

AQUATIC FUNGI OF ICELAND:
BIFLAGELLATE SPECIES

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Aquatic fungi of Iceland: Biflagellate species

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Abstract. Fifty six species of biflagellate (zoösporic) fungi are recorded from Iceland. These represent 16 genera in 9 families of 5 orders. Structural features and variational patterns of several taxa (and species complexes) are reported. A number of representatives have not been named, or are only provisionally identified, but they are usually accorded formal descriptions and their taxonomy is discussed fully. Experimental work with isolates of *Achlya* and *Aphanomyces* resulted in culturally-induced structural modifications in certain groups of taxa. Save in a few cases where new information has been brought to light, species previously reported from Iceland are noted merely by citations to the literature. No new taxa are proposed.

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INTRODUCTION

The first report of biflagellate aquatic (zoösporic) fungi in Iceland was that by Larsen in 1932. *Saprolegnia ferax* (Gruth.) Thuret was reported from Möðruvellir where it had been collected on a butterfly larva, and in a garden at Reykjavík, *Phytophthora infestans* (Mont.) deBary was detected on potato leaves. The second account appeared in 1960, this being a brief record by Höhnk of species collected near Geysir and in the vicinity of Hveragerdi. He collected ten species (seven in the genus *Pythium*) of which only seven were given binomials. None of the fungi in either Larsen's or Höhnk's papers was described or illustrated.

In 1964 I began to survey the aquatic fungi in Iceland in an attempt to determine something more comprehensive about the aquatic mycoflora than had been previously recorded. An initial report of 17 species was issued in 1968. This was followed by papers dealing in part with biflagellate species (Howard, 1968; Johnson and Howard, 1968; Howard and Johnson, 1969), and with particular taxonomic groups among the biflagellate fungi: Johnson (1971, 1972), Howard, *et al.* (1970), and Johnson, *et al.* (1973). In these papers some species were given descriptive treatment and were illustrated. Some additional accounts have been prepared; these are referred to in the appropriate group in the systematic treatment to follow.

In a companion paper (Johnson, 1973a), I gave information on the occurrence of aquatic fungi in Iceland and of methods for collection, isolation, and preservation of specimens. These matters are not repeated here. Techniques that deviate from those given earlier, or methods specifically used for experimental work with these biflagellate fungi, are

accorded full treatment with the species to which they are applicable.

In conformity with the account of the uniflagellate taxa, I am emphasizing species variations noted among the biflagellate fungi. If there is a unique aspect to the aquatic mycoflora in Iceland it is that it contains a surprisingly large number of morphological variants of common species. So striking have some of these variations been that extreme caution in the systematics of the species has been practiced. No new taxa are described, and a number go unnamed because sufficient evidence is not at hand to allow proper placement and confident identification. To better convey concepts, illustrations are purposely abundant (although not all taxa are illustrated).

For the most part, the fungi treated in this account are represented by preserved specimens (on slides or in vials) in the collections of the Museum of Natural History in Reykjavík. Preserved specimens from gross cultures are on occasion supplemented in the collections by plants from pure or experimental cultures (often unifungal). Detailed collection data accompany these specimens, and are not repeated here save in abbreviated form where necessary.

Unless stated to the contrary, the characterizations of fungi were derived from gross, unifungal, or pure cultures grown on the appropriate substrates in 40 ml of sterile tap water incubated at 23–25° C. In all formal descriptions, the numbers in parentheses represent the 70% median of 200 measurements or counts (derived from five preparations). No median figures are given in instances where sparse growth would not permit this number of determinations. In these cases, only the ranges are given. Wherever practicable, qualitative information is supplemented by

quantitative data. Such data are also of the 70% median of 200 observations or counts unless otherwise noted. Before being measured, actively swimming spores were killed by exposure to fumes of osmic acid for one minute. Encysted or quiescent spores were measured as living cells.

SYSTEMATIC ACCOUNT

The biflagellate aquatic fungi known to occur in Iceland are distributed in five orders: Plasmodiophorales, Saprolegniales, Leptomitales, Lagenidiales, and Peronosporales. The sequence of treatment in the following account generally follows that used by Sparrow (1960).

PLASMODIOPHORALES

Plasmodiophoraceae

OCTOMYXA

Octomyxa sp. (Figs. 1–4)

Two species have been described in this genus, one in *Achlya glomerata* Coker (Couch, et al., 1939) and a second in *Brevilegnia* sp. and (by artificial inoculation) *Geolegnia inflata* Coker and Harvey (Pendergrass, 1948). The *Octomyxa* from Iceland is the first member of the genus known to invade a species of *Aphanomyces*. A description follows.

Plasmodium occurring in obovate to cylindrical swellings at the ends of the host hyphae; segmenting to form sporangia or resting spores. Sporangium globose, subglobose, or ovate; thin-walled; provided with a single narrowly or broadly papillate exit tube opening by a broad, somewhat irregular apical pore; 8–14 μ in diameter. Planonts endogenously formed; provided with 2 laterally(?) inserted, heterokont flagella; 6–7 μ long by 2–3 μ in diameter. Resting spores spherical, smooth-walled; occurring in clusters of 8 (rarely less); 6–7 μ in diameter; germination not observed.

This fungus was collected twice (Herb. No. 1541, 1542) in *Aphanomyces* (?) *laevis* on snakeskin bait in gross cultures 10 weeks old. The *Octomyxa* was induced to discharge planonts when the bait was flooded with fresh, sterile tap water containing 0.01% potassium tellurite, but I could not isolate the host and transfer it with its parasite to fresh bits of pretreated bait (for method, see Johnson, 1973a). In view of these old — and correspondingly sparse — specimens that could not be separated out from gross culture, I choose not to name the *Octomyxa* at this time.

SOROSPHAERA

Sorosphaera sp. (Figs. 5–7)

Howard (1968) collected the first specimens of this fungus in thalli of *Hyphochytrium catenoides* Karling from a soil sample taken near Thingvellir. He experienced difficulty in identifying the fungus, but because its resting spores aggregated into a sphere assigned it to *Sorosphaera*. Since the fungus commonly produced 12 resting spores in each cluster, Howard regarded it as an undescribed species. The name he applied is a *nomen nudum*.

This peculiar fungus again appeared in one collection of *Hyphochytrium catenoides* on cellophane bait in a soil sample from the base of an escarpment at Thingvellir. Howard's specimens (Herb. No. 446) were scanty; the same may be said for my material. The following combined description of the plants in the two collections is therefore necessarily incomplete.

Sporangia small, spherical or subspherical, thin-walled; occurring in sporangium-like swellings of the host or in somewhat distorted, fusiform, intercalary swellings (sori); 2–several in a sorus; usually walled-off from a portion of the infected host plant; opening by deliquescence (or fragmentation) of the wall; 6–9 μ in diameter. Planonts not observed. Cystosori 8.1–10.2 μ in diameter; yellowish brown; borne in small, intercalary, irregularly fusiform swellings; usually consisting of 12 pyramidal resting spores (rarely 9 per cyst-

osorus), 2.8–3.7 μ in diameter, arranged in a hollow or solid sphere or in an irregular cluster; each resting spore surmounted by a small, hyaline, inconspicuous collar; enveloping membrane not observed; germination not observed.

The cystosori, made up of small, pyramidally-compressed resting spores (Fig. 7) are distinctive. I found these cells to occur very sparsely (2–4) only in small, intercalary swellings of the host thalli. In H o w a r d's specimens the cystosori were very numerous, on the contrary, and developed in large swellings of the *Hyphochytrium*.

The apical collar of the resting spore conceivably relates this fungus to *Sorosphaera veronicae* Schroeter, but his species may not always possess such a structure. The known taxa in *Sorosphaera* evidently do not have cystosori consisting so regularly of 12 resting spores.

The characteristics of resting spore shape, their aggregation pattern, and the apical collars support an assignment in *Sorosphaera*. If the Iceland fungus is properly placed (provisional at the moment) it is the first member known to occur in another aquatic fungus. Other species are parasites of vascular plants.

