., Phycologia australica. London. 1858–1863.
5. HOOKER, J. D., Handbook of the New Zealand flora. London. 1867.
6. KJELLMAN, F. R., in ENGLER and PRANTL'S Die natürliche Pflanzenfamilien 1^2:Leipzig. 1897.
7. KÜTZING, F. T., Phycologia generalis. Leipzig. 1843.
8. LAING, R. M., Observations on the Fucoideae of Bank's Peninsula. Trans and Proc. New Zealand Inst. **18**:303–311. *pl. 10.* 1885.

9. LINNAEUS, C. VON, Mantissae Plantarum. Holmiae. 1767.
10. MITCHELL, M. O., and WHITTING, F. G., On *Splachnidium rugosum* Grev., the type of a new order of algae. Phyc. Mem. **1**:1–10. *pls. 1–3.* 1892.
11. MURRAY, G., Introduction to the study of seaweeds. London. 1895.
12. ———, On the cryptostomata of *Adenocystis, Alaria,* and *Sacchorhiza.* Phyc. Mem. **2**:59–63. *pl. 16.* 1893.
13. OLTMANNS, F., Morphologie und Biologie der Algen. Jena. 1905.
14. ROE, M. L., The development of the conceptacle in *Fucus.* BOT. GAZ. **61**:231–246. *pls. 14–17.* 1916.
15. SAUVAGEAU, C., Sur la sexualité hétérogamique d'une Laminaire (*Saccho-rhiza bulbosa*). Compt. Rend. Acad. Sci. **161**:796–799. 1915.
16. ———, Sur les débuts du développement d'une Laminaire (*Sacchorhiza bulbosa*). Compt. Rend. Acad. Sci. **161**:740. 1915.
17. SMITH, A. L., and WHITTING, F. G., Notes on the sori of *Macrocystis* and *Postelsia.* Phyc. Mem. **1**:84–86. *pl. 20.* 1895.
18. SUHR, J. N. VON, Beiträge zur Algenkunde. Flora **24**:257–298. 1840.

EXPLANATION OF PLATES XIV–XVIII

All the drawings were made with the aid of the Abbe camera and reduced one-half in reproduction. For figs. 1–21, original magnification was 1580; for fig. 22, 790; and for figs. 23, 24, 1050.

FIG. 1.—Modified superficial cell, showing heavy coat of mucilage which distinguishes initial row from other border cells.

FIG. 2.—Two-celled stage of initial row.

FIG. 3.—Three-celled stage of same.

FIG. 4.—Two stages in development of initial rows; a two-celled stage at right and an older stage at left in which some of the cross-walls have been resorbed.

FIG. 5.—A linear row of the thallus, showing mucilage coat characteristic of an initial row.

FIG. 6.—An initial row in which cross-walls have been almost completely resorbed; traces of old walls still distinguishable.

FIG. 7.—A cut showing how initial row is usually terminated by sister cells, one of which usually fails to mature but sometimes initiates a young hair, as in fig. 8.

FIG. 8.—An initial row together with a young hair.

FIG. 9.—Basal portion of a branch of an apical hair which has become an "initial."

FIG. 10.—Lateral branch and basal portion of apical hairs which have become "initials."

FIG. 11.—Basal portion of an old apical hair in which cross-walls have been resorbed; the upper portion (unshaded) will be shed later.

FIG. 12.—An ordinary vegetative hair characteristic of apical region.

FIG. 13.—A completely involved linear row of the thallus with outer portion showing resorption of cross-walls and loss of nuclear detail.

FIG. 14.—Two initial rows which are modified young hairs.

FIG. 15.—An initial row including a linear row of the thallus together with a terminal hair; entire structure shows more or less disintegration and loss of cross-walls.

FIG. 16.—A stage which begins to show characteristic "filiform appendage" at basal end of initial row; almost all the cross-walls have been resorbed and original cell contents have disintegrated into granular patches.

FIGS. 17, 18.—Showing how interior cells of thallus pull away and release the "filiform appendage" from pressure.

