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A COMPARATIVE MORPHOLOGICAL STUDY OF THE MYXOMYCETE FRUCTIFICATION

by

GLADYS E. BAKER

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Morphological studies of slime molds have consisted mainly of taxonomic investigations and developmental studies. External characters have been used in taxonomy as well as those internal characters which are readily seen by microscopic examination of the sporangia. The early workers in the field based their classifications primarily on external appearances. DeBary (1, 2, 3) was the first to emphasize microscopic details. Rostafinski in his monograph revolutionized the system by using almost entirely internal characters as the basic principles of his classification. Later both external and internal characters were correlated in taxonomic descriptions, as in the works of Lister (7) and Macbride (8).

Rostafinski followed closely the work of DeBary, his teacher. His *Sluzowce* (10) is beautifully and profusely illustrated. Among his figures is a fair proportion of diagrams of the internal structure of sporangia. In many cases, though finely executed, these do not include sufficient detail to be of value except for purposes of general orientation. Of those illustrations that do attempt to show clearly the internal relations, many are inaccurate. These drawings were not made directly from sections, but were reconstructions, which would account for such inaccuracies.

Massee (9) also includes several illustrations of fructifications in section, but his figures are of even less value. Lister and Macbride chiefly illustrate external views, spores, and capillitial characters. To such figures as are found in these books reference will be made later.

Very few authors have included diagrams of sections of mature forms. The purpose of this work has been to show as nearly as possible the nature and the exact relations of the chief structures of the mature sporangia, such as the walls, capillitium, columella, and stalk. Spore characters have not been considered. Sixty-four species representing thirty-three genera have been studied. Both Lister and Macbride have been followed for generic and specific

descriptions. With a few exceptions, Macbride's synonymy and classification have been accepted.

Material for the work was taken largely from the mycological herbarium of the State University of Iowa. The collections range in age from one to twenty-five years. Unfortunately, many collections in the herbarium do not have complete collection data—in many instances, especially, the date is omitted. However, the majority of the material used was collected within the last five years. It was supplemented by several collections of fresh material made in the fall of 1931 near Iowa City. Sections of *Badhamia rubiginosa* (Chev.) Rost. were cut from a 1928 herbarium collection and from sporangia killed in Bouin's fluid in the fall of 1931. No essential differences between the two were noted. Dried material gave results as satisfactory as those obtained with fresh specimens.

All studies were made from sections cut in paraffin, with additional whole mounts whenever necessary. The earlier sections made from herbarium collections were first soaked in 95% ethyl alcohol, swelled in a dilute solution of potassium hydroxide, washed, and dehydrated by a butyl alcohol series, using the grades recommended by Zirkle (12). Later, it was found more satisfactory to put the sporangia on moist filter paper in covered petri dishes, where they were left over night. In this way no potassium hydroxide was used, the sporangia being transferred directly to the first of the butyl series. Sections from material treated by the second method preserved to a greater extent the wall and external calcareous deposits. All slides were stained by a short triple method—safranin, crystal violet, and aqueous orange G. Measurements of spores from sporangia dehydrated in both ways were within Lister's or Macbride's limits.

Sporangia collected in the field were killed in Bouin's fluid for twenty-four hours, washed and dehydrated in the same way as the herbarium material. Sections cut twenty microns thick proved the most satisfactory, especially for capillitial characters.

As it was found impractical to make the drawings on a common scale, the magnifications are given for each. All drawings were made directly with a Zeiss microscope and a camera lucida, with the exception of figures 1, 4a, 27a, 42, 43, 44, and 56, which were reduced to suitable sizes from camera lucida originals. The drawings included here are representative of sporangia in the particular collections used. Undoubtedly, there is a great deal of variation,

particularly in size, form, and amount of lime present, in different collections of the same species. An effort was made to select collections which were typical of the species. Though at times the diagrams of different species are remarkably similar or structurally very simple, yet the drawings are presented to afford correlation of the essential characters. No attempt has been made to discuss generic characters. For each species a description of its characters and a drawing or more when needed, have been included.

It has been impossible to achieve conclusive results concerning the nature of the aethalioid forms, except in the case of *Dictydiaethalium plumbeum* (Schum.) Rost., for which several young stages of material were available. It is hoped that all the so-called aethalioid slime molds will be studied in their entire development to determine their exact form.

The types of fructifications are defined according to the conceptions of Martin. These include: the aethalium—hypothetically the most primitive form, in which all or a considerable part of a given plasmodium is involved, and in which differentiation has not proceeded to the delimitation of separate sporangia; the pseudoaethalium—in which the sporangia are delimited, but borne in compact and more or less attached groups; the plasmodiocarp—approaching the sporangiate type and formed of the principal veins of the plasmodium; the sporangium—the typical erect fructification representing only part of the plasmodium.

This study was suggested by Professor G. W. Martin and completed under his direction in the mycological laboratory of the State University of Iowa.

The list of species studied is as follows:

PHYSARALES

Physaraceae

1. *Fuligo septica* (L.) Gmelin
2. *Fuligo muscorum* Alb. and Schw.
3. *Badhamia macrocarpa* (Ces.) Rost.
4. *Badhamia utricularis* (Bull.) Berk.
5. *Badhamia rubiginosa* (Chev.) Rost.
6. *Physarum serpula* Morgan
7. *Physarum lateritium* (Berk. and Rav.) Morgan
8. *Physarum sinuosum* (Bull.) Weinm. ex Fr.
9. *Physarum cinereum* (Batsch) Pers.

10. *Physarum melleum* (Berk. and Br.) Massee
11. *Physarum citrinum* Schum.
12. *Physarum globuliferum* (Bull.) Pers.
13. *Physarum penetrale* Rex
14. *Physarum nucleatum* Rex
15. *Physarum didermoides* (Ach.) Rost.
16. *Physarum compressum* Alb. and Schw.
17. *Physarum flavicomum* Berk.
18. *Physarum gyrosum* Rost.
19. *Physarum polycephalum* Schw.
20. *Craterium leucocephalum* (Pers.) Ditm.
21. *Craterium leucocephalum* var. *scyphoides* Lister
22. *Craterium minutum* (Leers) Fries
23. *Physarella oblonga* (Berk. and Curt.) Morgan
24. *Leocarpus fragilis* (Dickson) Rost.
25. *Cienkowskia reticulata* (Alb. and Schw.) Rost.

Didymiaceae

26. *Mucilago spongiosa* (Leyss.) Morgan
27. *Didymium squamulosum* (Alb. and Schw.) Fries
28. *Didymium minus* Morgan
29. *Diderma radiatum* (L.) Morgan
30. *Diderma spumarioides* Fries
31. *Lepidoderma tigrinum* (Schrad.) Rost.
32. *Colloderma oculatum* (Lipp.) G. Lister

STEMONITALES

33. *Stemonitis fusca* Roth
34. *Stemonitis axifera* (Bull.) Macbride
35. *Comatricha nigra* (Pers.) Schroet.
36. *Comatricha suksdorfii* Ellis and Everh.
37. *Diachaea cerifera* G. Lister
38. *Diachaea leucopodia* (Bull.) Rost.
39. *Enerthenema papillatum* (Pers.) Rost.
40. *Enerthenema melanosperum* Macbride and Martin
41. *Lamproderma violaceum* (Fries) Rost.
42. *Lamproderma arcyrionema* Rost.

CRIBRARIALES

43. *Licea biforis* Morgan
44. *Licea minima* Fries
45. *Licea variabilis* Schrad.
46. *Lindbladia effusa* (Ehr.) Rost.
47. *Tubifera ferruginosa* (Batsch) Gmelin
48. *Enteridium splendens* (Morgan) Macbride
49. *Dictydiaethalium plumbeum* (Schum.) Rost.
50. *Cribraria argillacea* Pers.

LYCOGALES

51. *Lycogala epidendrum* (L.) Fries

TRICHIALES

52. *Margarita metallica* (Berk. and Br.) Lister
53. *Listerella paradoxa* Jahn
54. *Ophiotheca wrightii* Berk. and Curt.
55. *Ophiotheca vermicularis* (Schw.) Massee
56. *Perichaena depressa* Libert
57. *Arcyria globosa* Schw.
58. *Arcyria denudata* (L.) Wettstein
59. *Arcyria cinerea* (Bull.) Pers.
60. *Hemitrichia vesparium* (Batsch) Macbride
61. *Hemitrichia serpula* (Scop.) Rost.
62. *Hemitrichia clavata* (Pers.) Rost.
63. *Trichia varia* Pers.
64. *Oligonema nitens* (Libert) Rost.

Fuligo septica (L.) Gmelin. Figs. 4a, 4b.

The aethalial fructification of *Fuligo septica* is usually large and pulvinate. Its wall is membranous and rugose, with numerous calcareous deposits throughout, but especially abundant laterally and basally. Within are spores and capillitium. The latter consists of many membranous knots, some quite decidedly calcareous, others not, but all more or less connected by fine threads.

It has been customary to refer to this slime mold as an aethalium. On the basis of Martin's terminology it is an aethalium, but in an opposite sense from standard definitions. There is no evidence in sections of mature specimens that the membranous expansions

represent vestigial sporangia. More probably they represent pseudocapillitium formed as the result of degenerating protoplasm.

Of published illustrations of this species, Rostafinski's deserve the first consideration. Figure 97 in his monograph presents a view of the central stratum of the aethalium, showing the vein-like protoplasmic areas characterizing its development. Figs. 101 and 104 show equally well the separate details of the capillitium. But his diagram of a median section, fig. 106, achieves scarcely more than location of the different layers of the fructification. Massee has a meaningless diagram of such a section, but neither Lister nor Macbride illustrates the species in this way.

Fuligo muscorum Alb. and Schw. Fig. 1.

Fuligo muscorum forms irregular fructifications that are pulvinate or elongate in habit. An individual fructification consists of interwoven tubes, often regarded as sporangia, but more probably representing vein-like regions of the plasmodium or closely combined plasmodiocarps. A single membranous wall bearing some lime fuses basally with the delicate membranous hypothallus. Besides the internal walls, a true capillitium of lime nodes and short threads is present.

It is perhaps justifiable to regard this form as an aethalium, at least until more definite results are obtained. The only illustrations of the species are in Lister's *Monograph*.

Figure 1 represents a median vertical section.

Badhamia macrocarpa (Ces.) Rost. Fig. 2.

Sessile, subglobular sporangia are typical of this Badhamia. Its single, somewhat rugulose wall is membranous, with here and there lime inclusions. The capillitium is not entirely badhamioid, but in part approaches the physaroid type, for its calcareous tubes and knots are often connected by short, fine threads.

Only external appearance, spores, and capillitium have been illustrated by Massee and Rostafinski. Lister has an excellent series of this type, but Macbride has no drawings of the species.

A view of a section cut through an entire sporangium is given here.

Badhamia utricularis (Bull.) Berk. Fig. 5.

The sporangia of this species are subglobular and in contrast with those of the preceding species are large and stipitate. A very

delicate membrane serves as the peridium. On its exterior are numerous calcium granules, usually quite round and marked with radial striae. Small clumps of calcium granules are scattered in the wall at intervals. A weak, slender, fibrous stalk—its edges roughened by loose ends, and about two-thirds the sporangium height—supports the sporangium. There is no hypothallus. The capillitium is moderately broad, flattened, and expanded at the axils. Occasionally fine threads connect larger knots. Its arrangement is not intricate: it simply forms a uniform network in the interior. The spores often remain in clumps of three or more, or are entirely free, depending upon the particular sporangium.

Rostafinski and Lister illustrate the capillitial and growth characters in an excellent series of drawings. Neither Massee nor Macbride made drawings for this species.

Badhamia rubiginosa (Chev.) Rost. Fig. 6.

This species, clearly a Badhamia, has a definite stipe rising from a discoid hypothallus. Its sporangia are obovoid, bounded by heavy membranous walls which are confluent with the walls of the columellae and the stalks. The fusiform columella, a continuation of the stalk, attains three-fourths of the sporangium height, becoming broadest about one-third below its apex. Both columella and stalk are filled with lime granules. The capillitium is a rugged network of broad tubes, densely charged with lime and extending from columella to wall.

Badhamia rubiginosa is of common occurrence, yet in the standard works on slime molds one usually finds illustrated only gross characters and separate details. Rostafinski attempted a median view of a sporangium, but his figure is quite inaccurate.

Figure 6 is an internal view of a mature sporangium, showing the relations and structure of the wall, columella, and capillitium.

Physarum serpula Morgan. Figs. 8a, 8b.

This is a plasmodiocarpous form that is terete in section. The wall is membranous and filled with irregularly distributed lenticular lime granules which take a heavy stain. The capillitium is abundant, almost badhamioid, consisting of large irregular knots and bands, connected by short, fine threads. The capillitial knots contain lime granules, though less profusely than the wall.

The specific nature of these granules is not emphasized in the literature. However, Lister's illustration of the capillitium and

wall suggests their presence. Macbride's description of the capillitium as "charged with polygonal nodules of lime" probably refers to these granules, though they are decidedly not polygonal. When a portion of a sporangium is mounted on a slide, the granules appear perfectly clear, with a slight yellowish cast.

Physarum lateritium (Berk. and Rav.) Morgan. Fig. 3.

The sporangia of the collection studied are sessile and subglobose. The single, thin, rugulose membrane that forms the peridium has occasional calcium granules in its outer edge. At the base the wall is somewhat thickened, forming a more or less distinct hypothallus. Internally, the capillitium forms a close net of fine threads and rounded calcareous knots of varying size and shape.

Although this species is easily separated from *P. cinereum* by color, and by character and size of spores, the distinctive differences in their internal morphology are very slight. The nodes of *P. cinereum* are a bit more angular than those of *P. lateritium*.

Physarum sinuosum (Bull.) Weinm. ex Fr. Fig. 15.

Short plasmodiocarps or distinct sessile sporangia are found in this Physarum. The particular sporangia sectioned are laterally compressed, varying little in width from base to apex, a character that is typical though not constant. There is a double wall, the outer layer of which is broad and rough, breaking irregularly at the apex for dehiscence. Apically it is thicker and covers the spore mass after the outermost part has split. The inner layer is a membrane of variable width to which the capillitium is attached. The capillitium is a freely branching system of large lime knots and slender short threads.

In Rostafinski's monograph, Plate V, fig. 91, there is an illustration of the species in section. It is not altogether accurate, but it is the best diagram in the literature. The basal portion of the sporangium is least correct; in all the sections examined the walls are continuous at the base. Massee has a small sketch which suggests only the manner of dehiscence.

Physarum cinereum (Batsch) Pers. Fig. 17.

This very simple, sessile, subglobose fructification is borne on a hypothallus. The sporangial wall is fine and membranous with

heavy calcareous deposits at intervals on the outside. Typically physaroid capillitium extends throughout the sporangium.

For all practical purposes, this species is adequately illustrated in Lister. A diagram of structure simply enables one to correlate its internal and external characters at a glance.

Physarum melleum (Berk. and Br.) Massee. Fig. 9.

This species is representative of the columellate Physarums. The sporangia are globose on a stalk that is about equal in height to the sporangium. A thin membrane forms the peridium, becoming confluent at the base with the wall of the stalk. The columella is a conical extension of the stalk. Both stalk and columella are finely vesicular, almost cellular in appearance. The capillitium consists of delicate hyaline threads originating along the entire length of the columella, sometimes expanded at the axils or connected with large angular lime knots.

No essential differences between this species and *Physarum citrinum* were revealed by this method of study. However, there are several characters which quite definitely separate the two for taxonomic purposes.

Physarum citrinum Schum. Fig. 10.

Short, stout stipes bear the subglobose sporangia of *Physarum citrinum*. The single membrane of the peridium, relatively thin, is often coated on the outside with calcareous deposits. The stalk appears cellular in section, due to many fine interlacing membranes. A short tapering extension of the stalk within the sporangium serves as the columella from which the capillitium arises. The latter consists of slender straight threads and lime knots of various sizes and shapes.

This species is distinguished from *Physarum melleum* chiefly by reason of its yellow stipe. In their morphological make-up the two species are quite similar. Neither species is adequately illustrated for structure. Lister has excellent views of habit; neither Rostafinski nor Macbride illustrates it; Massee has a habit sketch of *P. citrinum*. The diagrams given here emphasize the similarities in these Physarums.

Physarum globuliferum (Bull.) Pers. Fig. 12.

The sporangia are globular, erected on long slender stalks, two-thirds the total height of the fructification. Inside the sporangium,

the stalk forms the short, conical columella. Varying amounts of lime are clustered on the surface of the sporangium. The sporangium wall is a single membrane, so thin that little remains after sectioning, especially when dried material is used. This membrane is confluent with the stalk. The stalk itself is composed of a homogeneous matrix surrounded by a membranous wall, and containing calcareous deposits, these granular or at times clearly crystalline. In some sporangia this deposit of calcium is very abundant, occurring in dense clumps from the base of the stalk to the sporangium, but apparently not in the columella. When a stalk is placed in weak hydrochloric acid, the lime dissolves, leaving the horny or membranous matrix. The capillitium is comparatively lime free. Though there are occasional lime filled knots, many are limeless; all knots are connected by fine threads.