SAPROLEGNIALES

Members of two families are treated: Saprolegniaceae and Thraustochytriaceae. Earlier (J o h n s o n, 1968) two species of a third family, Ectrogellaceae, were reported. *Ectrogella perforans* Petersen was found in one collection of a species of *Striatella*. Specimens in a sample of *Pinnularia* sp. were infected by *Aphanomyopsis bacillariacearum* Scherffel. Neither of these fungi has again been recovered. D i c k (1971) assigns *Aphanomyopsis* to a new family, Leptolegniellaceae.

Saprolegniaceae

H o w a r d, *et al.* (1970) published an illustrated treatment of 35 species (8 genera) of this family, and proposed some taxonomic

changes. Subsequently, representatives of *Brevilegnia* (a genus not included in the 1970 account) were reported (J o h n s o n, *et al.*, 1973; J o h n s o n, 1974). S e y m o u r and J o h n s o n (1973a) collected an unusual oömycete in rotifer eggs. The fungus (described but not named) produced sporangia and eccentric oöspores by segmentation of a non-myceloid thallus. The plants had saprolegniaceous affinities but were not assigned formally to this family. *Leptolegniella keratinophilum* Huneycutt, collected on snakeskin bait (H o w a r d, *et al.*, 1970), has been removed from the Saprolegniaceae by D i c k (1971) and placed in the Leptolegniellaceae.

ACHLYA

Morphological variations in 12 species of *Achlya* from Iceland have already been described (H o w a r d, *et al.*, 1970). A quantitative and qualitative analysis of the *Achlya spiraculis* Johnson-*A. papillosa* Humphrey complex (J o h n s o n and S e y m o u r, 1974b) resulted in reduction of the former to synonymy. An unusual form of *A. racemosa* Hildebrand (with secondary or "satellite" oögonia) has been recovered in Iceland soils (J o h n s o n, 1973b).

The collections of water molds from Iceland contained a sizeable assortment of unidentified Achlyas, or ones assigned provisionally to "intermediate" status between known species. The unnamed specimens either failed to produce the sexual apparatus, or could not be isolated into pure culture. These fungi are excluded from consideration.

Achlya americana Humphrey (Figs. 108–110)

Known from an earlier account by H o w a r d, *et al.* (1970) this species and some closely related forms were analyzed quantitatively and qualitatively by J o h n s o n and S e y m o u r (1974a). Twenty-one isolates (joined by three prominent features that identify *Achlya americana*) were characterized. Two additional Achlyas from soil have yielded to

isolation techniques; these nearly identical plants (Figs. 108–110) are believed to be further variants of Humphrey's species.

On hempseed (pure cultures, 40 ml of tap water, 23–25° C), the fungi produced spherical to pyriform oögonia on short, lateral stalks (Fig. 108). Each oögonium contained 10–14 (median 70%) small, eccentric oöspores that did (Fig. 109) or did not (Fig. 110) fill the oögonial cavity. The oögonial wall was pitted (Fig. 110) or irregular, or both (Fig. 109), but pits were sometimes limited only to those points where the antheridial cells were attached. Among the 14 colonies examined, 83–91% of the antheridial branches were monoclinal (and of near origin as in *Achlya americana*); the remainder were declinal. The antheridial filaments were usually conspicuously branched (Fig. 108) and the often very prominent antheridial cells were attached by projections to the oögonium wall. In some subcultures, the sympodial branches arising below some sporangia terminated in antheridial cells, but the frequency with which this occurred was noticeably variable (1.7–13%).

In general aspect, the sexual apparatus of the two isolates is very similar to that of *Achlya americana* (Howard, *et al.*, 1970; Johnson, 1956; Humphrey, 1893). The isolates digress from *A. americana* chiefly in three characteristics: the irregular inner wall surface, the large antheridial cells, and the conversion of sympodial hyphae into antheridial branches. That declinal antheridia may also occur in the Iceland plants is a further variation from *A. americana* as Humphrey originally described it, but forms with such branches have already been admitted to the species (Johnson, 1956; Coker and Matthews, 1937). If interpretation of *A. americana* by Johnson and Seymour (1974a) is correct, the species also produces (though rarely or infrequently) androgynous antheridial branches. The limits of *A. americana* have thus been broadened over the years since its dis-

covery, and the species now would easily admit my specimens.

The two fungi from Iceland are remarkably like *Achlya* sp. 1, described from two collections in Michigan (Johnson, 1956). At the time this unnamed taxon was reported, I noted its similarity to *A. americana* (among other species), emphasizing, however, that sympodial branches ending in antheridial filaments constituted an important though not unique feature of the fungus. The Iceland plants have this characteristic, but not in the frequency noted for the unnamed *Achlya*. This suggests, of course, that the conversion of sympodial branches to antheridia is not necessarily a constant feature in the individuals in which it occurs. Accordingly, there is even stronger evidence in the Iceland specimens for identifying *Achlya* sp. 1 with *A. americana* than was apparent from characterization of the Michigan material, and the two taxa are therefore combined. Modifying the limits of *A. americana* to include the two fungi from Iceland does not make it an unwieldy or unrecognizable species.

Achlya bisexualis Coker and A. Couch

The mating strains (Herb. No. 2712, 2716) occurred in two separate soil samples from one locality near Straumsvík. This dioecious species is adequately described and illustrated elsewhere (Johnson, 1956). Some of the unidentified *Achlyas* that did not produce oögonia or antheridia are possibly mating strains of this species or of *Achlya ambisexualis* (Johnson, 1956).

Achlya debaryana Humphrey

(Figs. 111–115)

Three isolates (Herb. No. 1580, 1613, 9057) constitute the sole records of this controversial species in Iceland. The following description was derived from a characterization of pure cultures of the three specimens (Figs. 111–113) grown on hempseed at 25° C in 40 ml of tap water.

Mycelium diffuse, extensive; two-week-old

colony 1.5–2.1 cm in diameter, principal hyphae stout, moderately branched. Gemmae absent. Sporangium fusiform, cylindrical, or naviculate; renewed sympodially; 80-(266-375)-623 μ long by 12-(21-27)-31 μ in diameter. Planonts discharged in an achlyoid fashion; spore mass persisting; encysted spores 9-11 μ in diameter. Oögonium spherical or pyriform; lateral or terminal, rarely intercalary; 31-(68-93)-112 μ in diameter. Oögonial wall smooth on outer surface, pitted, unpitted, or slightly irregular and pitted on the inner surface. Oögonial stalks stout, straight, curved, or bent; generally 1–2 times the oögonium diameter, in length. Antheridial branches usually monoclinal, and of distant (83%) or near (17%) origin; infrequently (11%) diclinous; slender, slightly irregular, simple or branched. Antheridial cells large, cylindrical or broadly fusiform; attached by short or long projections to the oögonial wall; fertilization tubes present but not persisting. Oöspores eccentric, spherical; usually filling the oögonium; 1-(8-12)-32 in number 13-(22-26)-34 μ in diameter; germination not observed.

Pure cultures of the three isolates grown in tap water showed a definite preponderance of monoclinal antheridial branches of distant origin (see description), and these were not profusely branched (Fig. 113). Gross cultures, similarly, had exhibited monoclinal antheridial branches, but 80–94% of these were of near origin, and usually were densely branched. The individuals were thus obviously variable in these two characteristics at least. To determine something of the degree of variability, I propagated colonies of one isolate (No. 9057) in 40 ml of a sterile 1:1 mixture of pond water and soil extract.

Pond water was collected from a shallow lake (Ellidavatn), and filtered through cheesecloth and sterile, absorbent cotton. Approximately 100 g of potato garden soil was steeped (with occasional stirring) in 1 liter of cold tap water for 6 hours. The water was filtered in the same manner as the pond water, and then reconstituted to 1 liter. Equal

portions of the pond water and soil extract were mixed and autoclaved (121° C, 20 minutes).

Oögonium size, wall structure, stalk length, and oöspore number were the same in the experimental colonies of isolate 9057 (Figs. 114, 115) as in the control plants grown in tap water. The 70% median oöspore size was slightly higher (24–28 μ) in the experimental plants. This contrasts with the relative constancy of oöspore size in, for example, specimens of *Achlya americana* (Johnson and Seymour, 1974a), and members of the *A. spiracaulis*-*A. papillosa* complex (Johnson and Seymour, 1974b). In the modified culture conditions, the antheridial filaments of isolate 9057 were profusely branched (Figs. 114, 115) and, when monoclinal, were of near origin (less than 18% originated more than 200 μ from the stalk of the oögonium to which they were attached). Monoclinal branches prevailed, and only infrequently were diclinous ones produced. No androgynous antheridial branches were observed.