FIG. 19.—A young conceptacle with young septate hairs.

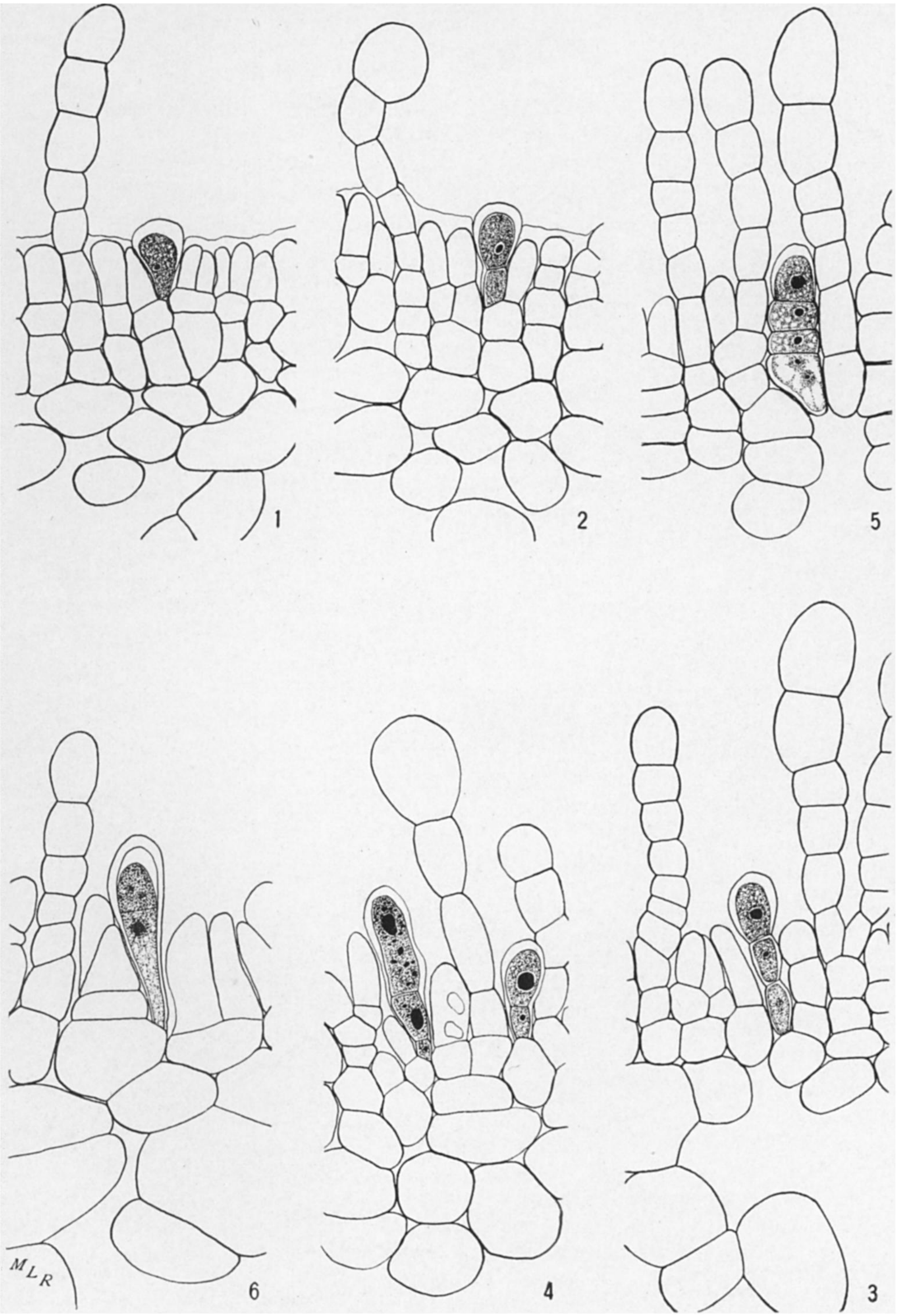
FIG. 20.—A later stage of a conceptacle with development of septate hairs.