Rostafinski, fig. 86, diagrams the internal structure in a manner that implies that the stalk and columella are completely calcareous.

Figure 12 is typical of conditions in the various sporangia of a herbarium collection determined by Macbride.

Physarum penetrale Rex. Fig. 19.

This Physarum is very similar in its structural plan to *P. globuliferum*. The sporangia, in this form, are ellipsoidal, standing on long slender stalks, two-thirds the total height. The single wall is limeless, in contrast with that of the preceding species, though there may be a few calcareous deposits. Inside, the conical columella extends two-thirds the height of the sporangium, then broadens apically. Capillitium arises along the entire columella and radiates to the wall. It consists of slender threads with scattered lime knots and triangular axillary expansions.

Lister's illustrations of the species are the only ones in recent works. Her figure b, plate 36, which was designed to show internal structure, is not clear enough to show detail.

Figure 19 is drawn from sections cut from a 1926 collection of Brandza's, typical except that the particular sporangium drawn is somewhat flattened rather than oval.

Physarum nucleatum Rex. Fig. 7.

Physarum nucleatum is so named from the presence of a central mass of lime. Typically the fructification consists of a slender, solid stalk, a little more than half the total height, and a sub-

globose sporangium, bearing some lime on the outside. In the center is the large mass of lime from which the close capillitial net of fine threads and scattered lime knots radiates.

Only one author, Lister, illustrates this species. Her figures are beautifully drawn and the detailed drawing of the "nucleus" and capillitium shows clearly enough their relation to each other.

Physarum didermoides (Ach.) Rost. Fig. 14.

The sporangia of this Physarum are ovoid and shortly stalked. Their walls are composed of three layers: the outermost a heavy calcareous shell, most of which is destroyed in sectioning; a middle, delicate membrane to which the calcareous layer is attached; and a heavy membrane on the inside, that at times is closely combined with the middle membrane or may be widely separated. Short, delicate, membranous stalks support the sporangia, which may be more or less united in groups. In the center of each sporangium there is a large mass of lime bounded by a membrane of variable thickness. It is supported by very fine threads with numerous rounded lime nodes which radiate throughout the sporangium.

Rostafinski has a splendid drawing of the species in section, though his material apparently lacked the central lime mass. The character of the wall appears two-fold in contrast with the three layers described here. Macbride states that if the calcareous cap is present, the central lime mass is lacking. Both were clearly present in the material used.

Physarum compressum Alb. and Schw. Fig. 13.

Fan-shaped sporangia, the result of lateral compression, are characteristic of the stipitate forms of *P. compressum*. Sections were cut parallel to the flattened surface and also at right angles to it. As no fundamental differences were apparent only the former section is illustrated. The wall is membranous, bearing closely adhering lime granules on the exterior. The stout, somewhat furrowed stalk is coarsely granular in section, and encrusted on the outside with lime. A network of fine short threads and variously shaped lime knots is typical of the capillitium, which is attached on all sides.

In Rostafinski's monograph there is a clear-cut sectional diagram. The character of the stalk is too regular and there is a suggestion

of a columella, but aside from that it leaves nothing to be desired. No other sectional drawings of this species were found.

Physarum flavicomum Berk. Figs. 11a, 11b.

Nodding, slightly flattened sporangia are borne on tall slender stalks free from calcareous deposits. The walls are single membranes with inclusions of pellet-shaped bodies in the region of the stalks. These stain red with safranin and are irregularly distributed, as are the lenticular granules in *P. serpula*, but in this species they are larger. At times they are present in the upper part of the stalk. The capillitium is a simple net of threads with axillary expansions and small angular lime knots.

Figure 88 in Rostafinski illustrates very nicely the general plan of this species, though the sporangium is not complete. There is nothing in it to indicate the presence or nature of the curious granules mentioned above.

Physarum gyrosum Rost. Fig. 18.

According to Macbride's classification, this is one of the Physarums in the Tilmadoche group. The sporangia are massed, labyrinthine and fused, forming almost an aethalioid mass on a common hypothallus. Their walls are simple and non-calcareous. Within, the capillitium, consisting of extremely fine threads with large fusiform lime nodes, is oriented transversely to the walls.

No illustrations besides Lister's very excellent series were found. This, however, does not include a sectional view.

Physarum polycephalum Schw. Fig. 16.

The sporangia of *Physarum polycephalum* are gyrose and dichotomously lobed. There is a fine capillitium with calcareous nodes here and there through the sporangial head. The stalk is membranous with an internal granular deposit, non-calcareous. There is no membrane separating it from the sporangium. The wall is membranous and in this case with little calcium, owing probably to the fact that the sporangia used were matured in a moist chamber.

A life history of this species has been worked out by Howard (5). It is interesting to note from his work that there is no membrane between sporangium and stalk at any stage, and that the fructification is not compound in that all the lobes are continuous with the central portion, even though by very small openings.

Craterium leucocephalum (Pers.) Ditm. Fig. 25.

The small, obovoid, stalked sporangia of *Craterium leucocephalum* open by irregular circumscission. The outer layer of the double wall is slightly thinner in the upper portion, and membranous with a few lime granules in vesicular pouches. Some lime is free on the surface. The inner wall is a thin membrane. At the base the walls are thicker, almost cartilaginous. The cartilaginous stalk, from a small hypothallus, is confluent with the outer wall. In the center of the sporangium there is a pseudo-columella of aggregated lime granules, unevenly distributed and bounded by a fine membrane. It is supported by the capillitium of fine branching threads interspersed with moderate sized lime granules.

Massee illustrates a median vertical section of this, but it is not accurate. No lime occurs in the stalk as there indicated; the threads are too heavy; and the columella is unlike any seen in the present study. Excellent habit sketches are included in both Rostafinski and Lister.

Craterium leucocephalum var. *scyphoides* Lister was studied but there is so little difference between the typical species and this variety that the variety was not illustrated.

Craterium minutum (Leers) Fries. Figs. 22, 23, 24.

Sporangia from three different collections were sectioned. The first, a Brandza collection (No. 41, August 1927), is characterized by goblet-shaped, stalked sporangia (fig. 23). Dehiscence is by a regular lid, not inserted but dome-shaped. The lid itself is thinner than the sporangium wall. There are occasional lime deposits on the inner side of the peridium. The stalk is thick and confluent with the wall. No pseudo-columella is present, but the lime knots of the capillitium are very large and irregular.

An Oregon collection made by M. E. Peck has short, broad sporangia that are almost fan-shaped in section (fig. 22). The wall is double—the inner, a calcareous layer; the outer, membranous merging into cartilaginous at the junction with the stalk. There are the same layers in the lid, but it is thinner and bears crystalline lime nodules on the outside and in the wall itself. The lime knots are smaller than in the preceding specimen, but there is no pseudo-columella.

Another collection reveals the typical *C. minutum* form with inserted lid (fig. 24). There is a much thinner calcareous inner

layer than in the sporangia of Peck's collection, though it is undoubtedly present on the inner side of the membranous layer. The outer wall of the sporangium and the wall of the stalk are distinct at the base of the sporangium, but merge farther up. The stalk is cartilaginous. A true lid, more or less calcareous, is present. It is depressed with a prominently projecting rim. The capillitium consists of small lime knots and fine threads. In the center the lime unites to form a pseudo-columella.

Rostafinski's illustration of this species is beautifully drawn, but highly diagrammatic. The internal character is correct, but the wall is too schematic to be of scientific value. According to his diagram, there are three layers in the wall—the outer seemingly cartilaginous; a more or less calcareous middle layer; and an innermost membrane to which the capillitium is attached. Such a wall was not found in any of the material studied. All three variations described are illustrated.

Physarella oblonga (Berk. and Curt.) Morgan. Fig. 21.

This slime mold has cylindrical stipitate sporangia that are hollow from apex to base. The wall is membranous and single. On the interior it forms the spurious columella which is continuous with the hollow stalk. The inner and outer walls fuse at the base of the sporangium to form the wall of the stalk. Filiform capillitium, rarely forking, extends from the inner to the outer wall. Trabeculae, stout calcareous bands, have broad attachments on the outer wall. A few continue directly across to the interior wall, but the majority taper to a fine point and are connected with the inner wall by short threads. The trabeculae are persistent on the outer wall when the sporangium opens.

Rostafinski, Appendix, figure 243, has illustrated a median vertical section in an entirely satisfactory way. Other authors contribute necessary details and habit views.

Cienkowskia reticulata (Alb. and Schw.) Rost. Fig. 26.

Plasmodiocarpous in habit, this species is attached to its substratum by a narrow base. The single wall is membranous and free from lime except at the points of attachment of the calcareous plates which are at right angles to the axis of the fructification. The capillitium is a loose network of fine threads with numerous

free, pointed, and curved ends. These threads are connected at times with the calcareous plates.

No diagram of internal morphology was found. Figure 26 represents a plasmodiocarp sectioned at right angles to the plates.

Leocarpus fragilis (Dickson) Rost. Fig. 20.

Sporangia from two different collections were sectioned, but only one illustrated as there were no differences other than size and shape. The sporangia are large, obovoid and stipitate. There are three layers in the wall. The outer layer is thick, cartilaginous, and brittle, so that in sectioning it may split in a shingle-like fashion. It is continuous with the stalk. Innermost is a membrane to which the capillitium is attached. Between this membrane and the cartilaginous layer, there is a heavy amorphous calcareous deposit. The stalk is very slender, filiform, and weak, rising from a hypothallus common to several sporangia. The capillitial element is double—one system of very fine threads with the majority of its nodes limeless and another of large calcareous tubes. Both occur in all parts of the sporangium and are occasionally connected, though more often quite distinct.

There is a good drawing of the wall with capillitium attached in Rostafinski, figure 93.

Mucilago spongiosa (Leyss.) Morgan. Figs. 27a, 27b.

The fructification of this species is aethalioid, composed of labyrinthine tubes with membranous walls, the whole interspersed with calcareous deposits. A broad cortex of calcium crystals surrounds the outside. These are for the most part densely clustered along fine membranes which originate from the apical ends of the sporangium-like veins and form a loose reticular cortex. A similar arrangement, though not so extensively developed, is found at the bottom. Internally, the calcium crystals are especially aggregated along the walls. A spongy hypothallus connects the entire fructification with the substratum.

Figures 27a and 27b are drawn from vertical sections.

Didymium squamulosum (Alb. and Schw.) Fries. Fig. 30.

The stalked sporangia of this species when sectioned make particularly fine slides. They are hemispherical, deeply umbilicate beneath, and on the exterior are covered with crystals, most of

which are stellate, though a few are flattened. The wall is a single membrane of varying thickness. The deeply furrowed and channelled stalk is heavily coated with lime nodules both inside and outside. At the base it is confluent with the hypothallus. A vesicular expansion at the top of the stalk, filled parietally with lime granules, forms the columella. Slender, flexuose threads, the capillitium, radiate from wall to wall. The character of the stalk varies, for in some specimens it is not so deeply furrowed nor so heavily lime crusted.

Massee has a small illustration which does not adequately suggest internal structure. In Rostafinski there is a well drawn series, yet it is inaccurate for the character of the stalk and columella.

Didymium minus Morgan. Fig. 33.

The sporangia of *D. minus* are hemispherical and umbilicate like those of *D. squamulosum*, but their stalks are four-fifths the entire height, solid and cartilaginous. The columella is a vesicular expansion filled with lime granules and a few fine membranous threads. The capillitium of sparingly branched, flexuose threads, reaches from the columella to the inner wall. Some threads that are decidedly larger than the others branch to form small ones.

Rostafinski's unexcelled illustration of *D. farinaceum* (synonymous with *D. melanospermum*) shows a very similar structure.

Diderma spumarioides Fries. Fig. 29.

Sessile, hemispherical sporangia, umbilicate beneath, characterize the fructification. The wall is double, composed of an outer calcareous crust and fine inner membrane. A membranous, convex columella with its numerous membranes giving it a cellular appearance is continuous with the stalk, which is constitutionally the same. There may be occasional deposits of lime granules in both. The slender branching threads of the capillitium radiate from columella to wall. There may be a calcareous layer on the upper surface of the hypothallus, which is continuous among many sporangia.

Rostafinski depicts a series of sporangia of this species with their hypothallus and columellae heavily encrusted with lime. Such a decidedly calcareous condition was not found in any of the material used, though it may occur, of course.

Diderma radiatum (L.) Morgan. Figs. 31a, 31b.

From a Colorado collection, sections were cut of sporangia ranging from stalked to almost sessile forms. A true double wall was not found, the typical case apparently consisting of outer and inner membranes enclosing a homogeneous, amorphous, calcareous mass. As these are so closely combined and almost indistinguishable at times, it seems doubtful to interpret this as a three-fold wall. The stalk, when present, is stout, membranous, becoming cartilaginous near the base. There are occasional calcium deposits in it. Columella and stalk are continuous, the former a convex expansion of the stalk. The capillitium is sparingly branched, flexuose, and attached to the inner membrane and wall.

Some specimens seem to lack the outermost membrane, in which case the wall could perhaps be called double.

There are illustrations of this species in section in Rostafinski, but they are morphologically inaccurate.

Lepidoderma tigrinum (Schrad.) Rost. Fig. 28.

This handsome slime mold has large hemispherical sporangia, deeply umbilicate, on stout furrowed stalks, two-thirds the total height. The wall is single, cartilaginous and covered with large granules or scales of calcium. A few of these scales are covered by membranes, but the majority are free. In section, the stalk is reticulate and vesicular, with crystals of calcium in the lacunae. The columella, as in other Didymiaceae, is an expansion of the stalk. Its furrows are much smaller and the lime nodules more numerous than in the stalk. Typical capillitium radiates abundantly from wall to wall. On close examination the calcium scales are seen to be closely appressed, not firmly embedded. In early stages it is possible that they are covered by very fine membranes.

Figure 159, Rostafinski, is the best median sectional view in the literature, though it is not correct for the structure of the columella.

Figure 28 was drawn from a Washington specimen collected by Macbride.

Colloderma oculatum (Lipp.) G. Lister. Fig. 32.

Unlike any other slime mold, the sporangia of *Colloderma oculatum* are encased in a heavy gelatinous sheath which forms the outer wall of the fructification. In places it has heavy granular deposits. Within this sheath, the usually sessile spore mass is en-

closed by a single membrane which is very delicate. The sporangia are ellipsoidal or subglobose with flattened bases from which the capillitium arises. This consists of branching, anastomosing, straight threads, slenderer near the surface.

Lister supplies the only illustrations of the species.

Figure 32 shows a median vertical section.

Stemonitis fusca Roth. Fig. 40.

Characteristically the sporangia of this species are cylindrical, obtuse at both ends, slender, and stalked. The stalk, slender and about one-fourth the total height, comes from a small hypothallus. At the extremity of the columella—a continuation of the stalk within the sporangium—several primary branches of the capillitium are given off. The network of capillitium extends from the columella to the surface by primary branches which anastomose and gradually become finer to form a peripheral net with angled meshes.

Criticisms of the illustrations of this species in Massee, Lister, and Macbride, would be much the same as those mentioned in connection with the following species.

Stemonitis axifera (Bull.) Macbride. Fig. 41.

Sporangia of this species are exceedingly long and slender with slightly acuminate apices. The slender stalk, which rises from a hypothallus, is about one-third the entire height and is continued within the sporangium as a columella. In the sporangium, the columella extends nearly to the apex. Larger primary horizontal branches connect with a fine angular peripheral net. There are many free ends on the surface by which the wall, early evanescent, is supposedly supported.

Lister does not recognize this species as *S. axifera* but as *S. ferruginea* Ehrenb. Massee also refers to it under that specific name. This however, is merely a matter of synonymy. Massee includes among his illustrations a bit of the net from the columella to the surface, but the primary branches seem too heavy in proportion to the peripheral net and the transition between the two too abrupt. Lister's figure showing the same structure is confusing as it represents the entire body. A diagram of a median longitudinal section is of greater value in orientation. One would scarcely be able to separate *S. axifera* and *S. fusca* on the basis of the illustrations of the capillitial net in Macbride.

Comatricha nigra (Pers.) Schroet. Fig. 36.

The globose, somewhat flattened sporangia of the collection used stand on solid tapering slender stalks about three times the sporangium height. At times there is a continuous hypothallus among the sporangia. The stalk is continued within the sporangium about three-fourths of its height. It gradually tapers and divides almost directly into the finer surface network through a few intermediate heavy branches. Heavy primary threads proceed horizontally from the columella, branching and anastomosing to form the finer surface network. The net is dense only at the surface. There are a few free ends resembling short barbs on the outside.