The identification of my isolates with *Achlya debaryana* is provisional, as is the status of the species itself. The history of the taxonomy of *A. debaryana* and some remarks on its structure are recorded elsewhere (Johnson, 1956).

Not having seen specimens alleged to be *Achlya debaryana*, but judging solely from the literature available at the time, I limited the concept of the species to those individuals having unpitted oögonia and monoclinal antheridial branches of remote origin (Johnson, 1956). Subsequently, Milanez and Beneké (1968) reported *A. debaryana* from a single collection in Michigan. They contributed some vital and significant quantitative data for the species. In their specimen, the oögonia were 25-90 μ in diameter (usually 50-75 μ) and the oöspores were predominantly 22-26 μ in diameter. Their isolate produced 2-7 oöspores per oögonium, and they reported that the oögonial walls were unpitted. The sizes of the oögonia and oöspores recorded by these investigators for

their specimen are in remarkably close agreement with those of the Iceland plants. In the latter, however, the oöspore number is slightly higher than in the Michigan isolate. A later report of *A. debaryana* by B e n e k e and R o g e r s (1970) refers specifically to the unpitted oögonia and the remote origin of the antheridial branches.

Obviously, some fungi (B e n e k e and R o g e r s, 1970) identified with *Achlya debaryana* possess the two characteristics which I proposed (J o h n s o n, 1956) were necessary to delimit the species. By identifying the Iceland specimens as this species, I contradict my earlier account and conclusions, but in the specimens at hand, their general configuration leaves no doubt that they are very near *A. debaryana*. On the other hand, the report by B e n e k e and R o g e r s of plants that agree exactly with my earlier interpretation of *A. debaryana* argues against including my specimens from Iceland in this species.

An important factor in the identity of the Iceland specimens is that of the extent to which isolate 9057 responded to culture. Monoclinous antheridial branches of near origin were produced in gross culture and in pond water-soil extract, but such branches had a distant origin in colonies grown in tap water. Branches of near origin are more suggestive of *Achlya americana* than of *A. debaryana*, and point to an even closer relationship of the two taxa than previously (J o h n s o n, 1956) suspected. The quantitative and qualitative analysis by J o h n s o n and S e y m o u r (1974a) of some isolates revolving about *A. americana*, leaves some doubt that even this species is properly circumscribed. Until adequate limits are set on *A. americana*, it seems unwise to equate *A. debaryana* fully with it. Additional *debaryana*-like isolates need to be manipulated experimentally in several environmental conditions before the status of the species can be settled. The remarks in the subsequent account of *A. klebsiana* are pertinent to this point.

Achlya cambrica (Trow) Johnson
(Figs. 102–107)

This species was collected on five previous occasions in Iceland (H o w a r d, *et al.*, 1970). Two additional isolates (Herb. No. 3703, 3708), with some characteristics at variance with those of the species, have been recovered.

Oögonia of the specimens at hand are more abundantly pitted (Fig. 103) than has been described for the species. Chiefly, however, the two isolates differ from *Achlya cambrica* (J o h n s o n, 1956) in the origin and nature of the antheridial branches. These are usually (68–73%) diclinous, and openly (Fig. 107) or compactly (Fig. 106) branched. By contrast, diclinous branches were rare in the previously collected specimens from Iceland (H o w a r d, *et al.*, 1970), but when these were present, they were simple or only sparingly branched. Monoclinous antheridia predominated in the various specimens described by J o h n s o n (1956), and in those recovered by H o w a r d, *et al.* (1970). The antheridial cells in isolates 3703 and 3708, though laterally appressed or attached by projections to the oögonial wall, are larger and more prominent than previously reported for this species. Some antheridial cells (Fig. 106), in fact, are indistinguishable from those commonly produced by *A. americana* (Fig. 108).

Admitting to *Achlya cambrica* the two isolates with a preponderance of diclinous antheridial branches allies that species even closer to *A. flagellata* than earlier (J o h n s o n, 1956) suspected. The presence of wall ornamentations in *A. cambrica* and their alleged absence in *A. flagellata* may indeed be the only feature that can be used to separate the two taxa.

Achlya colorata Pringsheim
(Figs. 97–99)

This appears to be a relatively common species in wet soils from the marshy edges of lakes and streams. In their usual expression the Iceland plants have very prominent, multiple, androgynous (Figs. 97, 99) or exi-

gynous (Fig. 98) antheridial branches. In contrast to a prior description of this species (Johnson, 1956), I find the inner surface of the oögonial wall to be smooth generally.

Achlya flagellata Coker

As indicated by Howard, *et. al.* (1970), *Achlya flagellata* is not common in Iceland. In late 1972, I collected several specimens of an *Achlya* identified tentatively as Harvey's (1942) *A. californica*. Representatives of these collections were compared with two isolates of *A. flagellata*, all specimens being grown in pure culture under similar environmental conditions: 40 ml tap water, 23-25° C incubation. The fungi identified as Harvey's species had more abundant antheridia than did *A. flagellata*, but otherwise were accommodated readily within the limits of Coker's species (Johnson, 1952). *Achlya californica*, itself a *nomen nudum*, is therefore merely one of several variants of *A. flagellata*.

Achlya inflata Coker (Fig. 118)

Recovered twice in soil samples from the lava field east of Thingvellir (Herb. No. 3307, 3313), and once from soil and debris in a rearing pond at Kollafjörður (Herb. No. 1662). *Achlya inflata* is easily recognized by the large, spherical oögonia and declinous antheridial branches. The antheridial cells (Fig. 118) of the Iceland specimens are often larger than those of the Michigan plants described by Johnson (1956).

Achlya klebsiana Pieters (Figs. 116, 117)

Most specimens (from Iceland) identified as *Achlya klebsiana* agree well in their overall characteristics with the expanded limits of the species (Johnson, 1956) with two exceptions. Up to 54% of the oögonia in the Iceland plants have monoclinal antheridia, and 20-35% of these branches are of near origin (Fig. 116). The most recent description of *A. klebsiana* (Johnson, 1956) states that about 30% of the antheridia are monoclinal, but nearly always of distant ori-

gin. In *A. klebsiana* it is evidently rare for the oögonia to be pitted other than at points where the antheridial cells are attached, or to be unpitted. Pitting is extremely variable in the specimens at hand: some oögonia are devoid of pits, some have these only under the points of attachment of the antheridial cells, and others are pitted elsewhere as well.

The general configuration of the sexual apparatus in the Iceland specimens of *Achlya klebsiana* grown in tap water at 23-25° C is similar to some of the responses of *A. debaryana* (Figs. 115, 116) in modified culture conditions. Moreover, when *A. klebsiana* is propagated in a soil extract medium (see discussion under *A. debaryana* for method of preparation), the antheridial filaments become profusely branched (Fig. 117) and irregular. A similar response (Fig. 114) occurs with isolates of *A. debaryana*. With respect to oöspore and oögonium size, *A. klebsiana* and *A. debaryana* are obviously indistinguishable from one another.

The foregoing observations support the view that *Achlya debaryana* and *A. klebsiana* are possibly expressions of a single species. Johnson (1956) had suggested this disposition even though he had not seen specimens of Humphrey's species. In the isolates at hand, I can find only one characteristic on which to separate the two species: fewer oöspores (4-6, median 70%) in *A. klebsiana* than in *A. debaryana* (8-12, median 70%). This is at best a tenuous separation.

Among the *Achlyas* isolated from various habitats in Iceland were several plants identified merely as *Achlya klebsiana-flagellata*. These specimens had particular combinations of characters that related in part to one species and in part to the other. Some isolates, for example, had a preponderance of declinous antheridial branches (characteristic of both *A. klebsiana* and *A. flagellata*), produced androgynous antheridia like those of *A. flagellata*, yet had maturing oöospheres as in *A. klebsiana*. In still other features used in identification, namely, oögonium and oöspore size, and wall pitting pattern, the "*klebsiana*-

flagellata" isolates could be assigned confidently to either species.