FIG. 21.—The hair pit stage of the conceptacle.

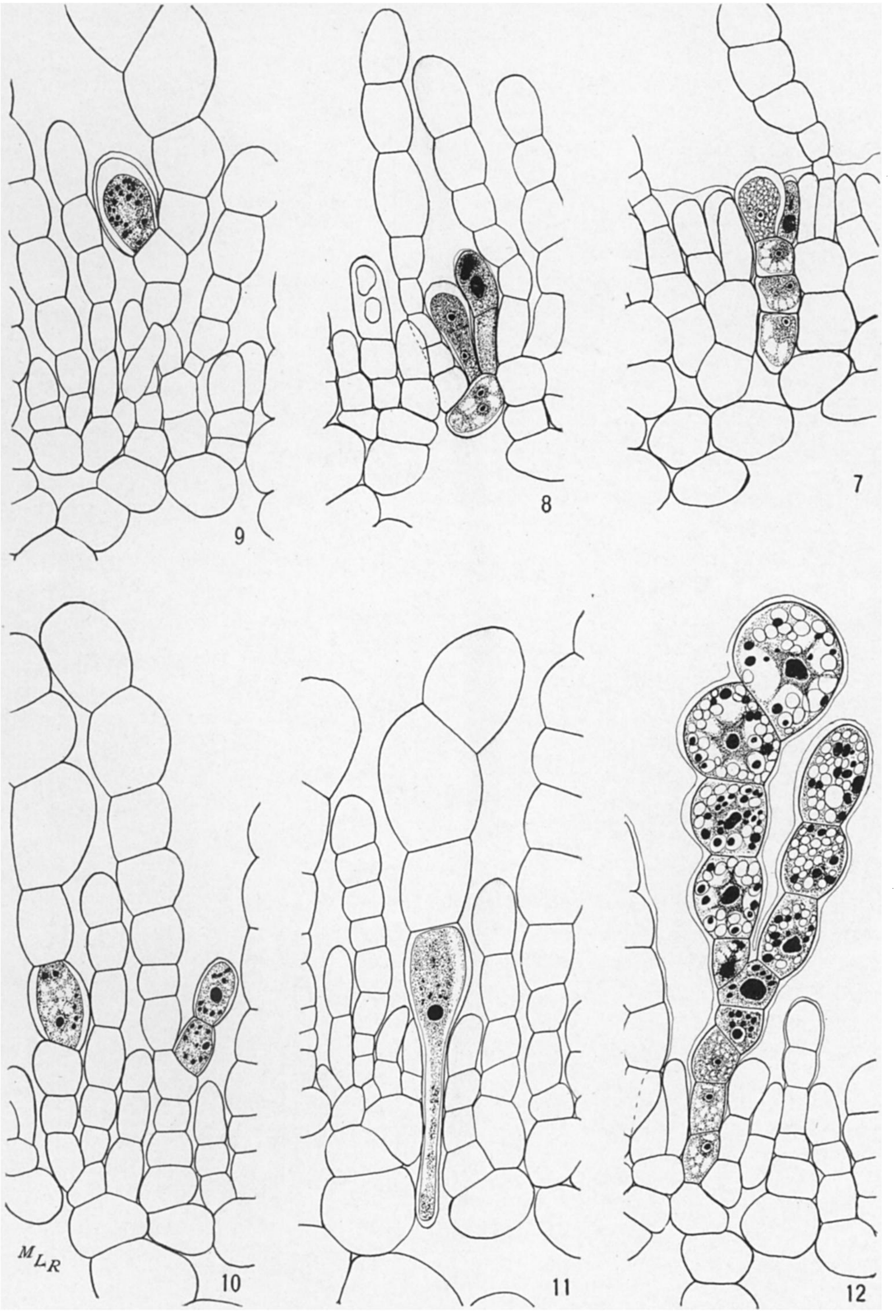
FIG. 22.—A mature conceptacle, showing various stages of reproductive sacs (gametangia ?) and a few fragile hairs; old hairs have been shed.