DeBary (2) has a good illustration of the species, although a view of a section would be less confusing than an illustration of an entire sporangium such as he has drawn.

Comatricha suksdorfii Ellis and Everh. Fig. 39.

In this form the sporangia are large, cylindrical, and obtuse at both ends. A short, rather stout stipe rises from a small hypothallus. For a short distance the stipe is latticed in a manner similar to that of some Lamprodermas. The columella extends nearly to the apex of the sporangium, where it expands into a membranous web-shaped structure from which heavy capillitial threads originate, or simply divides into several main threads as in *C. nigra.* The capillitium is a very dense network attached along the length of the columella. The primary branches are heavy, but soon anastomose and branch throughout the sporangium. The entire net is closer than that of *C. nigra,* in which the main branches are quite conspicuous. At the outside there are many free ends, pointed, long and slender.

In distinguishing between *Comatricha suksdorfii* and *Comatricha nigra,* the gross characters such as the size, shape of the sporangium, and length of the stalk, are the most outstanding. Of the detailed characters the numerous free ends of the network of *C. suksdorfii* and their size and shape are significant, as is also the dense, closely branched net. It does not seem probable that a distinction could be made on the basis of the columellae for there seem to be no constant differences for that character.

Of the illustrations of *C. nigra* in extant works, Lister's are good for growth habits; Rostafinski's series is suggestive of sporangial variation; Macbride has a good picture of the structural

character in its entirety. For *C. suksdorfii,* also, Macbride offers the best figures.

Diachaea cerifera G. Lister. Fig. 38.

This interesting slime mold is stipitate, with subglobose sporangia which often have large waxy collars at their base. These collars, which resemble a huge cushion in section, are of a rough heterogeneous nature with a smooth outer layer. The entire structure takes a heavy stain with crystal violet. The single, delicate sporangium wall merges at the base into the collar. With the collar the stalk is over one-half the total height. It originates as a slender stalk and gradually expands to meet the collar with which it is confluent. Rigid, straight threads, comprising the capillitium, extend from the base to the walls in a fan-like manner. There is some branching. At the points of attachment to the wall, both above and below, the threads often become abruptly finer.

Lister gives the only description and illustration of the species. As usual, she includes splendid habit views and detailed drawings of capillitium and spores, but nothing to indicate its general construction.

Diachaea leucopodia (Bull.) Rost. Fig. 35.

The ovoid, obtuse sporangia are bounded by single, very thin, membranous walls. They are borne on stalks, one-third the total height of the fructification, which are lime filled and bounded by a thin membrane. The columella is a continuation of the stalk, also lime filled, extending well into the sporangium. Fine threads comprise the capillitium that radiates from the columella to the peridium. The nodes are limeless. At the points of attachment to the columella and peridium the threads are finer, especially at the peridium.

This genus is clearly differentiated from the two preceding genera by the characteristic limy stalk and the persistent peridium. It is allied to them by the capillitium, which sometimes forms a net to support the wall. Lister classifies the genus with the Physaraceae between the Physarums and Didymiums and suggests that it may be a connecting link between the Calcarineae and Stemonitaceae.

Massee illustrates and describes *D. leucopodia,* but gives no figures aside from habit and spores. He places the genus among

the Didymieae. Macbride has no illustrations of this species. Lister's figures give an adequate representation of its separate characters. Two partly opened sporangia in figure a, plate 99, show general internal construction. Rostafinski's figure 178 is the nearest approach to the diagrammatic representation of the internal structure. But, as in Lister's drawing, the result would be more satisfactory if only a section of the sporangium were shown.

Enerthenema papillatum (Pers.) Rost. Fig. 37.

One of the determining characters of this genus is the delicate membranous peridium which persists for only a short distance around the apical concave disc. The stalks of the globular sporangia are about equal to the sporangium height. In section the stalk is latticed from the hypothallus to the origin of the columella. The solid columella is merely an extension of the stalk within the sporangium. It tapers gradually to the apex, then expands again to form the disc from which all the capillitium originates. Its long flexuose threads extend downward with some branching; they are free in mature specimens.

Rostafinski does not include this species among those illustrated in his monograph, but Massee, Macbride, and Lister all have satisfactory pictures of it.

Enerthenema melanospermum Macbride and Martin. Fig. 34.

This species is strikingly larger than *E. papillatum*, although it resembles it in many ways. As in the smaller species the sporangia are globular, have a thin membranous wall, persisting only apically, and are stalked. However, at the point of origin of the sporangium wall the stalk is expanded in a large node. Stalk, node, and columella are all continuous. The very large apical disc bears the capillitium.

There are no important differences between this and *E. papillatum* as shown in section, except size and the presence of the large node at the junction of stalk and wall.

Lamproderma arcyrionema Rost. Fig. 48.

The globose sporangia of this form have a delicate persistent membrane. The stalk, about equal in height to the sporangium, is latticed internally. Within the sporangium, the columella ex-

tends practically half way. At its apex it divides into several primary branches from which smaller capillitial threads lead off. These threads are freely branched and anastomose to form a round-meshed net, with some free ends. There seem to be no attachments to the peridium. It is interesting to note that the stalk is latticed —a condition not readily seen in gross examinations.

Lamproderma violaceum (Fries) Rost. Fig. 49.

This species has many characters in common with the preceding one. Though the stalk is longer than in *L. arcyrionema,* it is structurally the same. At the junction of the sporangium and stalk, on each side of the columella and between it and the wall, there is a comparatively large, membranous area. This may be peculiar to the collection studied, though the sporangia appear otherwise normal. The capillitium arises from the apical region of the columella and for some distance along it. The net is made up of straight smooth threads, anastomosing and branching, and forming a close surface net. Its ends are mostly free and quite fine at the tips.

There are few figures of these two species. In Rostafinski, there is a small diagram of *L. violaceum,* figure 64, indicating the extent of the columella and the origin of the capillitium from it; he does not illustrate *L. arcyrionema.* Massee drew the same species, but not to any great advantage. On the other hand, Macbride illustrates *L. arcyrionema* with the wall entirely removed; this does not give a complete picture of the structure. Both are represented in Lister, but the results are rather confusing as the entire sporangia are drawn. These Lamprodermas retain their walls well enough to justify their illustration and description in such a stage.

Licea variabilis Schrad. Fig. 47.

Typically this is a large, sessile, pulvinate form without a hypothallus. Its lack of capillitium is characteristic of the genus as a whole. In this species there is a double wall—the outer layer thick, rough, and cartilaginous; the inner thin, delicate and membranous. Dehiscence is irregular.

In the literature this species is often described as *L. flexuosa,* as in Massee and Lister. Lister does not recognize the presence of two walls, but prepared sections confirm Macbride's observations of a double wall. The rough outer layer is closely appressed to

the thin inner membrane. It is more or less deciduous and is, therefore, often lacking in places.

No illustrations representing structure were found.

Licea minima Fries. Fig. 45.

A Colorado collection furnished the material for the study of this species. Its sessile, hemispherical sporangia are small and have no hypothallus. A single thick, cartilaginous wall opens by one or more predetermined lobes. The "peg-like warts" as described by Lister, are clearly visible on the inner sides of the lobes in the upper portions of the sporangium, but they do not occur on the lateral walls or along the base. They are pendant, like stalactites, and in places are abundant.

Licea biforis Morgan. Figs. 46a, 46b.

The fusiform sporangia of *L. biforis* are extremely small. There is a comparatively thick wall which opens by a longitudinal fissure at the top. Lister's comparison to a "date-stone" is apt. In section the lobes of dehiscence are tapered but rather blunt at the margins. Within the sporangium, the spores exhibit a regular radial arrangement. This shows to best advantage in section, for it can hardly be determined by an entire mount.

The walls of *L. minima* and *L. biforis* are very similar. Lister calls the former cartilaginous and the latter membranous. Again (6) he described the wall of *L. biforis* as similar to that of *L. flexuosa,* though with fewer external deposits. Judging from sections made from a collection of Morgan's, this is incorrect. When Lister's definition of cartilaginous is applied to these species as seen in section, both are apparently cartilaginous.

Illustrations of these species in Lister are sufficient for habit and detail. The sectional diagrams shown here illustrate more clearly the exact manner of dehiscence.

Lindbladia effusa (Ehr.) Rost. Figs. 42, 56.

A Pennsylvania collection of the species shows individual sporangia that are short stipitate. There is but a single layer of them, mostly free, though at times several are closely compressed. Short, rugulose stalks connect the sporangia with the well-developed hypothallus. The outer and innermost layers of the hypothallus are

thickened. The thin membranous walls of the sporangia are confluent with the stalks.

In another collection, from Nebraska, (no. xxvi), the sporangia are superimposed in several layers, forming a pulvinate pseudoaethalium. The whole structure rests upon a membranous hypothallus. The sporangia are cylindrical, though often much compressed. As in the former collection, the walls are membranous, with scattered, very fine plasmodic granules which take a clear red stain with safranin. It is possible to distinguish the individual walls of the sporangia even when they are closely appressed.

These two collections are suggestive of the extremes of variation in the genus and species. The sporangial forms resemble Tubifera; the plasmodic granules in the walls ally *L. effusa* to the Cribrarias, though it has no net.

Nothing can be determined from Macbride's picture, plate 12, figures 1 and 2. Lister has a good sectional view. Massee and Rostafinski have no illustrations of the species.

Tubifera ferruginosa (Batsch) Gmelin. Fig. 43.

This is a pulvinate pseudoaethalium with crowded cylindrical sporangia, more or less angled by pressure. Several layers of sporangia are superimposed upon each other. The walls of the individual sporangia are distinct, though tightly appressed in the inside areas. A heavier wall, common to all sporangia, bounds the exterior. The whole is borne on a loose, spongy hypothallus.

Macbride's illustrations are of no help, and Lister's are good only for habit and general orientation. Massee's also are unsatisfactory; Rostafinski does not illustrate the species.

Enteridium splendens (Morgan) Macbride. Fig. 44.

This pulvinate fructification is seated on a well developed hypothallus. It is bounded by a rather heavy wall or cortex, which merges basally with the hypothallus.

Internally, the whole mass is pierced by many membranous irregular bands that are expanded at the angles and at their junction with the cortex. These bands have been regarded as the walls of the numerous sporangia which make up the aethalium. Studies of mature forms give no basis for such a conclusion; rather, sections of this stage suggest that the whole is a very closely combined group of numerous plasmodial veins whose walls form the bands.

Both Macbride and Lister have regarded this form as closely related to Reticularia. Wilson and Cadman (11) after a thorough cytological and morphological study, concluded that Reticularia was not an aethalium, as no evidence of sporangial walls appeared. They termed it a sporangium that had become partially septate. This idea seems slightly far-fetched, for if it is a sporangium the bands within should develop in a fashion similar to capillitium. By their own account these are not the product of secretions but the result of protoplasmic degeneration during development and after meiosis.

On the basis of Martin's terminology, Enteridium is an aethalium and not a pseudoaethalium—(the latter term is comparable to the aethalium of Wilson and Cadman). If the bands in Enteridium are formed of protoplasmic remnants they may be regarded as pseudo-capillitium.

None of the illustrations in extant works give entirely satisfactory representations of internal structure.

Dictydiaethalium plumbeum (Schum.) Rost. Figs. 57-62.

A mature fructification of this species is pulvinate, although much flattened, on a membranous hypothallus. It is composed of cylindrical sporangia so compressed as commonly to become hexagonal, but often pentagonal or quadrangular. From the material available, young and mature stages of several different collections were studied. These gave evidence for the following points:

For each sporangium there is a membranous wall which is early evanescent. These are so closely appressed that they appear as one save at the corners. The sporangia may be four, five, six, or rarely seven sided. There are as many threads present as there are sides to a sporangium. They lie to the inside of the membranous walls and in cross-section they appear shield-shaped with the less arcuate side joined with the wall. This characteristic shape is seen in both young and mature stages, though in the latter the wall has disappeared. In longitudinal sections of mature specimens, the threads are seen to bear numerous minute spines and projections.

Apically the threads are clearly confluent with the sporangial caps, but below they do not attain the base. Many threads are in actual connection at the top, but none was found in similar junctions at the base. Either they end in a bulbous expansion or they join with other threads of the same sporangium, about one-twelfth

of the way or less from the bottom. When the basal membrane is removed, soaked in 95% alcohol, cleared, and mounted, no broken ends or other indications of thread attachment are evident.

Serial sections of young material reveal that near the base the threads gradually spread apart, become elongate in section, and finally fuse. There are no threads present in the very last sections. Only at the apex can the threads be said to mark the angles. There they come very close together at the corners of the sporangia. In the longitudinal sections one sees that the membranes definitely extend the entire length of the fructification and are attached to the floor.

The sporangial walls are commonly described as vestigial and represented by threads extending from the dome-shaped apex of each sporangium to the base. From the foregoing, it is doubtful if they are really part of the wall.

In the reconstruction of the mature pseudoaethalium, such as this, several things are outstanding, but especially the regularity and symmetry of its structure. The numerous sporangial caps give rise to as many vertical threads as there are sides to a sporangium. These extend nearly to the bottom, but end by a bulbous expansion or by uniting with other threads of the same sporangium. At the base there is a membrane with small extensions at right angles to it, indicating the points of attachment of the membranous sporangium walls, early evanescent. The entire structure is filled with spores. Below is a large, membranous hypothallus.

Among extant illustrations, Rostafinski's stand first, although they are highly diagrammatic and not too accurate. His figure 25 represents the general appearance of a section of an entire pseudoaethalium, though in reality the domed apices are more closely compressed and the bases more flattened than Rostafinski has shown them to be. His figure 30 is an artificial diagram correctly illustrating the design as seen in cross-section below the apex, but not accurate in detail.

Macbride's figure showing construction is inaccurate in that the threads do not reach the base as there implied.

Lister includes among her illustrations one of the floor of the pseudoaethalium showing the bases of the sporangia, figure 152e, and one of the caps with threads attached. The former condition is seen easily when a bit of the basal membrane is torn off and mounted. The second diagram depicts some of the threads joined

at their extremities, a fact which is suggestive of the condition mentioned previously. However, one would infer from Miss Lister's description that she intended this to represent basal attachment.

There are a few illustrations in Massee, but they do not contribute to the knowledge of the structure.

Beyond doubt, the presence of definite walls in the early stages makes this a pseudoaethalium. It appears that the threads do not continue to the base, in which case the question arises as to their function and homology. It is hoped that this very interesting form with its unusually perfect symmetry will soon be studied thoroughly in its entire development.

Cribraria argillacea Pers. Fig. 53.

From a Morgan collection of 1895, sections were made of sessile, gregarious sporangia on a distinct hypothallus. A single wall was found to be continuous over the entire sporangium, heavier at the base than in the upper portion where there are small thickenings on the inner side. These probably represent the net. The wall itself is bounded by a membrane on the exterior, but the inner surface is free—a layer of rough heavy granular deposits. Aggregations of these plasmodic granules form the thickened areas. In *Lindbladia effusa* the plasmodic granules are scattered, but in this Cribraria they are distributed throughout in dense clusters.

Massee, Macbride, and Lister show only entire sporangia, spores, and portions of the net.

Lycogala epidendrum (L.) Fries. Figs. 50a, 50b.

Lycogala epidendrum is one of the commonest and best known of the slime molds. The fructifications are large and sessile, dehiscing irregularly at the apex. They are surrounded by a crust or cortex of two layers which retain their identity throughout, although closely compressed in the basal portions. Of the two, the inner layer is the more homogeneous. In places it is very broad and may be separated from the outer one; again it is joined by irregular strands and tubes to the outer layer. A very fine, but distinct, membrane separates it from the spore region. On the surface there are occasional protoplasmic extrusions, usually completely covered by membranes of the outer layer. In young stages, before these protoplasmic areas are definitely pushed to the outside, the nuclei appear perfectly normal. When these areas are

completely cut off, degenerating nuclei are often visible. At maturity, only rarely are nuclear remnants distinguishable in the protoplasmic extrusions. In the upper part of the wall a few vesicles or tubes were observed, but these are more frequent in the basal region. The mature fructification contains spores and capillitum. The latter arises from the outer layer of the cortex, pierces through the inner one and is continued within. It is tube-like, often quite flat, freely branched at times, long or short, usually much wrinkled, and has round free ends.

This type of fructification can be considered only an aethalium. Since it was not studied developmentally, there is no evidence to support the idea of its being a single sporangium. Subsequent studies to determine the origin of the capillitium should be undertaken to reveal the true nature of the fructification.

There are many descriptions and studies of this genus and species in the literature. As early as 1859, DeBary (1) wrote of it and illustrated his paper with remarkably accurate drawings. However, considering the figures in some of the more recent works, it is perhaps justifiable to present a diagram of a complete aethalium as it appears in section.