Repeated attempts to sort out these *Achlyas* into reasonably recognizable species units invariably ended in indecisive naming. A few of the more troublesome isolates were propagated in various modified culture conditions (such as staling water and soil extract, and temperatures of 18 and 30° C), but the resulting morphological responses of the fungi were inconclusive in their bearing on identification. As appears to be the case in *A. americana*, for instance (Johnson and Seymour, 1974a), the limits of *A. klebsiana*, *A. debaryana*, and *A. flagellata* are also far from settled.

(?) *Achlya megasperma* Humphrey

There is but one collection (Herb. No. 10616) of a fungus provisionally identified as this species. Originally thought to be a *Saprolegnia*, the specimen occurred on hempseed in company with hyphae of *S. ferax*. When isolated, however, by single-hypha transfer to cornmeal agar and (subsequently) to hempseed, no sporangia were produced in the pure cultures. Subcultured colonies also failed to form sporangia when propagated in sterile or nonsterile soil extract (18 or 25° C).

The oögonia usually contain 4–6 subcentric oöspores 44–54 μ in diameter (median 70%), and are attended by declinuous or monoclinal (distant origin) antheridial branches. These characteristics relate the specimens to *Achlya megasperma* rather than to either *Saprolegnia uliginosa* Johannes (no antheridia) or *S. megasperma* Coker (smaller oöspores). Until other representatives are cultured and the sporangia characterized, the fungus cannot be identified satisfactorily.

Achlya (?) *oblongata* var. *oblongata* deBary (Figs 146–152)

Watermolds provisionally assigned to deBary's variety appeared in five samples from various localities. Since the characteristics of these specimens in pure culture were

in close accord, I believe that the isolates are not merely aberrant forms. A composite description of the five isolates (Herb. No. 577, 10423, 10772, 10979, 11245) propagated as pure cultures on hempseed in 40 ml of tap water (incubated at 23° C) follows.

Mycelium diffuse, extensive, colony reaching 2 cm diameter on hempseed, in one week. Gemmae abundant; terminal or intercalary, single or catenulate; globose, pyriform, obovate, cylindrical, or irregular, and occasionally (when intercalary) laterally bulged at one end; apparently functioning as sporangia or oögonia. Sporangia very uncommon; cylindrical or fusiform, straight or curved; sympodial renewal rare, the branch below a sporangium usually bearing oögonia or gemmae, or both; 96–277 μ long by 13–41 μ in diameter. Planonts discharged in an achlyoid fashion; spore mass usually falling away from the exit orifice; encysted spores 9–(10–11)–13 μ in diameter. Oögonium usually broadly obovate, occasionally cylindrical, spherical, pyriform, or laterally bulged; usually terminal or intercalary, occasionally lateral; obovate ones 60–(120–148)–171 μ long by 53–(74–90)–133 μ in diameter, spherical ones 73–(80–94)–118 μ in diameter; cylindrical ones 50–(66–79)–87 μ long by 24–(35–41)–53 μ in diameter; basal septum occasionally elongated into one or two narrow, simple or once-branched projections into the oögonial cavity. Oögonial wall smooth; unpitted or (rarely) with very small pits under the antheridial cells; in some large, obovate oögonia, wall is thin near the basal portion, but otherwise usually of equal thickness throughout. Oögonial stalks simple, stout; about equal to the diameter of the oögonium, in length. Antheridial branches declinuous, very slender, usually not persisting; branched or simple. Antheridial cells small, simple or once-lobed; clavate or cylindrical; laterally appressed; fertilization tubes not observed. Oöspheres not maturing, variable in shape, but generally spherical, ovoid, ellipsoidal, or pyramidal, occasionally conforming to the shape of the laterally bulged oögonium or a

cylindrical one; rarely becoming thick-walled and then bearing internally a few large, scattered oil droplets; spherical ones 12–(22–28)–70 μ in diameter; 1–(10–14)–38 in number; maturation and germination not observed.

General configuration of the sexual apparatus and such particular features as origin and fate of the antheridial branches in the Iceland specimens are quite properly considered representative of *Achlya oblongata* var. *oblongata* (Johnson, 1956). Size and shape of the terminal and lateral oögonia, and number of oöspores, are features which my specimens have in common with this variety. The plants, however, also show prominent divergences from *A. oblongata* var. *oblongata*.

None of the oöspores of the Iceland fungi matured into any recognizable oöspore type, although they are known to do so, though infrequently (Johnson, 1956), in *Achlya oblongata* var. *oblongata*. Moreover, deBary's variety does not have the extreme range of sizes and shapes expressed by the oöspores of the specimens at hand. In addition, *A. oblongata* var. *oblongata* has unpitted oögonia whereas in my plants pits may occur, although they are rare. None of the previous accounts of deBary's variety describes the oögonial wall as being thin in its basal portion, but this feature characterizes my isolates in part. The conspicuous basal septum extensions (Figs. 146, 148) in the Iceland fungi are not known to be characteristic of the variety *oblongata*.

Growth of the isolates in several modified culture conditions was extremely poor, and the results showed little that could be used for taxonomic purposes. Pure cultures propagated in tap water had fewer spherical (and lateral) oögonia (Fig. 151) than did those specimens forming oögonia in a 1:1 mix of sterile soil extract and tap water. In tap water alone, the fungi generally produced obovate or cylindrical oögonia (Figs. 146, 147, 149). To what extent this instance of variability reflects overall variation in the isolates is not

known.

Oögonia of the isolates resemble in some respects (Fig. 150) the configuration of the sexual apparatus in *Achlya intricata* (Bencke, 1948; Howard, *et al.*, 1970). In that species, also, the antheridial branches do not persist, and the antheridial cells are small. The oöspores in Bencke's species, however, mature into eccentric oöspores, and most oögonia are conspicuously lobed, hemispherical, or irregular. These characteristics do not permit identification of the Iceland specimens with *A. intricata*.

Equating the five isolates with *Achlya oblongata* var. *oblongata* remains provisional. Discovery of the oöspore type in other specimens of the Iceland plants would assist materially in a final decision on identity.

Achlya oligacantha deBary

(Figs. 119–133)

Specimens identified as *Achlya oligacantha*, a relatively poorly known species, appeared in seven collections (Herb. No. 1868, 1952, 3444, 6182, 6723, 10912, 10933). On isolation, only two representatives, Nos. 10912 and 10933, grew into vigorous colonies that could be characterized and manipulated experimentally. The account of this species is taken largely from the results of propagation of these two isolates. The characteristics of the species, derived from pure cultures on hempseed in tap water, are given in the following description.

Mycelium diffuse; two-week-old colony 0.8–1.7 cm in diameter. Gemmae absent. Sporangia very sparse; when present, cylindrical or fusiform, straight, curved, or bent; renewed sympodially; 280–743 μ long by 24–36 μ in diameter. Planonts discharged in an achlyoid fashion; spore mass usually falling away from the exit orifice; encysted spores 9–12 μ in diameter. Oögonium usually spherical or pyriform, occasionally ovoid, rarely angular, dolioform, or apiculate; lateral, terminal, or (rarely) intercalary; 38–(75–87)–161 μ in diameter. Oögonial wall generally smooth, but occasionally

(27–39%) sparsely ornamented; ornamentations small, papillate; unpitted, sparingly pitted, or with pits and broad, circular, thin areas on the inner surface. Oögonial stalks stout, generally curved or irregular, infrequently (12–27%) loosely coiled or strongly bent; rarely straight or branched; generally 2–3 times the öogonium diameter, in length. Antheridial branches, when present (absent on 20–38% of the öogonia) predominantly (65–73%) monoclinal and of near origin; rarely androgynous, infrequently dichlinal; slender, usually irregular, occasionally sparingly branched. Antheridial cells simple, cylindrical to clavate; laterally appressed, fertilization tubes usually absent. Oöspheres very infrequently maturing (1–8%): usually not filling the öogonium; 1–(10–16)–24 in number; 16–(23–27)–38 μ in diameter. Oöspores centric; spherical; 22–28 μ in diameter; germination not observed.

The general configuration of the sexual apparatus (Figs. 119–121, 130) of the specimens closely parallels previous descriptive matter (Johnson, 1956). The notable exception is in the nature of the öogonial wall. *Achlya oligacantha* is alleged (Johnson, 1956) to have unpitted öogonia; in the representatives at hand, pitted ones (Fig. 122) also occur.