FIG. 23.—The initial row as it appears in a conceptacle at stage shown in fig. 22.

FIG. 24.—Gametangium (?) just before discharge of contents.



ROE on SPLACHNIDIUM



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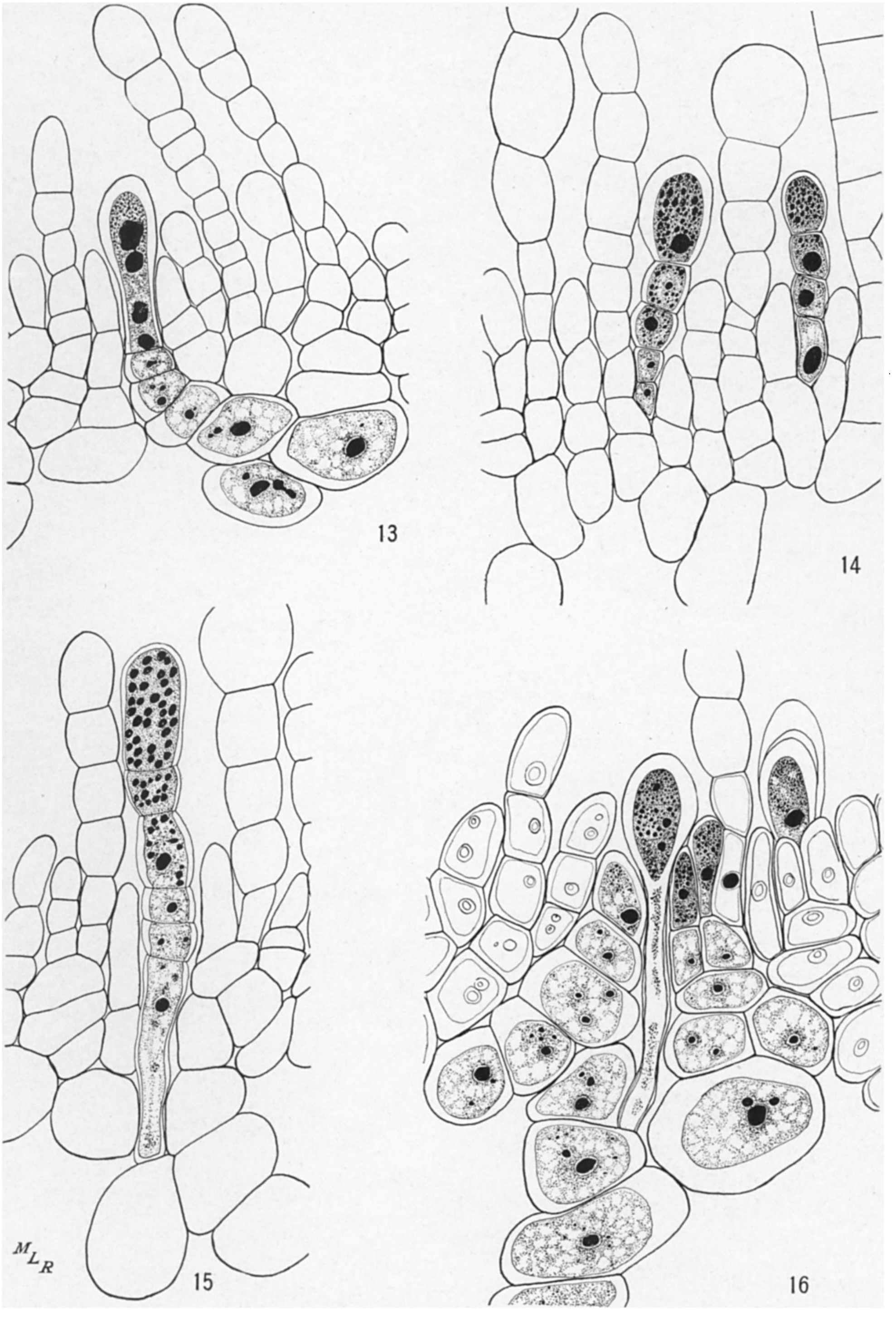