Margarita metallica (Berk. and Br.) Lister. Fig. 63.

Sections were cut from herbarium material of sessile, subglobose sporangia on a small hypothallus common to several fructifications. A single thin, membranous wall opens irregularly. The capillitium is composed of fine coiled threads infrequently branched and very infrequently attached. No actual attachments were distinguished in prepared material, but their presence was verified by a fresh mount.

According to Massee, who described the species as *Prototrichia chamaeleontina* but did not illustrate it, the threads are thickened at the points of attachment. Such thickenings have not been seen, and neither Lister nor Macbride refers to a similar condition. Rather, judging from Lister's illustration, plate 196, one would infer that the threads are finer at their attachments. No drawings representing the internal structure in its entirety were found in the literature.

Listerella paradoxa Jahn. Figs. 55a, 55b.

This small sessile form grows on *Cladonia*. It has a single, but

extremely heavy, membranous wall, rough with much attached refuse matter. Tapering lobes with rather blunt ends allow for dehiscence. The capillitium is definitely attached at the base, sides, and on the lobes near the opening. Near the junction with the wall the capillitium is slightly less moniliform than in the sporangium.

Miss Lister describes this species as having scanty capillitium "attached below and perhaps above." In sections made from material collected by O. Jaap, abundant capillitium was found with definite attachments near the apex, on the sides, and at the base. Miss Lister's figures show clearly the diagnostic features of habit, capillitium, and spores. The drawing of a portion of the wall, as there presented, indicates the character but not the thickness in proportion to the entire sporangium.

Ophiotheca wrightii Berk. and Curt. Fig. 69.

The plasmodiocarpous sporangia are sessile, terete, and more or less globose in section. Material collected locally was used for study. The wall consists of two layers: the outer thick, rough, granular, forming a crust; the inner smooth, thin, and subcartilaginous. There is no lime on the exterior nor is there a hypothallus. A loose network of long, sparingly branched threads with numerous large spines, constitutes the capillitium. In section no definite attachments to the wall remained, but they are easily seen when a bit of the wall is mounted separately.

Lister credits this species with two walls; if Macbride intended to recognize this condition, he did not make it clear. Considering other forms in which two walls are acknowledged, it seems justifiable to admit the presence of two walls in this species. No structural diagrams were found in Massee, Lister, or Macbride, but several excellent drawings of habit and separate details are available in these works.

Ophiotheca vermicularis (Schw.) Macbride. Fig. 64.

In the form of growth, this species resembles *O. wrightii*—both are plasmodiocarpous, sessile, and subglobose in cross-section. A heavy granular mass bearing many beautiful, angled calcium crystals on the exterior and a fine membranous inner layer constitute the double wall. The inner membrane is papillose on the innermost surface in young sporangia, but in older sporangia this is

not so distinct. Only by mounting a portion of the wall separately could the capillitial attachments be distinguished. In all sections the capillitium was very scanty.

Macbride writes of a single wall; Massee implies the same structure; but Lister describes two walls. Median sections confirm the latter view.

Lister does not separate the genus Ophiotheca from the genus Perichaena. One of his criteria of the latter genus is the presence of double walls. Macbride separates them on gross characters and especially by the manner of dehiscence. For this study Macbride's classification has been accepted. Whether one admits one genus or two, the walls of both these species of Ophiotheca are double.

Perichaena depressa Libert. Fig. 51.

Many flattened, sessile sporangia, closely crowded and angled as a result of pressure, characteristically grow together. Dehiscence is by a definite lid. The wall is double. The outer layer is thick and granular without a bounding membrane on the exterior. In the upper portion it forms the lid; on the lower side, in connection with the substratum, it serves as the hypothallus. Closely connected with this outer wall, is a thin membranous layer, continuous around the entire spore mass. After the lid is lifted laterally, this membrane remains in place over the spores. The capillitium is a branching system of slightly irregular threads that approximates a net. Its attachments are mainly in the upper part of the sporangium.

Rostafinski has no illustrations of this; Massee has shown only habit and spores. A doubtful growth habit is all that Macbride contributes. Lister's habit and details, which are good in themselves, do not adequately illustrate structure, such as the nature of the lid and its relation to the rest of the sporangium.

Arcyria globosa Schw. Fig. 66.

Characteristic stipitate, globose sporangia grow usually on *Castanea* burs. Its single membranous, slightly rugose wall, evanescent above, persistent below, is confluent with the wall of the stalk. No internal membrane separates the sporangium proper from the stalk. The latter is filled with a dense mass of spore-like cells which merge into the spore content. Massee refers to these as "large, irregular, angled cells," but in the material studied they are similar to the spores themselves in shape, although much larger.

Short arms parallel to the sporangium wall may be the bases of the capillitial attachments, but as often the attachments are typical—i.e. at right angles to the wall. Attachments are mostly in the basal part of the sporangium.

Massee and Macbride place this species in the genus Lachnobolus chiefly on the basis of capillitial attachment by arms, but Lister and Baskerville (4) agree in retaining it among the Arcyrias. Certainly its internal characters, such as the presence of spore-like cells in the stalk and character of the wall, seem to ally it with the latter group.

Arcyria denudata (L.) Wettstein. Fig. 54.

Stipitate sporangia rise from a small hypothallus. The sporangia are sub-cylindrical, slightly ovate. Above the calyculus the wall is evanescent. The calyculus itself is smooth and continuous with the wall of the stalk. The stalk, three-eighths the entire height, is filled from the base to the sporangium proper with spore-like cells. These spore-like cells are larger than the true spores and contain an inconstant number of nuclei—from one to five. The capillitium, forming a spiral network, is attached to the calyculus and to the inside of the stalk. Horizontal capillitial strands occur well down in the stalk. In the stalk and near the calyculus, the capillitium is comparatively smooth. In the expanded portion of the sporangium it is marked with cogs, ridges, or spines.

The majority of drawings of this form consist of habit sketches and details of capillitium and spores. Lister's figure a, plate 174, is the nearest approach to a structural interpretation.

Arcyria cinerea (Bull.) Pers. Fig. 52.

The particular sporangia of this species which were studied were elongated and stipitate. A thin, rugulose calyculus is all that remains of the sporangium wall, which is early evanescent. Spore-like cells fill the cylindrical stalk from the base to the sporangium. The capillitium branches freely and is attached to the calyculus and the stalk. In these regions it is much smoother than in the sporangium; the peripheral threads are especially spinose.

These three species of Arcyria are deserving of illustration, for there are no figures in the literature adequately showing their structure. Rostafinski's diagram of *Arcyria cinerea* in median

section shows very well the location of the spore-like cells, spores and wall, but lacks the capillitial details.

Hemitrichia vesparium (Batsch) Macbride. Fig. 67.

This slime mold is fasiculate, several clavate sporangia growing on a common stalk. The outer wall, the broader of the two, widens apically into a sheath-like cap, often delicately membranous. The inner wall is a thin membrane enclosing the spores. The stipe, common to several sporangia, is loose and reticulate. In height it is a little more than that of the sporangium itself. Below, the stalk is continuous with the narrow, flattened hypothallus. Within the sporangium the capillitium is apparently free. It is twisted, spinulose, with acuminate free ends.

No illustrations depicting these characters in their relations to one another were found in reviewing the literature. The purpose of figure 67 is to show internal and external structures as they appear in a median longitudinal section.

Hemitrichia serpula (Scop.) Rost. Fig. 70.

This is one of the sessile plasmodiocarpous forms of Hemitrichia, with a well developed rough hypothallus. In section the sporangia range from terete to ellipsoidal. According to Macbride's observations the wall is single. Lister describes it as double, which assertion is confirmed by the slides made for this study. The outer layer is rough, granular, and the inner is membranous. They are distinct though very closely combined. The capillitium, which is made up of sparingly branched, twisting threads, is attached mainly in the basal part.

Massee has illustrated only spores and habit; Macbride has no illustrations; Lister has good sketches of habit and detailed characters.

Hemitrichia clavata (Pers.) Rost. Figs. 68a, 68b.

The sporangia of *H. clavata* range from nearly sessile, globose forms to others that are decidedly stipitate and turbinate. A single membranous wall, smooth on the exterior and papillose on the interior, is continuous with the stipe. In those forms which are well stalked the stalk may be one-third the total height and almost uniform in width from base to apex. It is filled from the base to the sporangium with spore-like cells. No internal membrane separates

the sporangial content from that of the stalk, so that their contents merge. The capillitium is a dense net with occasional free ends and many branches. In those forms with a short stipe the capillitium is attached at the base of the stalk; in those with well developed stipes it may reach the base or arise from points near the base.

This species is distinct from *H. stipitata,* which Lister includes in it. On the basis of Baskerville's descriptions, the two are clearly separate species. There is a good drawing of an expanded sporangium in Rostafinski's monograph, figure 207.

Trichia varia Pers. Fig. 71.

The short, stipitate or sessile, subglobose sporangia of this slime mold are characteristic of the genus. In the stipitate forms the stalk is approximately one-half the total height. Structurally, it is reticulate and of a heavy granular nature, and continuous with the spongy hypothallus which is common to several sporangia. The walls of the sporangia are single, membranous, and slightly thickened toward the base, and merge into the outer layer of the stipe. Within the sporangium there are many free short elaters with acute ends.

No illustrations of internal structure were found. Though very simple in its plan of construction, a diagram is included to show the exact arrangement of its parts.

Oligonema nitens (Libert) Rost. Fig. 65.

Structurally this is a simple form. Single thin membranes bound the sessile subglobose sporangia which rest directly on the substratum without a hypothallus. Internally, the sporangia are filled with spores and short elaters which are entirely free.

Numerous illustrations of habit, spores, and elaters are available, but none representing the complete internal appearance has been found.

LITERATURE CITED

1. Bary, A. de, Die Mycetozoen. Zeitschr. Wiss. Zool. 10:88-175. 1859.
2. Bary, A. de, Die Mycetozoen. 1864.
3. Bary, A. de, Comparative Morphology and Biology of the Fungi, Mycetozoa, and Bacteria. Eng. ed. 1887.
4. Baskerville, E. L., Some misunderstood species of slime molds. In press.
5. Howard, F. L., The life history of *Physarum polycephalum*. Am. Jour. Bot. 18:116-133. 1931.
6. Lister, A., and G. Lister, Notes on Mycetozoa. Jour. of Bot. 42:129-140. 1904.
7. Lister, A., and G. Lister, A Monograph of the Mycetozoa, ed. 3. 1925.
8. Macbride, T. H., North American Slime-Moulds, ed. 2. 1922.
9. Massee, George, A Monograph of the Myxogastres. 1892.
10. Rostafinski, J., Sluzowce. 1875.
11. Wilson, M., and Elsie J. Cadman, Life history and cytology of *Reticularia lycoperdon* Bull. Trans. R. Soc. Edinb. 60:55-603. 1928.
12. Zirkle, C., The use of N-butyl alcohol in dehydrating tissue for paraffin embedding. Science 71:103-104. 1930.

PLATE I

Fig. 1. *Fuligo muscorum* Alb. and Schw. Section of an aethalium. x 7.

Fig. 2. *Badhamia macrocarpa* (Ces.) Rost. Section of a sporangium. x 48.

Fig. 3. *Physarum lateritium* (Berk. and Rav.) Morgan. Section of a sporangium. x 48.

Fig. 4. *Fuligo septica* (L.) Gmelin. a. Section of an aethalium. x 7. b. Detail of lateral wall at the base, showing the heavy calcareous deposits. x 68.

Fig. 5. *Badhamia utricularis* (Bull.) Berk. Section of a sporangium. x 60.

Fig. 6. *Badhamia rubiginosa* (Chev.) Rost. Section of a sporangium. x 60.

Fig. 7. *Physarum nucleatum* Rex. Section of a sporangium. x 48.

Fig. 8. *Physarum serpula* Morgan. a. Section of a plasmodiocarp. x 68 b. Detail of wall and capillitium. x 512.

PLATE I

PLATE II

Fig. 9. *Physarum melleum* (Berk. and Br.) Massee. Section of a sporangium. x 48.

Fig. 10. *Physarum citrinum* Schum. Section of a sporangium. x 48.

Fig. 11. *Physarum flavicomum* Berk. a. Section of a sporangium. x 48. b. Granules from the wall. x 1170.

Fig. 12. *Physarum globuliferum* (Bull.) Pers. Section of a sporangium. x 48.

Fig. 13. *Physarum compressum* Alb. and Schw. Section of a sporangium parallel with the flat surface. x 30.

Fig. 14. *Physarum didermoides* (Ach.) Rost. Section of a sporangium. x 48.

Fig. 15. *Physarum sinuosum* (Bull.) Weinm. ex Fr. Section of a sporangium. x 30.

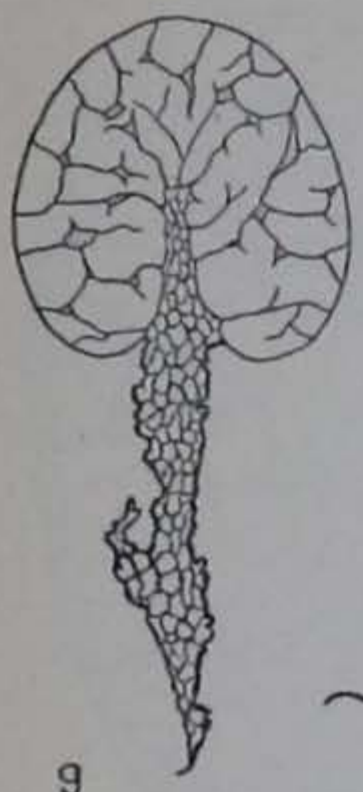
Fig. 16. *Physarum polycephalum* Schw. Section of a sporangium. x 30.

Fig. 17. *Physarum cinereum* (Batsch) Pers. Section of a sporangium. x 48.

Fig. 18. *Physarum gyrosum* (Rost.) Jahn. Section of a sporangium. x 30.

Fig. 19. *Physarum penetrale* Rex. Section of a sporangium. x 48.

PLATE II



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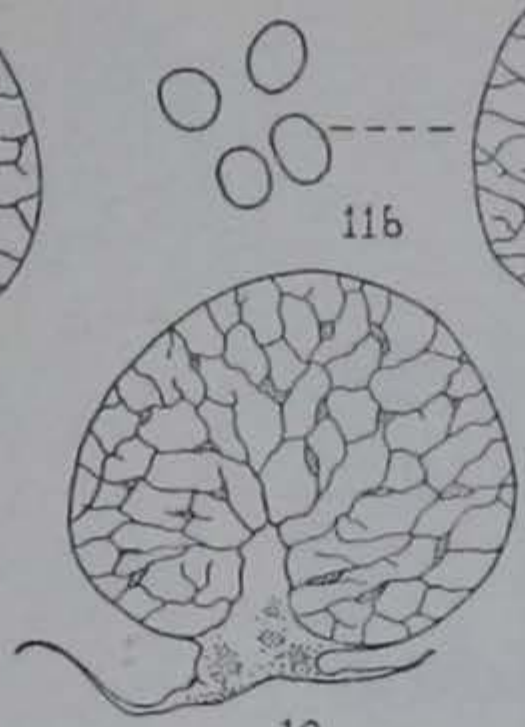

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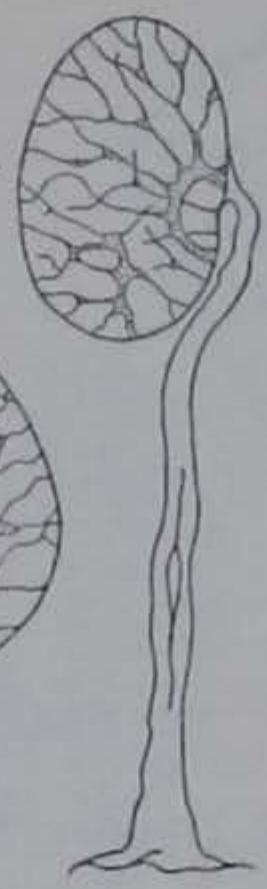

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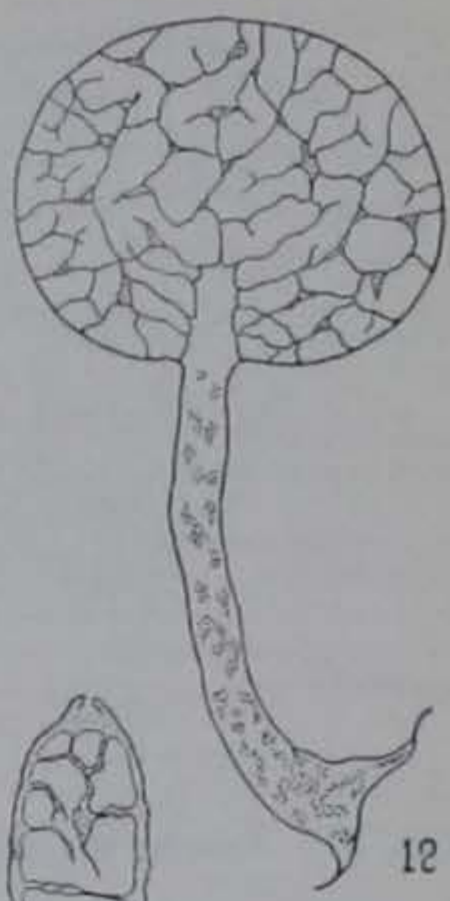