Milanez and Beneke (1968) report *Achlya oligacantha* from Michigan, but certain characteristics of their isolates diverge somewhat from an earlier (Johnson, 1956) circumscription. Some features of my plants are likewise at variance with their specimen. The Michigan material had unpitted öogonia, and the oöspheres matured into subcentric öospores (3–10 per öogonium). The few öospores that were formed by the Iceland specimens were centric. This difference in öospore structure may not be significant taxonomically, since it has been shown (Dick, 1969; Seymour, 1970) that a single species of watermold can have öospores of both types. The öospheres in the Michigan fungus aborted after maturing, and this contrasts sharply with the plants from Iceland

where maturation is usually rare. In the isolate examined by Milanez and Beneke, antheridia were abundant — they are sparse in the Iceland fungi — and androgynous ones predominated. My isolates generally had monoclinal antheridial branches. Moreover, it appears that most öogonia of the Michigan isolate were ornamented. In my fungi, on the contrary, the öogonia (in the tap water cultures) were most often smooth-walled. These substantial differences among the plants from the two localities need careful analysis when additional living cultures are at hand for direct comparison.

Howard (1968) concluded that *Achlya spiracaulis* was even more closely allied to *A. oligacantha* than had been earlier (Johnson, 1949) suspected. Later, Howard and his coworkers (1970) repeated this concept, even though they claimed that the two species could be separated on four characters: proportion of smooth-walled to ornamented öogonia, frequency of coiled öogonial stalks, fate of the oöspheres, and predominant öospore size.

In an experimental study of *Achlya spiracaulis* and *A. papillosa*, Johnson and Seymour (1974b) concluded that these two species were synonymous (*A. papillosa* had priority), but admitted that some plants in various cultures were suggestive of *A. oligacantha*. In particular, their data showed that coiling of the öogonial stalk and density of wall ornamentations in the *A. spiracaulis*-*A. papillosa* complex was highly variable. These same two features, of course, figure prominently in separating these species (now combined) from *A. oligacantha*. Lacking specimens for comparison, Johnson and Seymour did not arrive at any firm conclusions regarding the obvious similarities between *A. papillosa* and *A. oligacantha*.

Because of the demonstrably broad magnitude of variation in *Achlya papillosa* (Johnson and Seymour, 1974b) it was necessary to determine something of the variability of *A. oligacantha* (as it was presumably represented in the Icelandic flora) if it was to be

dealt with properly. Accordingly, I selected isolate 10933 as being the most representative of *A. oligacantha*, and propagated the fungus as a pure culture in 40 ml of sterile pond water and in 40 ml of a 1:1 mixture of sterile pond water and soil extract (see discussion under *A. debaryana* for method of preparation). The cultures were incubated at 18 and 25° C.

Oögonia in colonies grown in sterile pond water at 18° C exhibited striking variations in wall ornamentations (Figs. 125–129). There were proportionately more ornamented oögonia (51–66%) on these plants than on those grown in tap water (40 ml, 25° C) or other test conditions. The ornamentations varied from small, conical papillae (Fig. 128) to large, broadly conical ones (Fig. 126). In no instances, however, were the wall markings as dense as can develop on oögonia of *Achlya papillosa* (Johnson and Seymour, 1974b).

Specimens of *Achlya oligacantha* propagated at 25° C in the pond water–soil extract medium generally produced ovoid, smooth-walled (Fig. 123) oögonia on somewhat irregular stalks (Fig. 124). Ornamented oögonia were usually spherical, and had only a few, inconspicuous, papilla-like protrusions (Fig. 124). Much greater changes were induced in cultures grown in the pond water–soil extract medium incubated at 18° C (Figs. 131–133). In this environment, subcultures of the isolate (10933) of *A. oligacantha* produced (66–78%) large, pyriform or ovoid (Figs. 131, 133) to angular oögonia. These oögonia had 4–6 oöospheres (median 70%) in contrast to the usual number of 10–16 in specimens grown in sterile tap water culture and incubated at 25° C. Additionally, the oögnial stalks (and often the attendant antheridial branches as well) were very irregular, being contorted, twisted, or coiled. The laterally appressed antheridial cells were irregular and lobed, but either were not fully abstricted from the branch, or if so, did not appear to be functional (Figs. 131–133). Wall pitting was not affected by any of the culture conditions, nor

was the magnitude of oöosphere maturation noticeably changed over that detected in the control cultures (on hempseed, in 40 ml of sterile tap water, at 25° C).

If the performance of this one isolate is indicative of the species, it may be concluded that *Achlya oligacantha* is demonstrably variable in certain of its major structural features. Furthermore, the variation of this representative of the species, at least under the conditions employed, was clearly not in the direction of *A. papillosa*. The reaction of more numerous isolates obviously needs to be determined to test the reliability of this conclusion. Pending the results of a thorough study of more numerous specimens, I believe *A. oligacantha* should be recognized as a valid species. It appears to be separable from *A. papillosa*, as that species is now defined (Johnson and Seymour, 1974b), on characteristics expressed in pure cultures in tap water.

Achlya polyandra Hildebrand (Figs. 100, 101)

Not previously known from Iceland, this species was first collected (Herb. No. 2011) in 1969, followed by four other isolations (Herb. No. 3016 3800, 6493, 8061). With the exception of the general configuration of the antheridial branches, all specimens are in close agreement with the broadened description of *Achlya polyandra* proposed by Johnson in 1956. The plants from Iceland have multiple, very slender, much-branched antheridial filaments (Fig. 100, 101). Sparingly branched antheridia have also been reported for *A. polyandra*.

Achlya recurva Cornu (Figs. 94–96)

Collected on several occasions in soil samples, *Achlya recurva* is represented in Iceland by two known forms. One form is in all respects characteristic of the species (Johnson, 1956). The second form is a less common one, and has two prominent features not previously reported. Representatives of this form have a preponderance of very large

oögonia: the median diameter (70%) of these structures, exclusive of the truncate ornamentations (Fig. 94) is 65–88 μ . The oöospheres are correspondingly large, with a diameter (median 70%) of 25–28 μ . While 4–8 is the predominating range of oöspore number in the usual form of this species (Johnson, 1956) the plants with large oögonia have 10–12 (median 70%) oöspores. Small oögonia containing one (Fig. 96) or two oöspores, however, occur on the same hyphae as the large ones.

That *Achlya recurva* is more variable in certain features than expected (Johnson, 1956) is further illustrated by the isolate collected by Milanez and Beneke (1968). In their specimen the oöspores were generally large (25–35 μ in diameter) and few (2–4) in number. Nevertheless, in their plant (as in mine) the species retains its two chief characters: dense, truncate wall ornamentations and predominantly androgynous antheridial branches.

Achlya stellata deBary (Figs. 134–138)

Fungi identified as this species were collected on hempseed bait in soil samples from five localities (Herb. No. 578, 2310, 2381, 3452, 3610) and were subsequently isolated. The species was also found on roach wing bait on two other occasions (Herb. No. 3221, 3222), but could not be isolated. The identification of my plants with this species rests on the informative analysis by Dick (1960).

In resolving the uncertainties (Johnson, 1956) prevailing in the systematics of three very closely allied species, *Achlya spinosa* deBary, *A. stellata*, and *A. cornuta* Archer, Dick (1960) concluded that only two could be recognized as distinct entities (*A. cornuta* was reduced to synonymy with *A. stellata*). He separated deBary's two taxa on three grounds: sporangium structure, presence or absence of gemmae (none in *A. stellata*), and divergence in habitat. There are however, judging from Dick's account, far more pronounced differences between *A. spinosa* and *A. stellata* than these three. The

nature of the oögonium wall ornamentations (admirably figured by Dick) are quite different in the two species, and one (*A. stellata*) lacks an antheridial apparatus. This latter feature marks the Iceland specimens, and thus assures that their identity with *A. stellata* is correct (as that species is currently delimited).

Oögonia in the plants from Iceland are often less densely papillate than the isolates described by Dick, but the form of the ornamentations is unmistakably like that figured by him (Dick, 1960: text. fig. 2). In two of the isolates of *Achlya stellata* studied by Johnson, Rogers, and Beneke (1975), variations were induced in the oögonium wall ornamentations. In the modified environments the ornamentations were fewer in number, but larger, than on oögonia of plants grown in an ordinary tap water culture. In general configuration, these modified wall markings did not approach the lobed, wart-like, or bluntly papillate ornamentations of *A. spinosa*.