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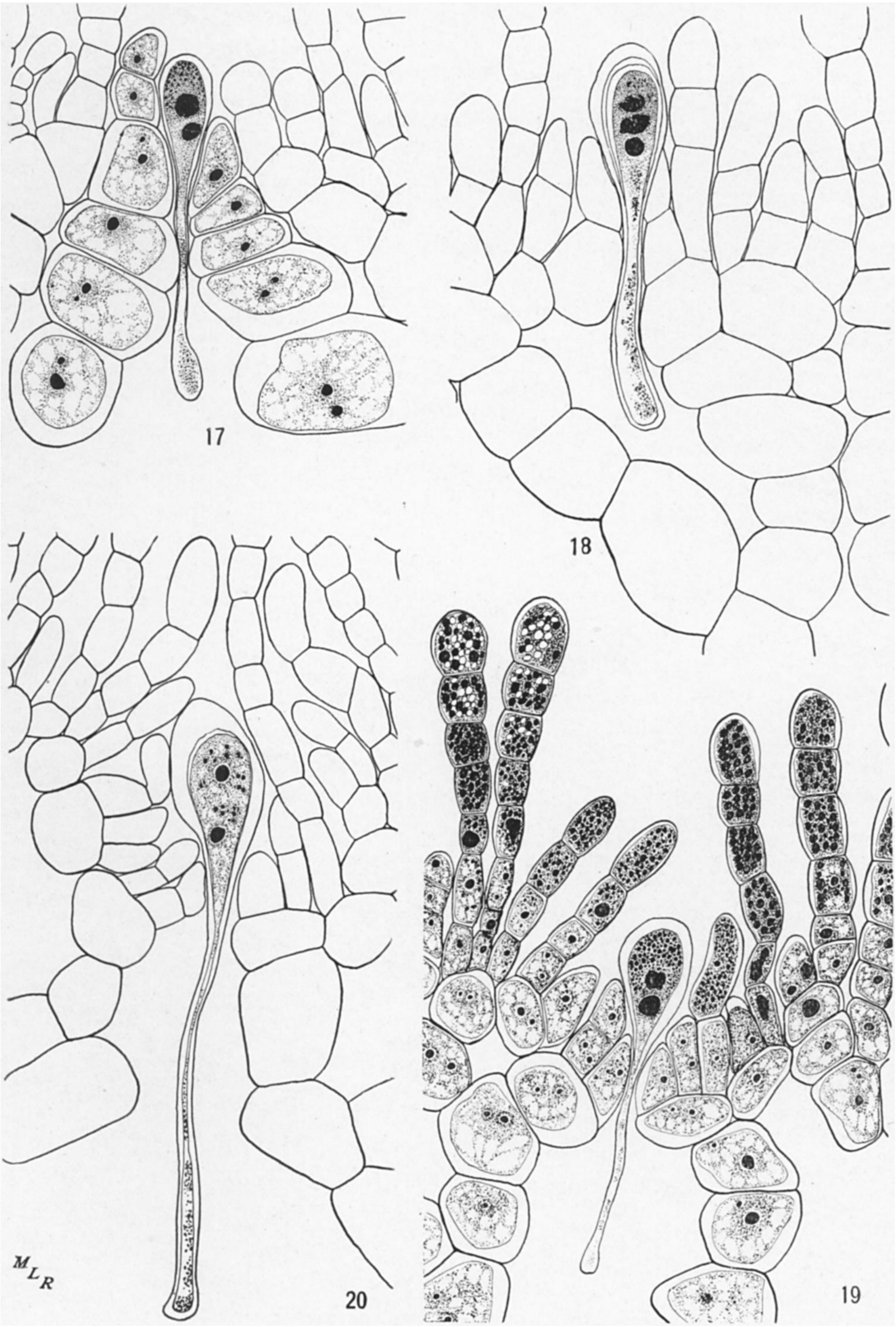