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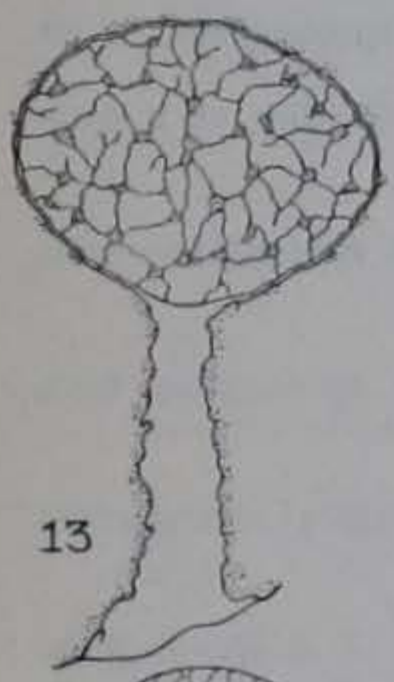

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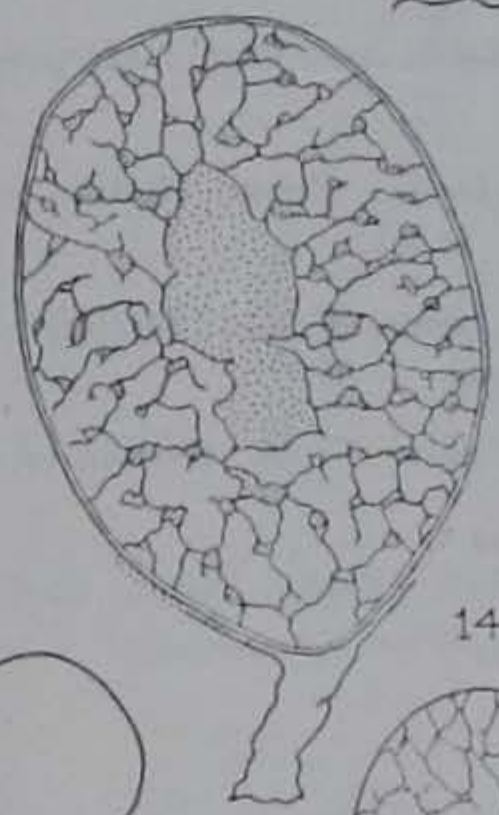

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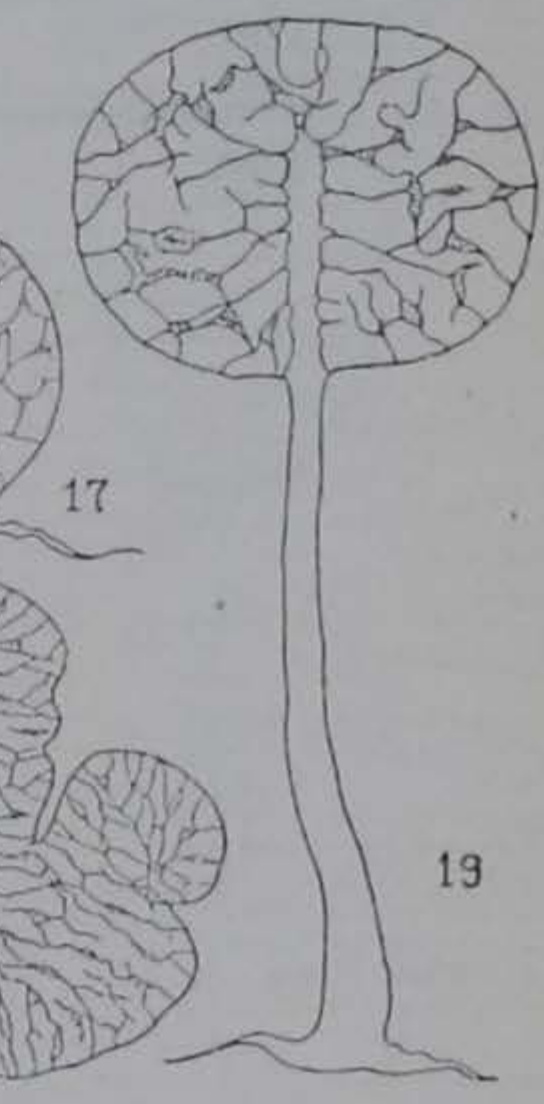

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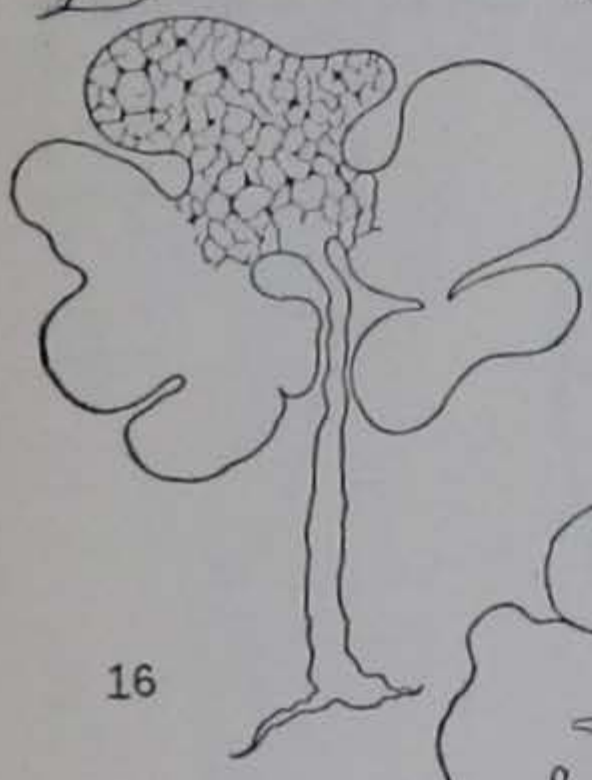

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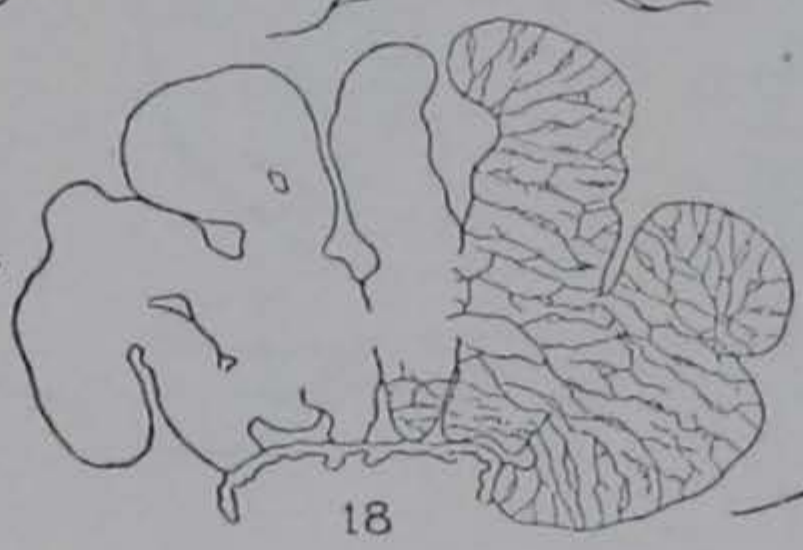

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PLATE III

Fig. 20. *Leocarpus fragilis* (Dickson) Rost. Section of a sporangium. x 30.

Fig. 21. *Physarella oblonga* (Berk. and Curt.) Morgan. Section of a sporangium. x 48.

Fig. 22. *Craterium minutum* (Leers) Fries. Section of a sporangium from a Peck collection. x 60.

Fig. 23. *Craterium minutum* (Leers) Fries. Section of a sporangium from a Brandza collection. x 60.

Fig. 24. *Craterium minutum* (Leers) Fries. Section of a typical sporangium. x 60.

Fig. 25. *Craterium leucocephalum* (Pers.) Ditm. Section of a sporangium. x 60.

PLATE III

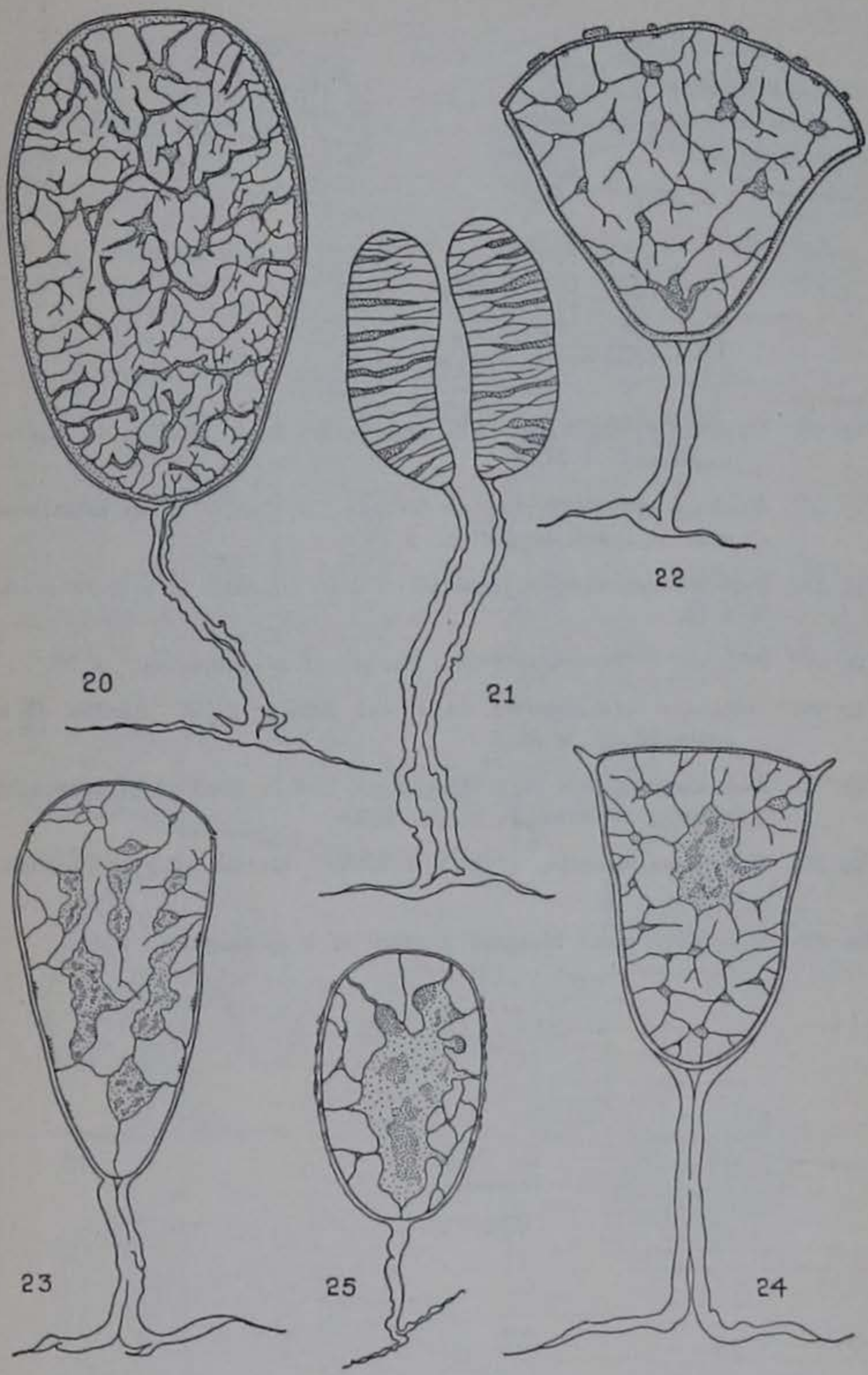


PLATE IV

Fig. 26. *Cienkowskia reticulata* (Alb. and Schw.) Rost. Section of a plasmodiocarp. x 48.

Fig. 27. *Mucilago spongiosa* (Leyss.) Morgan. a. Section of an aethalium. x 2. b. Detail of section. x 15.

Fig. 28. *Lepidoderma tigrinum* (Schrad.) Rost. Section of a sporangium. x 30.

Fig. 29. *Diderma spumarioides* Fries. Section of a sporangium. x 30.

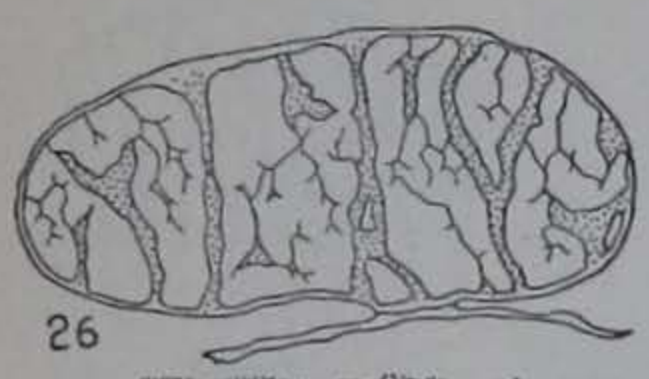
Fig. 30. *Didymium squamulosum* (Alb. and Schw.) Fries. Section of a sporangium. x 30.

Fig. 31. *Diderma radiatum* (L.) Morgan. a and b. Sections of sporangia showing variation in form. x 30.

Fig. 32. *Colloderma oculatum* (Lipp.) G Lister. Section of a sporangium. x 48.

Fig. 33. *Didymium minus* Morgan. Section of a sporangium. x 48.

PLATE IV



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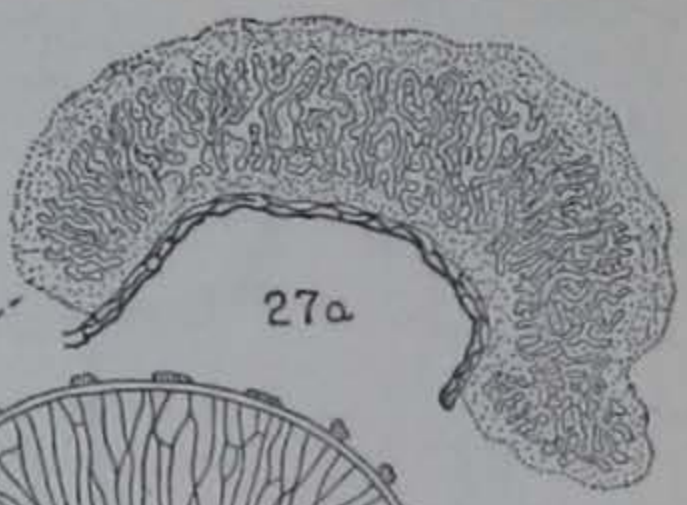

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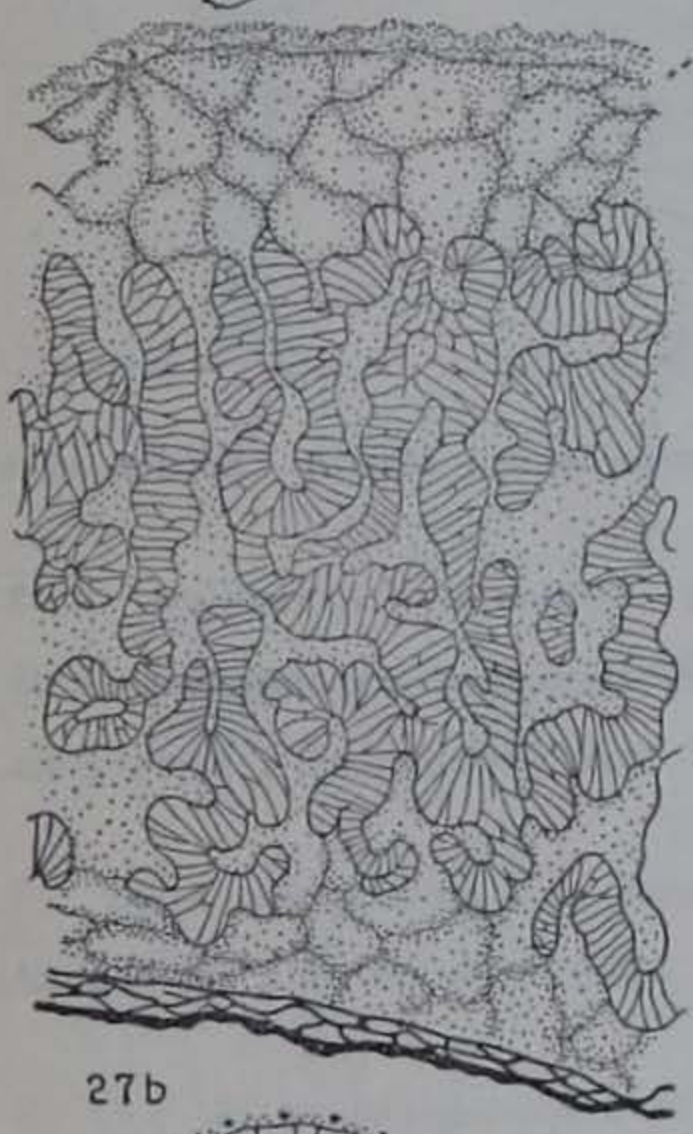