Achlya sp. 4144 (Figs. 139–145)

Four specimens (Herb. No. 4144, 4147, 4529, 8858) representing this unnamed taxon were isolated. A composite description derived from characteristics of pure cultures of these isolates grown on hempseed in tap water (incubated at 25° C) follows.

Mycelium diffuse, extensive; two-week-old colony 2.1–2.7 cm in diameter. Gemmae absent. Sporangia sparse; clavate or filiform; straight or slightly irregular; renewed sympodially or in a cymose fashion; terminal ones 141–287 μ long by 18–31 μ in diameter. Planonts discharged in an achlyoid fashion; spore mass persisting at the orifice; encysted spores 8–(9–10)–13 μ in diameter. Oögonium generally ovoid or broadly obovate, rarely angular or spherical, occasionally cylindrical (and then constricted) or broadly apiculate; lateral or terminal; 28–(45–57)–91 μ long by 24–(40–53)–66 μ in diameter. Oögonial wall smooth or provided with 1–4 large, broadly conical or cylindrical papillae; pitted

under point of attachment of antheridial cells. Oögonial stalks stout, short, slightly irregular; simple; in length, generally about equal to the predominating oögonium diameter; occasionally proliferating. Antheridial branches usually declinous, infrequently (14–23%) monoclinal; slender, usually branched and wrapping about the oögonium to which attached. Antheridial cells prominent, simple or sparingly branched; laterally appressed, or attached by projections of various lengths; fertilization tubes sometimes evident. Oöspheres seldom maturing; very small ones (up to 10 μ in diameter) occasionally occurring with larger ones; 1–(2–3)–5 in number; 18–(20–25)–43 μ in diameter. Oöspores, when produced, eccentric; same number and size as oöspheres; germination not observed.

Only one specimen (Herb. No. 4529) survived subculturing after isolation. This fungus was grown on hempseed in various mixtures of tap water and soil extract or pond water, or in staling water diluted 1:1 with tap water, and incubated at 18, 25, and 30° C. Save for the fact that the oögonia were sparse in all cultures at 30° C, there were no prominent changes induced in the characteristics of the isolate. Since only one isolate was available for culturing, this single modification hardly delimits the range of variability in the "species."

The production (though very uncommonly) of eccentric oöspores places this unnamed species in the *Euachlya* group (Johnson, 1956), but it is not readily accommodated within the limits of any of the known taxa. About 45% of the oögonia are provided with very large ornamentations (Figs. 141, 142, 144), a condition that recalls *Achlya cambrica* or *A. caroliniana* Coker (1910) to some extent. In *A. caroliniana*, however, the oöspheres generally mature, and antheridial branches, when produced, are about as frequently monoclinal as declinous. The failure of most oöspheres in the Iceland specimens to mature suggest an affinity of the plants to *Achlya flagellata*. In that species, however, ornamented oögonia are not known, and wall pitting

is much more variable than in *Achlya* sp. 4144.

Characterization of additional specimens, propagated in a variety of environments, is needed before *Achlya* sp. 4144 can be properly identified. Should other fungi representing this taxon be found to have a substantial (or major) proportion of oöspheres to mature, a relationship to *A. cambrica* should be suspected.

APHANOMYCES

Representatives of this genus are particularly common in Iceland, and are often to be found on chitinous or keratinized baits seemingly to the exclusion of other aquatic fungi. Individuals of the subgenera (Scott, 1961) containing species with ornamented or roughened oögonia appear to predominate, but the best known species of the genus, *Aphanomyces laevis* deBary, may be collected in a wide variety of habitats, especially if snakeskin is used as bait in the gross cultures.

Aphanomyces irregulare Scott was reported by me in 1968, and again in 1970 by Howard and his associates. Scott's species was considered synonymous with *A. scaber* deBary. Howard and Johnson (1969) collected *A. helicoides* von Minden from Iceland soil, and a species (which they did not name) on midge exuviae. Howard, *et. al.* (1970) found *A. norvegicus* Wille in Iceland, as well as a second unnamed species, this one with conspicuously expanded oögonial stalks. The latter was again collected by me, but no binomial has as yet been applied to the fungus. Although Howard and Johnson (1969) lightly dismissed *A. laevis* forma *keratinophilus* Ookubo and Kobayasi as a mere variant of *A. laevis*, Seymour and Johnson (1973b) resurrected the form, and raised it to specific rank.

Many additional specimens of the foregoing taxa have been recovered in Iceland as well as a number of variants of them. The following treatment reports readily identifiable species, and also deals with certain troublesome isolates, but fails to unravel

puzzling uncertainties surrounding their taxonomy. Scott's excellent monograph dealt authoritatively with many problems in the systematics of the genus, but could not foresee future problems which were sure to arise. The difficulties experienced with the isolation and identification of some of the specimens recovered in Iceland makes it quite evident that further monographic study is a necessity. For this reason, individuals go unnamed until the results of such a study are at hand.

Aphanomyces amphigynus Cutter
(Figs. 69–73)

Forms (or variants) of this species have appeared twice (Herb. No. 236, 2439) on onion skin bait in soil samples. The specimens were identified with Cutter's species primarily on two characters, namely, the sharply pointed spines on the oogonium wall, and the aplerotic oöspore.

There are two prominent contrasting features between my plants and the circumscription of the species provided by Scott (1961). Monoclinous antheridial branches occur with nearly sessile oogonia (Fig. 73) as the fungus develops on the onion skin substratum. Such branches are not described for *Aphanomyces amphigynus*. In the Iceland specimens the antheridial cells are much smaller than the very conspicuous ones usually formed by Cutter's species (Scott, 1961: pl. 7, figs. P–S).

Other species of *Aphanomyces* in Iceland may have acute wall ornamentations (see *A. scaber*, for instance). In these other taxa, however, such wall markings are not universally present, but they appear to be so in the *A. amphigynus* at hand. In view of the variation encountered (and induced) in the nature of the wall ornamentations in *A. stellatus*, for instance, the characteristic of shape in the markings may prove to be of no taxonomic worth. Since *A. amphigynus* had not been previously cultured (Scott, 1961), it is impossible to identify with certainty my plants from onion skin with the species as it

has been circumscribed. That the Iceland specimens show monoclinous antheridial branches on one substratum in gross culture, evidence that Scott's certainty of the validity of *A. helicoides* may be justified, but diclinous ones when isolated suggests a rather broad degree of variability.

Aphanomyces helicoides von Minden
(Figs. 74–78)

Having examined a number of specimens of *Aphanomyces* with smooth-walled oogonia, Howard and his associates (1970) expressed serious doubt about the validity of von Minden's species. They thought *A. helicoides* to be very closely allied to *A. laevis*, finding that in some of their plants the hyphal "knots" supposedly characteristic of the former only were absent or variable in occurrence. The other distinctive feature of *A. helicoides* — coiling of the antheridial branches — was present in varying proportions among their specimens. However, because some plants always retained some degree of antheridial filament coiling, and others had no such features, they retained *A. helicoides* and *A. laevis* as separate species.

Among several specimens of *Aphanomyces* with smooth-walled oogonia, collected since the account by Howard, *et. al.* (1970), two (Herb. No. 2874, 3099) bear directly on the identity of *A. helicoides* and *A. laevis*. In these plants (isolated on hempseed), the antheridial branches are consistently diclinous, and rather conspicuously and abundantly branched. Coiling of the antheridial filaments is variable in frequency and extent. In some oogonia the branches are loosely (Figs. 74, 76) or tightly (Fig. 77) wrapped about oogonial stalk and adjacent hypha (Figs. 76, 77), but many oogonia are attended only by uncoiled antheridia (Fig. 78). Neither isolate produced the hyphal conglomerates supposedly characteristic of *A. helicoides*.

One isolate, No. 2874, was propagated in soil extract and in pond water (see *Achlya debaryana*), but the fungus was not noticeably altered in either of these media. In this

isolate at least, the antheridial branch coiling identified with *Aphanomyces helicoides* is a stable characteristic. Thus, there is some *Aphanomyces keratinophilus* (Ookubo and Kobayasi) Seymour and Johnson (Figs. 8–14).