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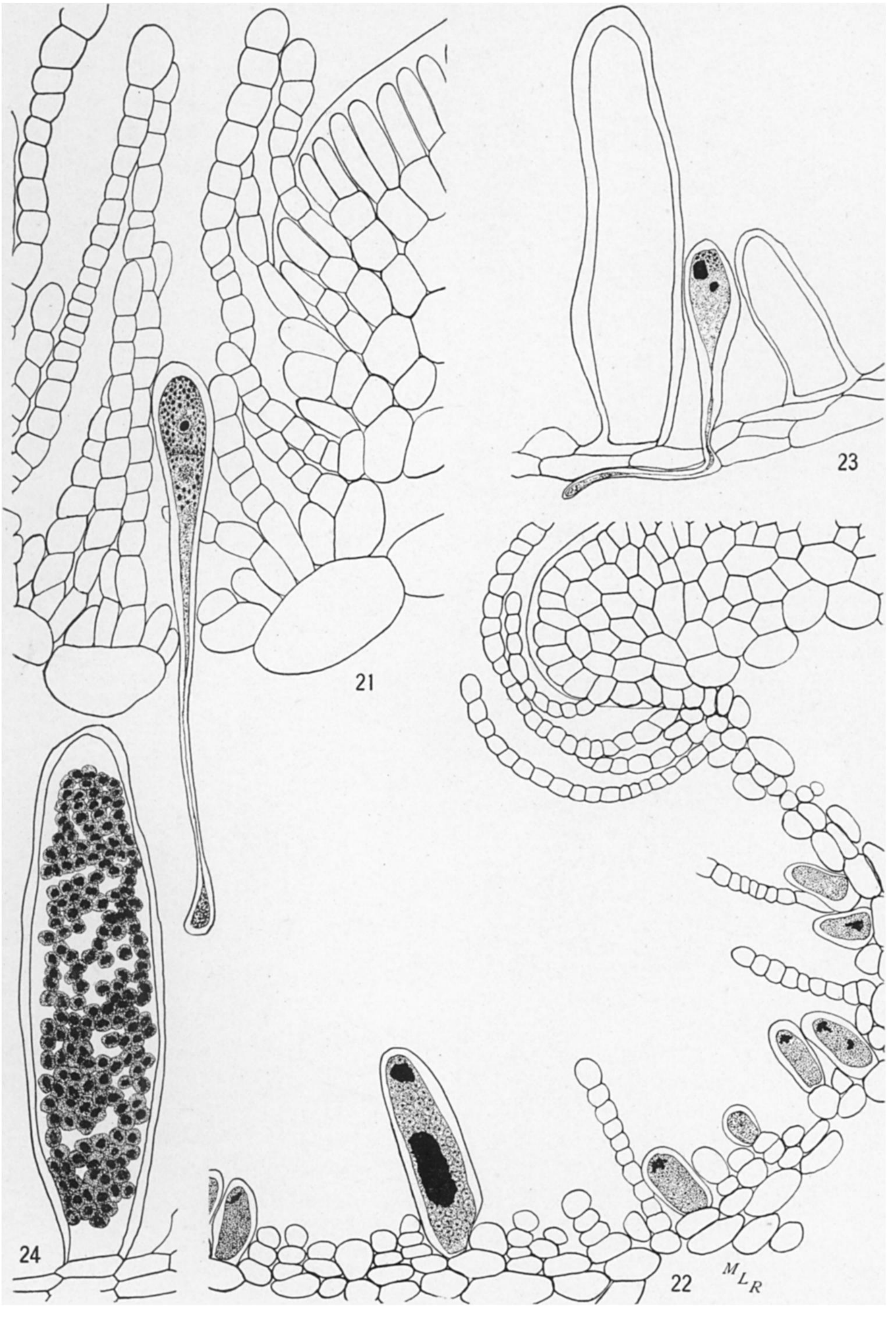

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