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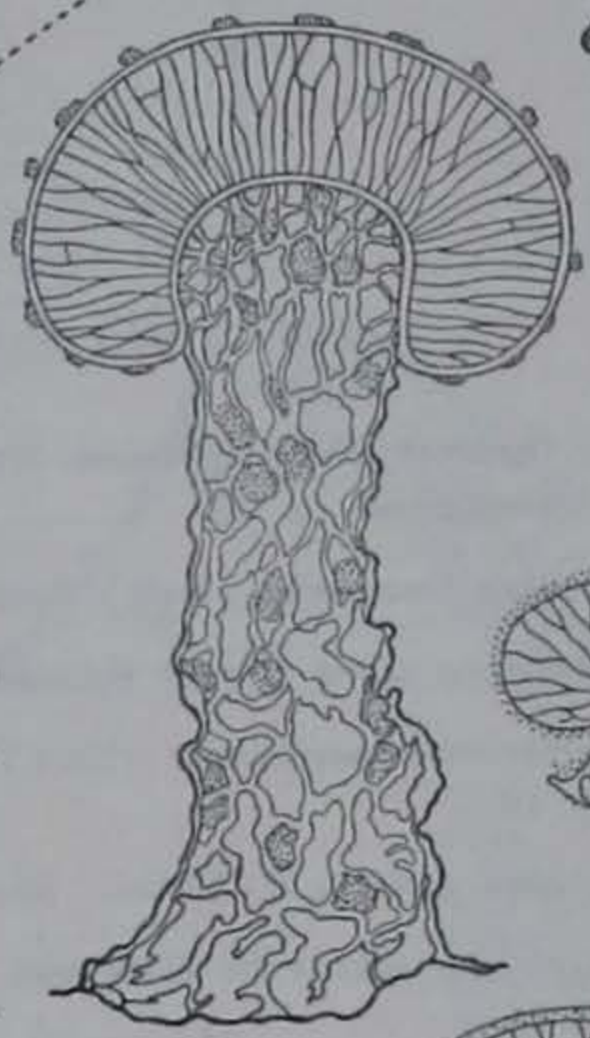

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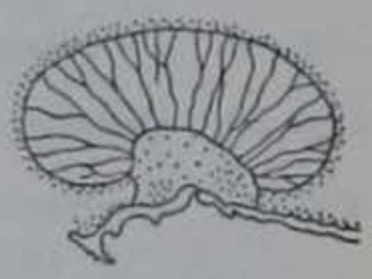

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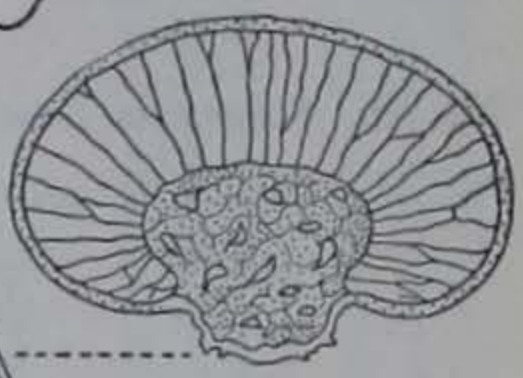

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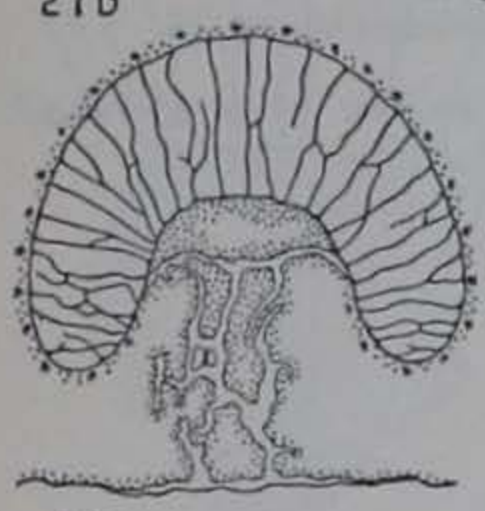

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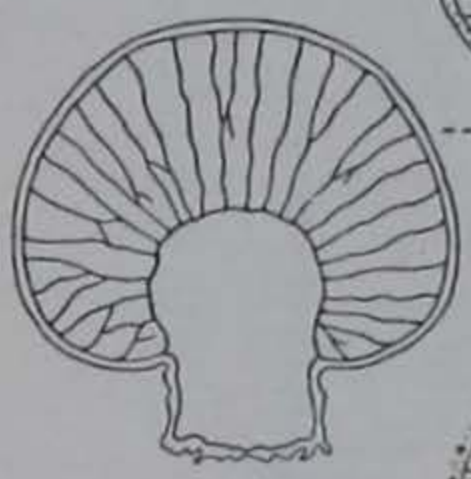

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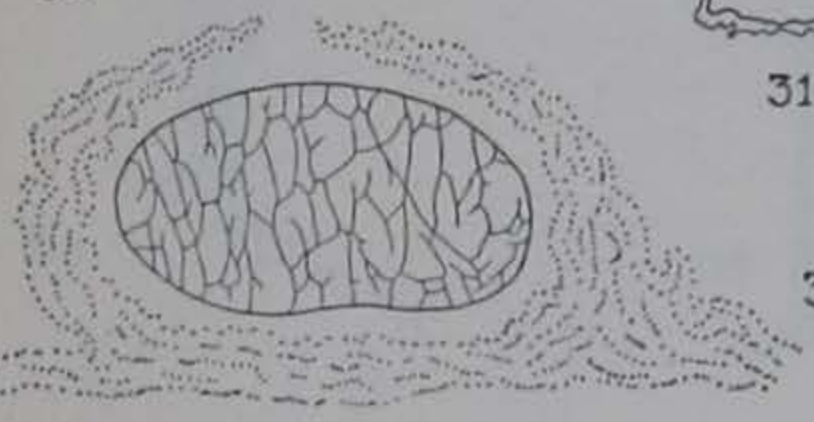

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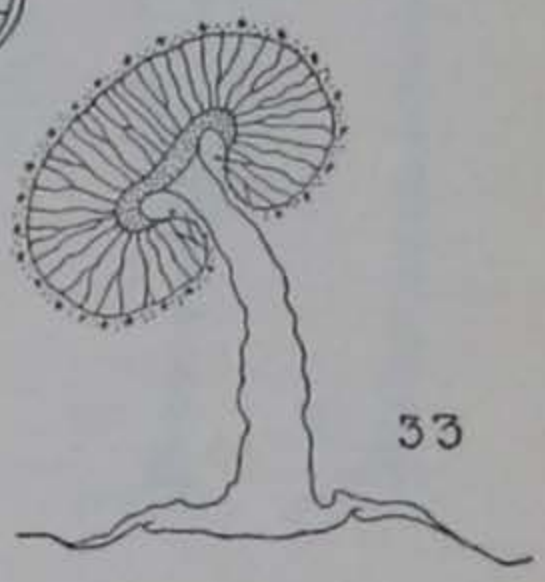

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PLATE V

Fig. 34. *Enerthenema melanospermum* Macbride and Martin. Section of a sporangium. x 30.

Fig. 35. *Diachaea leucopodia* (Bull.) Rost. Section of a sporangium. x 48.

Fig. 36. *Comatricha nigra* (Pers.) Schroet. Section of a sporangium. x 68.

Fig. 37. *Enerthenema papillatum* (Pers.) Rost. Section of a sporangium. x 48.

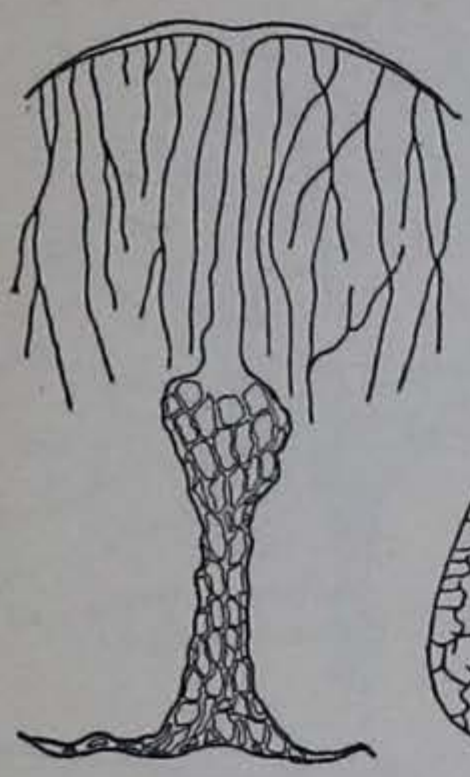
Fig. 38. *Diachaea cerifera* G. Lister. Section of a sporangium. x 48.

Fig. 39. *Comatricha suksdorfii* Ellis and Everh. Section of a sporangium. x 25.

Fig. 40. *Stemonitis fusca* Roth. Section of a sporangium. x 18.

Fig. 41. *Stemonitis axifera* (Bull.) Macbride. Section of a sporangium. x 15.

PLATE V



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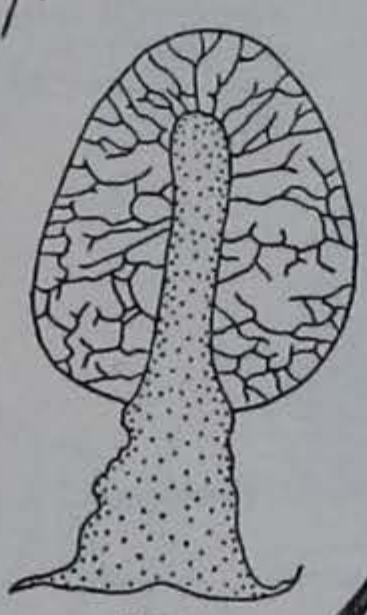

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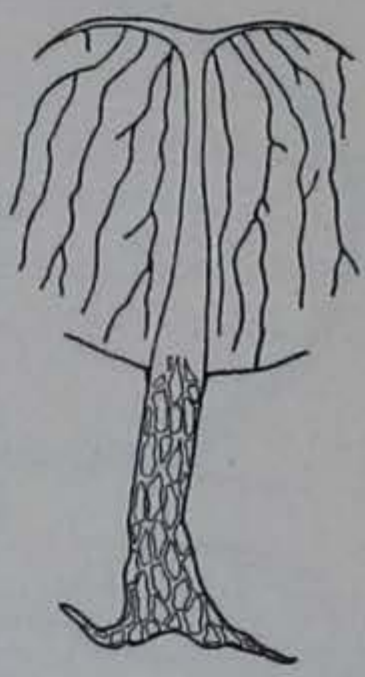

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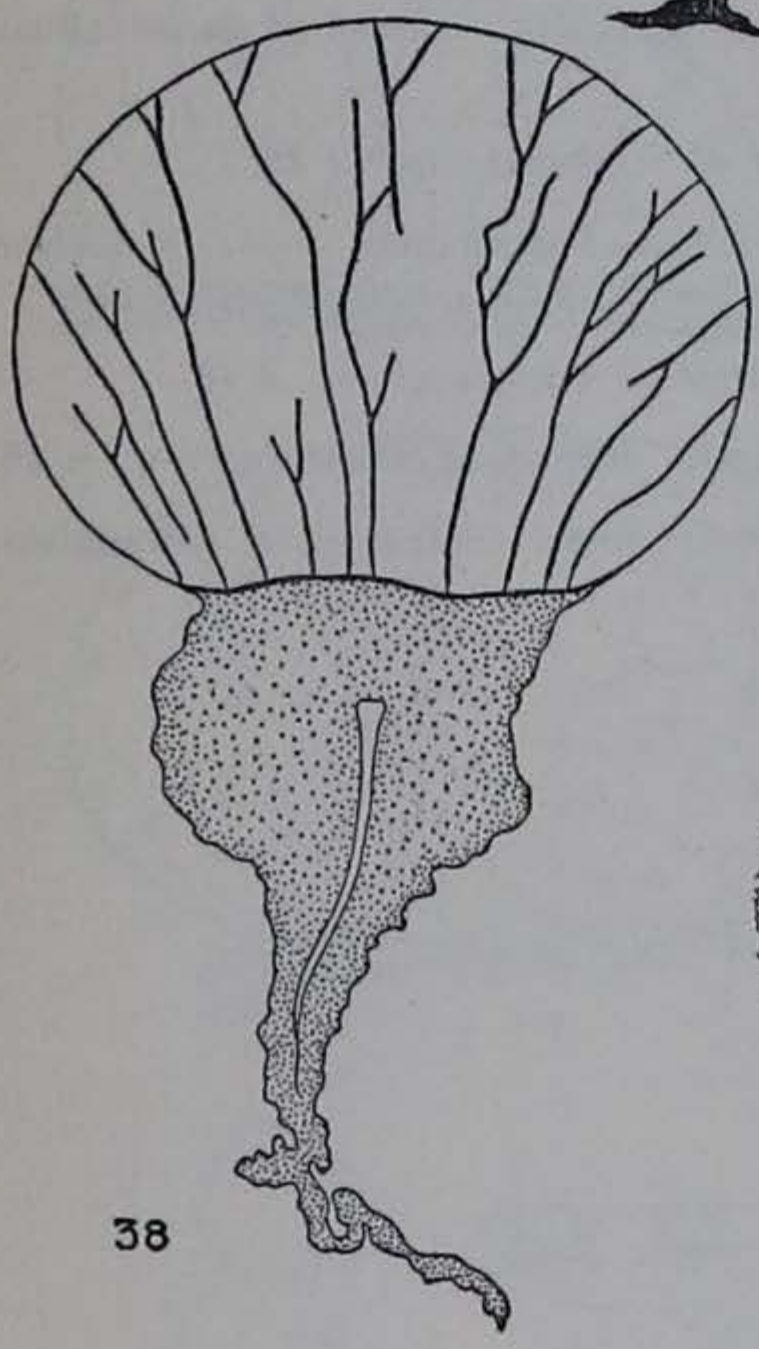

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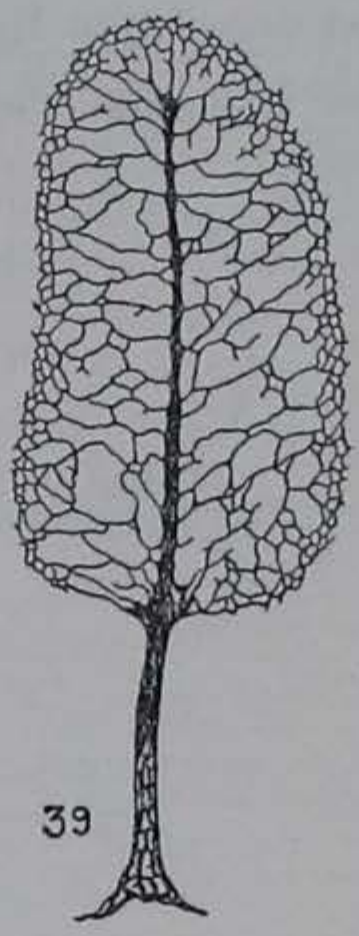

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PLATE VI

Fig. 42. *Lindbladia effusa* (Ehr.) Rost. Section of a pseudoaethalium. x 15.

Fig. 43. *Tubifera ferruginosa* (Batsch) Gmelin. Section of a pseudoaethalium. x 7.

Fig. 44. *Enteridium splendens* (Morgan) Macbride. Section of an aethalium. x 7.