There appears to be more than one form of this species. What are evidently the more "typical" plants (Ookubo and Kobayasi, 1955) have already been reported from Iceland. Two additional variants were recovered on human hair baited in various soil samples.

The commonest of the variants (Figs. 8–12) is identifiable by the fact that it produces only sessile oögonia (Fig. 8) on the substratum in gross culture. These oögonia, however, are very characteristic of the species both in size and in their physical relationship to the attendant antheridial filaments. The antheridia, usually much branched, are wrapped about and closely applied to the oögonia.

On two occasions this sessile form of *Aphanomyces keratinophilus* was propagated in unifungal culture on YPSS agar and human hair. Isolation from other fungi in the gross culture was accomplished as follows. Segments of infested hair from gross cultures were washed gently in a stream of tap water, and placed in dishes containing 20–30 ml of sterile pond water diluted 1:1 with tap water. Within 48 hours, new sporangia had formed and were sporulating. Encysted planonts were picked up with a very small loop, and streaked on the surface of one-quarter strength YPSS agar (Difco, dehydrated) containing 0.01% potassium tellurite. After 4–6 hours incubation at room temperature, the plates were examined and germinated spores with their hyphae transferred, together with a small block of agar, to sterile, plastic Petri dishes containing 2–3 ml of a sterile 1:1 mix of pond water plus 0.01% potassium tellurite. To the water surrounding the bit of hypha-infested agar, I added small segments of pretreated baby hair (see Johnson, 1973a, for method). These plates were incubated for 24–36 hours (at room temperature) at which time I added 20–30

ml of a 1:1 mix of sterile pond and tap water, and the cultures were then incubated (23–25° C) for an additional 3 weeks. Potassium tellurite was essential as a bacterial suppressant in the culture media. Cultures lacking this chemical quickly fouled, and the *Aphanomyces* would not grow into oögonium-producing populations. None of the attempts at isolation produced pure cultures.

On isolation, the sessile form of *Aphanomyces keratinophilus* usually produced short, emergent hyphae from the pretreated hair on which short-stalked oögonia (Figs. 9–11) were developed. In a few instances, the oögonial filaments were long (Fig. 12) much like those of the nonsessile form described earlier (Ookubo and Kobayasi, 1955; Seymour and Johnson, 1973b).

The second form (Figs. 13, 14) of *Aphanomyces keratinophilus* appeared (on human hair bait) in a single collection (Herb. No. 9593), but defied attempts at isolation. While this fungus had the various antheridial origin types described for the species (Seymour and Johnson, 1973b), these filaments were not often wrapped conspicuously and densely about the oögonia. The oögonia were small, and each contained a single, small (12–16 μ diameter) oöspore that did not fill the cavity. The oöspores of *A. keratinophilus* are generally 20–25 μ in diameter, and thus are substantially larger than those of the form.

The foregoing differences between the form (Herb. No. 9593) and the "typical" expression of the species are rather substantial. This suggests that the form, when recollected and isolated, may prove to be sufficiently distinct to be recognized as a separate taxon. The status of this form cannot be settled on the basis of a single collection known only from gross culture.

Aphanomyces laevis deBary (Figs. 79–86)

Like the two previous species, this one has been reported earlier from Iceland (Howard and Johnson, 1969; Howard,

et al., 1970). Among several subsequent collections of *Aphanomyces laevis* one isolate (Herb. No. 3102) stands out. When isolated and propagated on pretreated snakeskin (Johnson, 1973a) the fungus exhibited very large, globular, cylindrical, or bell-shaped antheridial cells. While the antheridial cells of *A. laevis* are usually large and conspicuous, they are most often clavate or vermiform as Scott (1961) illustrates them. A few oögonia (less than 11%) in the Iceland fungus were attended by coiled antheridial branches (Fig. 83) Although coiled antheridial filaments are the exception rather than the rule in *A. laevis* according to Scott (1961), even their occasional presence denotes a close similarity of this species with *A. helicoides*. The true alliance of these taxa will remain obscure until experimental evidence, gathered from a comparative study of a large number of isolates, is brought to bear on their taxonomy. It may be noted in passing that the planonts in my specimens emerge from their cysts to leave a poroid aperture (Fig. 86) much as Scott (1961) reports for the species. This is supporting evidence, however minor, for the decision to identify isolate 3102 with *A. laevis*.

Aphanomyces scaber—*A. irregulare*—*A. stellata* complex (Figs. 26–68)

The aquatic mycoflora of Iceland is generously supplied with representatives of *Aphanomyces* having ornamented oögonia. Howard, et. al. (1970) dealt with a scattering of such representatives, concluding perhaps precipitously that at least two species, *A. scaber* and *A. irregulare*, were synonymous. This decision was in accord with that proposed two years previously by Howard (1968).

Among more than 50 specimens of *Aphanomyces* collected from soil, water, and debris, and isolated on roach wing, snakeskin, or hempseed baits, either in pure or unifungal culture, eight have been particularly troublesome to identify. These eight provisionally identified isolates are treated as a single complex of species.

Isolate (Herb.) Nos. 2151, 3014, and 7908

are believed to represent *Aphanomyces scaber* (Figs. 47–52, 60–68), and isolate Nos. 762 and 3005 are identified as *A. irregulare* (Figs. 53–59). Two fungi, Nos. 815 and 2154, appeared to be most closely allied to *A. stellatus* (Figs. 38–46). Two other fungi (isolates No. 2892 and 7533), though unquestionably a part of this complex of three taxa, could not be identified with any reasonable certainty, and therefore were not given a binomial (Figs. 26–37).

The foregoing identifications require substantial comments. These, in turn, will point clearly to the current inadequacies in the taxonomy of these species with ornamented oögonia. To be sure, the most recent formal descriptions of the species (Scott, 1961) contain several characters of distinction traceable to the various taxa, but these may be traits that are shared by two or more entities. It is to ornamentation, therefore, that investigators have had to turn for identification purposes, and there has been little past agreement (Scott, 1961) as to the species limits afforded by characterization of ornamentation types, their density, and their patterns of distribution on the oögonium.

The three specimens (Figs. 47–52, 60–68) assigned to *Aphanomyces scaber* seem to have little in common except planont discharge pattern, antheridial branch origin, and size of oögonia and oöspores. Certainly in oögonium wall ornamentation these fungi appear to diverge into three distinct lines.

Isolate 7908 (Figs. 47–52) is thought to be most nearly representative of *Aphanomyces scaber* — as that species was recognized by Scott (1961) — than any other specimens at hand. The wall ornamentations of isolate 7908, though of varying density (Figs. 48, 49) and degree of development (Figs. 50, 51) among the oögonia, are generally narrowly conical, and terminate in a rounded tip. Such papillae immediately call into question the identity of the fungus with *A. scaber*. Scott's (1961: 53) description clearly defines the oögonium wall ornamentations as "... short, sharp-pointed spines up to 3.5 μ

in length . . ." The illustration accompanying the description, however, show (with one exception) oögonia with broad or narrow, conical papillae (rounded apex.) Even in the one oögonium depicted by Scott with sharply pointed spines, there are papillate ornamentations interspersed among them as well. This degree of variability pictured by him is at least generally matched (though it may also be exceeded) by that expressed in my isolate. In the Iceland specimens, also, the length (up to 12 μ) of the ornamentations (Fig. 50) exceeds that admitted to the species. However, a very few oögonia (Fig. 51) of isolate 7908 merely possess small protrusions that give the wall a roughened or irregular aspect. In the final analysis I am equating the Iceland plant with *A. scaber* more on the basis of illustrative rather than decriptive matter, and am admitting to the species a broader concept of ornamentation types than did Scott (1961) or deBary (1860).

The wall ornamentations on about 55% of the oögonia of isolate 3014 (Figs. 64–68) are small, conical (Figs. 64, 65), few in number, and rounded at the apex. In 9% of the oögonia the wall is merely irregular, or roughened, and possesses one or two papillae (Figs. 66, 67), while 32% of the oögonia are distinctly echinulate (Fig. 68). These variations occurred in cultures grown in the usual conditions of incubation: 23–25° C, and 40 ml of tap water. The echinulate wall ornamentations, of course, compare favorably with Scott's description of the wall markings in *A. scaber*, but are at variance with the illustrations he provided for the same species. With its roughened or irregular oögonia, isolate 3014 represents a tendency toward *A. irregulare*, and is very much like the *A. scaber* described and figured by Howard, *et al.* (1970: fig. 9). The general sparseness of the wall ornamentations on oögonia of 3014 does not fit well with either Scott's (1961) or deBary's concept of *A. scaber*, and casts doubt on the correctness of the identification of this Iceland plant.