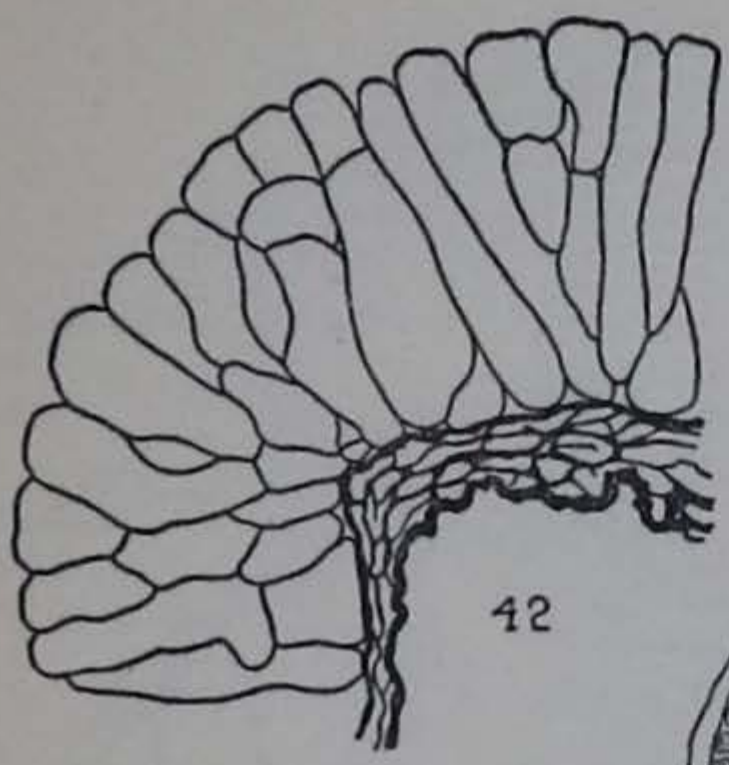
Fig. 45. *Licea minima* Fries. Section of a sporangium. x 48.

Fig. 46. *Licea biforis* Morgan. a. Sections of sporangia. x 48. b. Section of sporangium, with diagram of spore arrangement. x 235.

Fig. 47. *Licea variabilis* Schrad. Section of a sporangium. x 48.

Fig. 48. *Lamproderma arcyrionema* Rost. Section of a sporangium. x 48.

Fig. 49. *Lamproderma violaceum* (Fries) Rost. Section of a sporangium. x 48.



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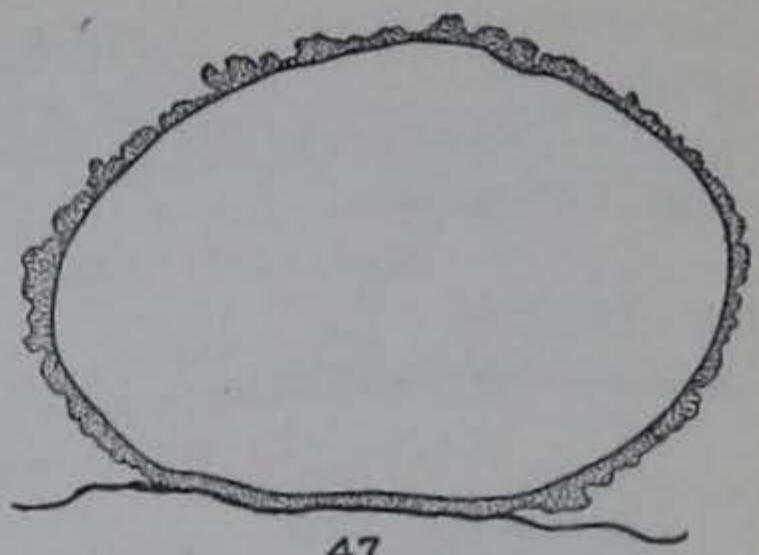

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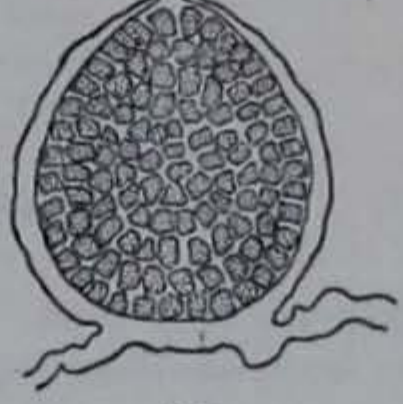

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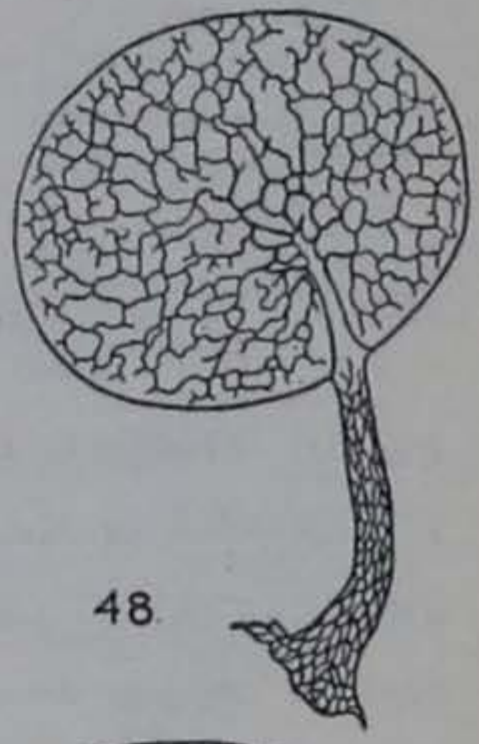

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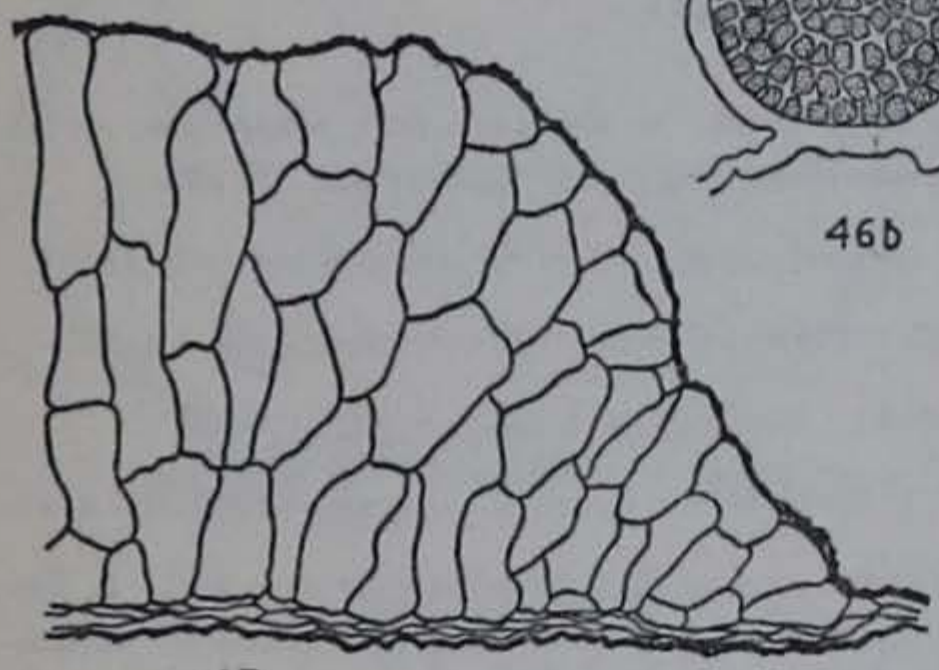

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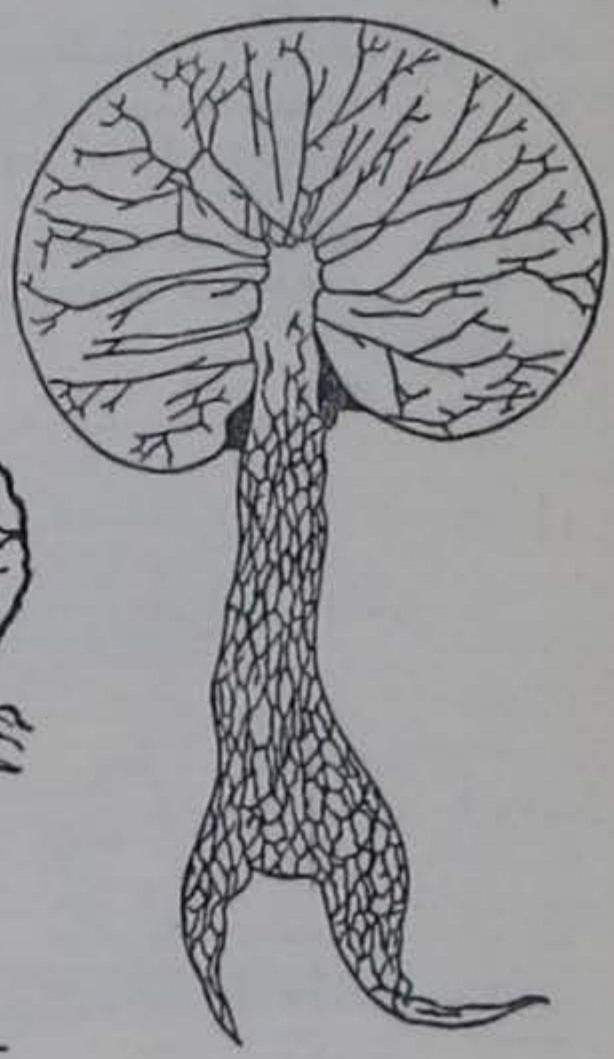

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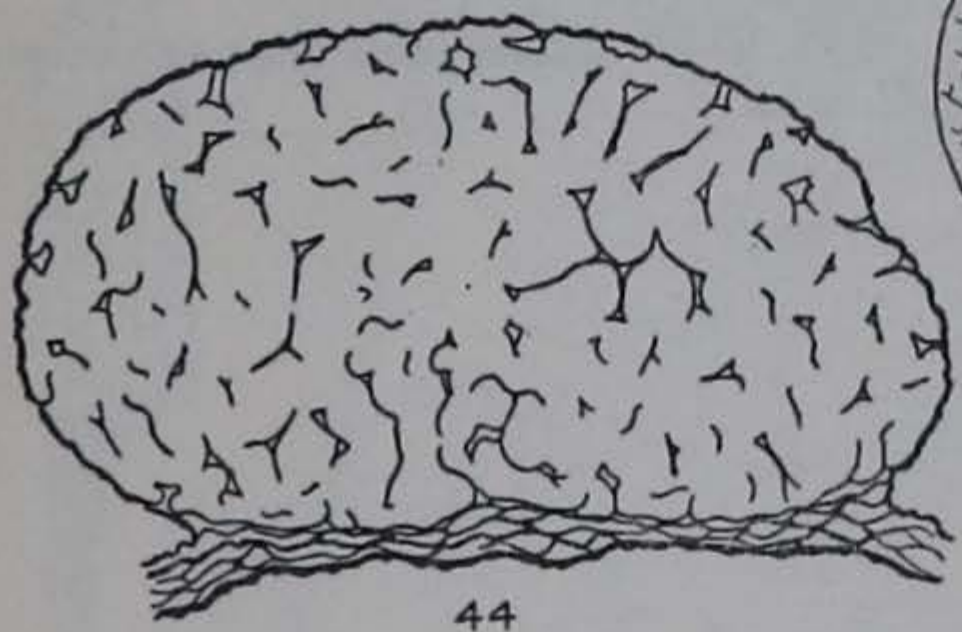

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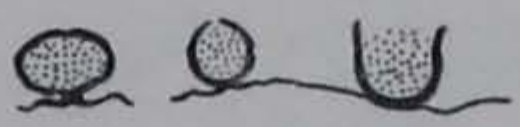

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PLATE VII

Fig. 50. *Lycogala epidendrum* (L.) Fries. a. Section of an aethalium. x 25. b. Detail of walls showing origin of capillitium. x 235.

Fig. 51. *Perichaena depressa* Libert. Section of a sporangium. x 48.

Fig. 52. *Arcyria cinerea* (Bull.) Pers. Section of a sporangium. x 18.

Fig. 53. *Cribraria argillacea* Pers. Section of a sporangium. x 48.

Fig. 54. *Arcyria denudata* (L.) Wettstein. Section of a sporangium. x 48.

Fig. 55. *Listerella paradoxa* Jahn. a. Section of sporangium. x 102. b. Detail of wall showing the margin of a lobe and point of attachment of two capillitial threads. x 525.

Fig. 56. *Lindbladia effusa* (Ehr.) Rost. Section of a fructification with distinct sporangia. x 15.

PLATE VII

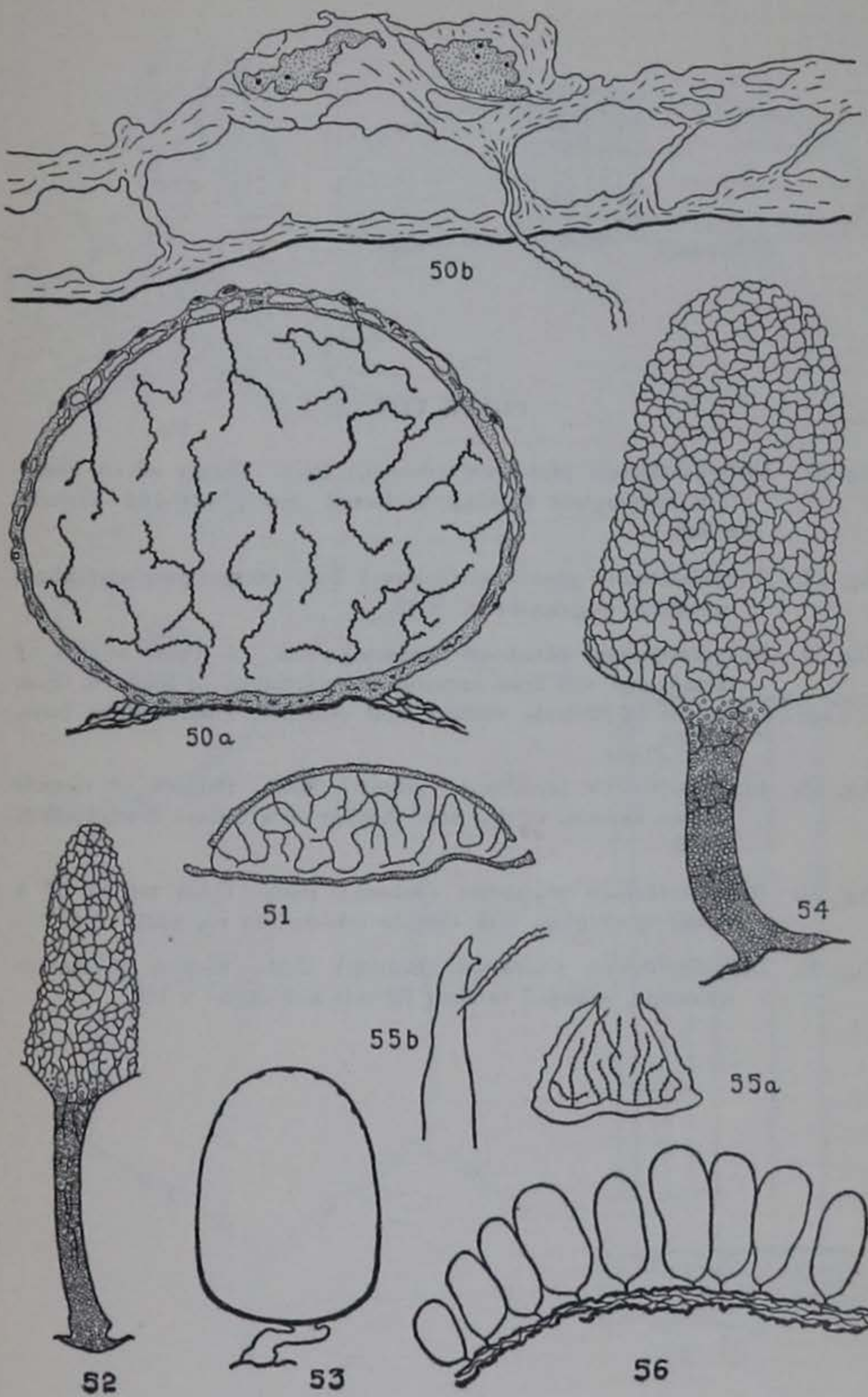


PLATE VIII

Fig. 57. *Dictydiaethalium plumbeum* (Schum.) Rost. Corner of an immature sporangium showing uncleaved protoplasm and threads. x 885.

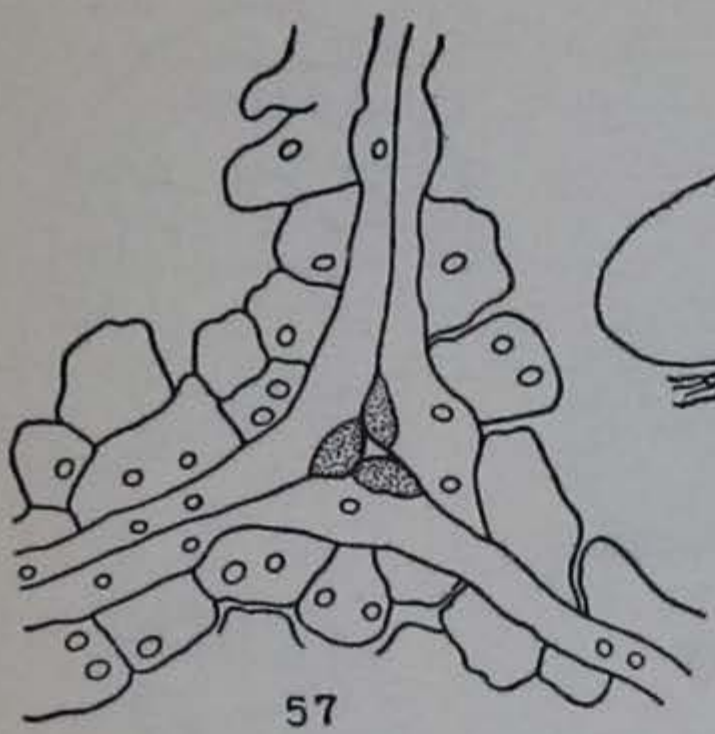
Fig. 58. *Dictydiaethalium plumbeum* (Schum.) Rost. Mature pseudoaethalium in section, diagrammatic. x 15.

Fig. 59. *Dictydiaethalium plumbeum* (Schum.) Rost. a. Cross section of threads and wall from immature fructification. x 1550. b. Cross section of threads without wall attached, from mature form. x 1550.

Fig. 60. *Dictydiaethalium plumbeum* (Schum.) Rost. Pattern of threads as seen in cross section near the top of a mature fructification. x 135.

Fig. 61. *Dictydiaethalium plumbeum* (Schum.) Rost. Cross section of a young sporangium with threads attached to the wall. x 525.

Fig. 62. *Dictydiaethalium plumbeum* (Schum.) Rost. Section of mature sporangia, enlarged to show threads and caps. x 102.



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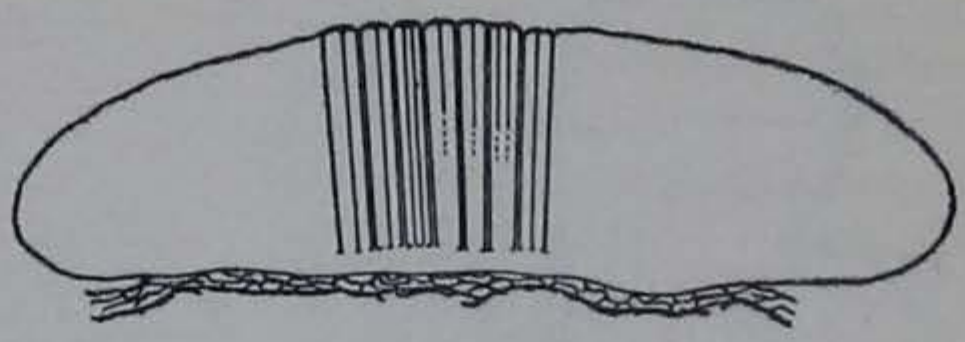

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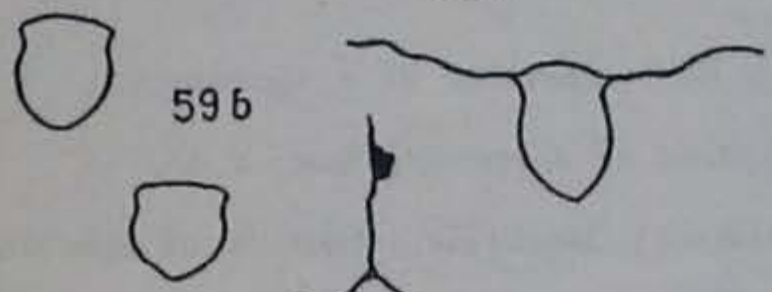

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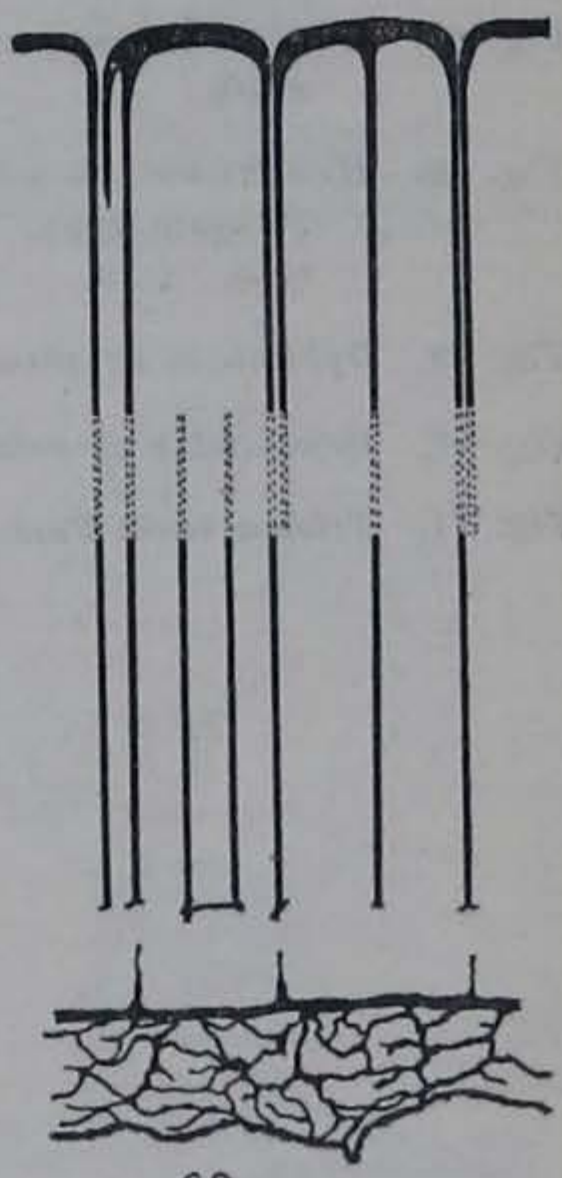

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PLATE IX

Fig. 63. *Margarita metallica* (Berk. and Br.) Lister. Section of a sporangium. x 48.

Fig. 64. *Ophiotheca vermicularis* (Schw.) Massee. Section of a sporangium. x 48.

Fig. 65. *Oligonema nitens* (Libert) Rost. Section of a sporangium. x 48.

Fig. 66. *Arcyria globosa* Schw. Section of a sporangium. x 48.

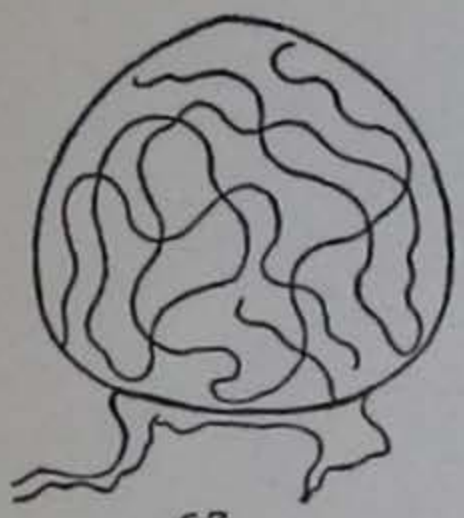
Fig. 67. *Hemitrichia vesparium* (Batsch) Macbride. Section of sporangia. x 30.

Fig. 68. *Hemitrichia clavata* (Pers.) Rost. a. Section of a sporangium, elongate type. x 30. b. Section of a sporangium, subglobose type. x 15.

Fig. 69. *Ophiotheca wrightii* Berk and Curt. Section of a sporangium. x 48.

Fig. 70. *Hemitrichia serpula* (Scop.) Rost. Section of a sporangium. x 48.

Fig. 71. *Trichia varia* Pers. Section of a sporangium. x 48.



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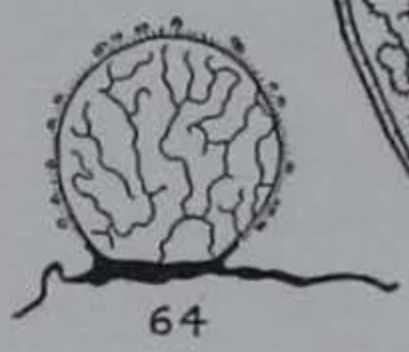

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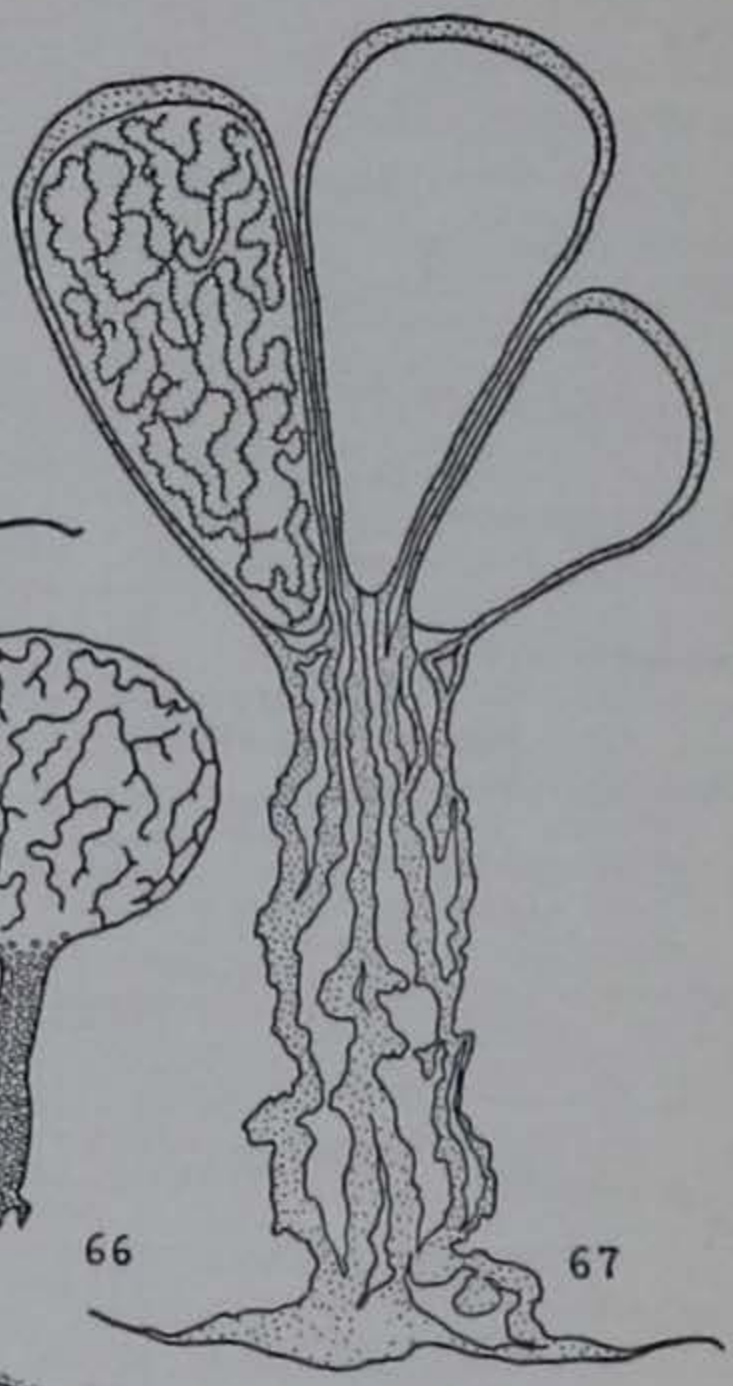

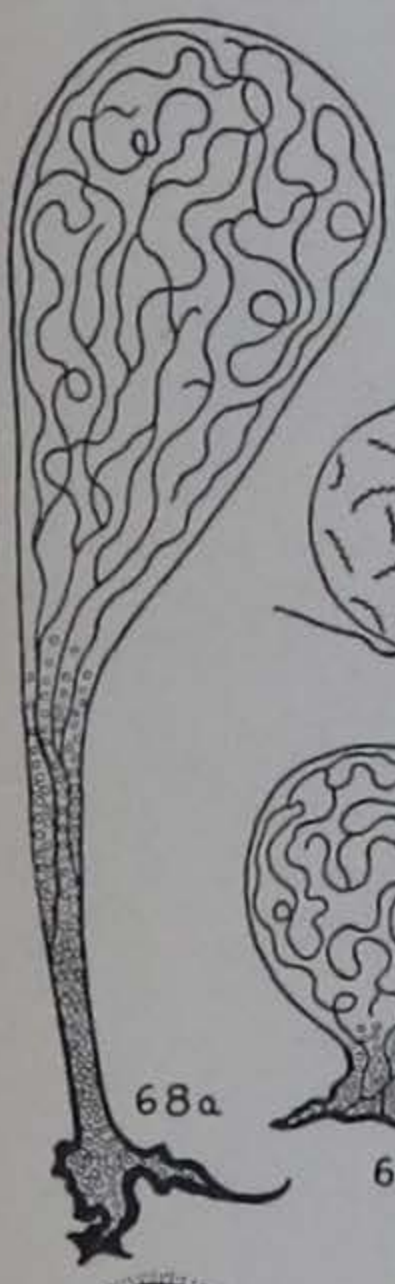

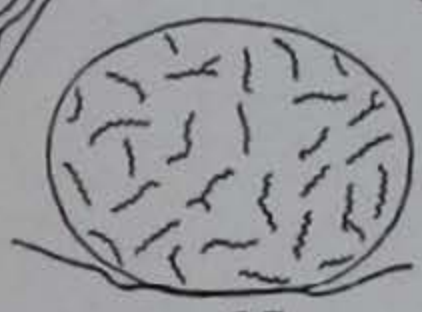

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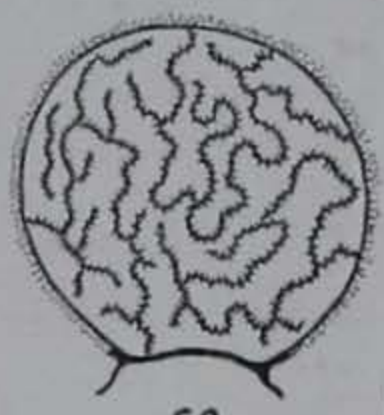

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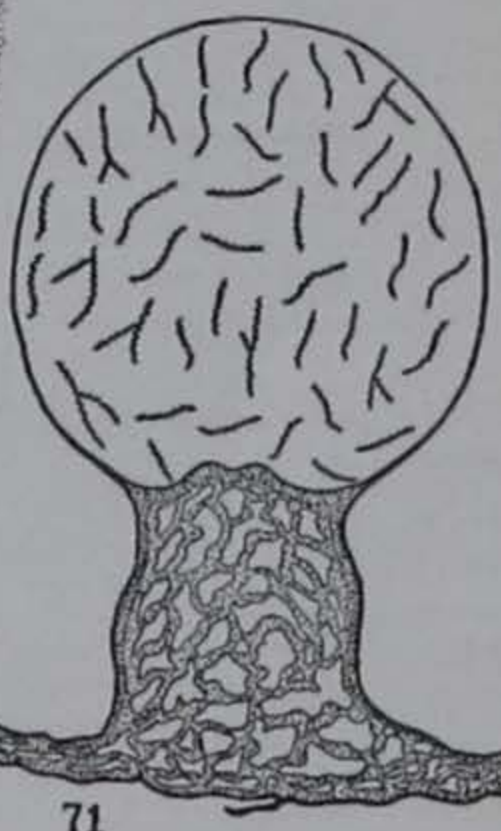

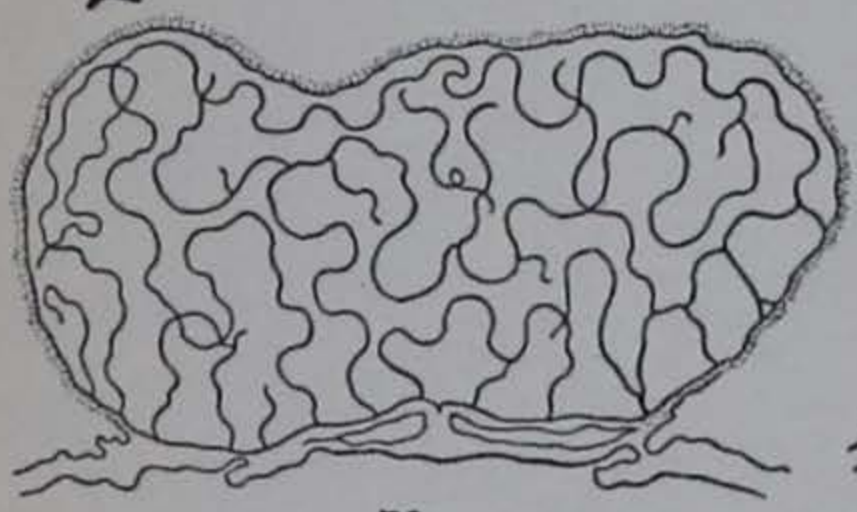

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