Short, broadly conical ornamentations,

rounded at the apex, are the exclusive type on about 30% of the oögonia (Fig. 60) of the third isolate of *Aphanomyces scaber* (Herb. No. 2151). Such projections occur on nearly every oögonium, and thus this type of ornamentation probably best characterizes this variant. Generally, the ornamentations in isolate 2151 are not as dense (Figs. 61, 62) as those produced on oögonia of isolate 7908 (Figs. 47, 48). With respect to density, but not to shape, the ornamentations of isolate 2151 are more nearly like those found in isolate 3014. Among the three fungi assigned to *A. scaber*, isolate 2151 stands out with respect to the magnitude of variation in its oögonium wall markings. These are sometimes projected into long, curved or bifurcate protrusions (Figs. 60–63).

Obviously, to admit isolate 2151 to *Aphanomyces scaber* broadens the description of that species very substantially. If the identification proves to be correct the species will then include representatives with low, broadly conical oögonial ornamentations. Should the *Aphanomyces* sp. reported by Kobayasi, *et al.* (1967) from the Alaskan Arctic prove to be a valid member of the genus, it would seem closely allied to this Iceland representative of *A. scaber*.

Scott's description (1961) of *Aphanomyces irregulare*, supplemented by the accompanying detailed discussion, leaves little question about the characteristics that constitute the species as he interpreted the taxon, and the nature of the specimens assigned there. Although *A. irregulare* occurs in Iceland, there are individual plants that have most features of the species yet digress enough to be identified with it only in great uncertainty. Two fungi (Figs. 53–59) illustrate this difficulty. While 61–73% of the oögonia are densely (Fig. 54, in part) or sparsely (Fig. 56) roughened or irregular, this condition is the result of many very small, wart-like papillae (Fig. 55). This is certainly a very different ornamentation pattern than Scott (1961) described for the species, yet the resultant oögonial irregularity is the same.

Isolates 762 and 3005 have an additional feature that is evidently not characteristic of *Aphanomyces irregulare* in the strictest sense: considerable variation in the size and density of the oögonial wall markings. The illustrations by Scott (1961) of this species show a very consistent ornamentation pattern, made up of wall protrusions that are rather regular in size. Nearly 11% of the oögonia in the two isolates I have named *A. irregulare* have distinctly narrow and long-conical (Fig. 58) ornamentations. These markings approach *A. scaber* (Figs. 47–50) as I interpret that species from the Iceland specimens at hand. Three to five per cent of the oögonia are irregular only in the upper half or third of the wall (Fig. 59). Such a feature has not been noted for *A. irregulare*.

The two fungi identified as *Aphanomyces irregulare* (No. 762 and 3005) grew very sparsely on isolation from gross culture, and then only on pretreated (Johnson, 1973a) roach wing. Consequently, the full range of variations expressed by these fungi is not known. It could be argued that the minute "papillations" (Figs. 53, 55) on the oögonia constitute a feature sufficiently unique to prevent an alliance of my plants with Scott's species. The alternative — to describe a new taxa on the basis of two rather variable isolates — is not warranted in my view. The limits of *A. irregulare* are of course extended rather broadly by the inclusion of the Iceland plants.

According to Scott (1961: 58) the oögonia of *Aphanomyces stellatus* are provided with " . . . bluntly conical tubercles up to 6.5 μ in length . . ." and this equates reasonably well with deBary's description and illustrations of this, the type species. In any case, the figures provided by Scott (1961: pl. 8, figs. J–L) show wall ornamentations that are perceptibly stouter and larger than those of either *A. scaber* or *A. irregulare* (Scott, 1961: pl. 7, figs. A–D, I–L). Two fungi from Iceland have been identified as *A. stellatus* (Figs. 38–46). Both specimens (No. 815 and 2154) were isolated onto hempseed from roach wing bait in gross culture, and colonies

with the sexual apparatus were developed (though very sparsely by isolate 815).

When first recovered, the specimens had oögonia that were usually very densely papillate (Fig. 39), but in form, these ornamentations were very much like those described by Scott (1961). When the fungi were isolated into pure culture and propagated in 40 ml of tap water at 23–25° C incubation, ornamentation density decreased (Figs. 40, 42) sharply. Nevertheless, the shape of these wall markings remained essentially the same as that found on oögonia in the gross cultures: short, broadly-rounded at the tip, and broadly-conical or nearly cylindrical (approaching the tuberculate condition recognized by Johnson, 1956). Thus, the tendency to from cylindrical rather than sharply tapering wall markings became the chief character on which I separated my specimens of *Aphanomyces stellatus* from the isolates of *A. scaber*. This is a very fine point of distinction, but it does seem to agree reasonably well with the concept of *A. stellatus* expressed by Scott's illustrations, and with the specimens collected in Greenland by Kobayasi, *et al.* (1971).

Since one of the isolates (No. 2154) identified as *Aphanomyces stellatus* grew readily on hempseed, I propagated specimens of it in various culture conditions: 20 and 40 ml amounts of sterile pond water, sterile soil extract, and a 1:1 mixture of the two, at 18 and 25° C; 20 and 40 ml amounts of a 1:1, 1:5, and 1:10 mix of sterile tap water and soil extract (incubated at 25° C); 50, 100, and 500 ml quantities of a 1:1 mixture of sterile tap water and sterile pond water (incubated at 18 and 25° C). The fungus grew in all of these environments, but pronounced morphological changes were exhibited mainly by plants that developed in cultures of soil extract or a mixture of soil extract and pond water.

In particular, two characters of isolate 2154 were modified. The oögonial stalks and most antheridial branches (irrespective of origin) were twisted, irregular, and contorted (Figs. 43–46), and many of the principal hyphae

were similarly changed. Substantial modifications were also induced in the oögonium wall ornamentations. These structures became quite large, often were broad and dichotomously or unequally branched, were sometimes bullate (*sensu* Johnson, 1956), and frequently were long, narrow, and curved or straight (Figs. 43–46). In 100 and 500 ml amounts of a 1:1 mixture of tap and pond water the density of ornamentations (at 18 or 25° C) was much less than that evident in soil extract cultures. Nevertheless, the pattern of these reduced (in number) ornamentations was indistinguishable from that marking oögonia produced by individuals grown in soil extract. None of the various combinations of culture conditions employed led to elimination of wall ornamentations nor to the production of oögonia resembling those of the *A. irregulare* or *A. scaber* specimens at hand.

In Iceland, the most frequently collected specimens of *Aphanomyces* with ornamented oögonia were ones producing stout, long, tubular, broadly cylindrical or conical markings each with a broadly rounded or nearly truncate apex. Two isolates, No. 2892 and 7533 (Figs. 26–37) were “typical” of these fungi. Although some oögonia of both isolates lacked antheridial branches (Figs. 26, 27), those that possessed such structures had ones of monoclinal, diclinal, or androgynous (16%) origin. Discharge of the planonts from their cysts was poroid (as in *A. laevis*). The oögonia of isolate 2892 were (exclusive of the wall ornamentations) 15–(18–21)–28 μ in diameter, and the oöspores were 10–(12–15)–23 μ in diameter. In isolate 7533, on the other hand, the oögonia and oöspores were larger: 18–(26–28)–39 μ in diameter (exclusive of the wall ornamentations) and 15–(21–24)–29 μ in diameter, respectively. I am inclined to dismiss this size difference as insignificant in view of the variability in general expressed by the species of *Aphanomyces* in Iceland’s soils and waters.

Isolate 7533 grew more vigorously on hemp-

seed than did 2892, and was therefore used in a series of culture manipulations patterned after those to which isolate 2154 of *Aphanomyces stellatus* was subjected. Isolate 7533 responded morphologically to cultures containing soil extract alone, or to extract in combination with pond or tap water. The resulting structural modifications (Figs. 35–37) were very similar to those developed by *A. stellatus* 2154: irregular, twisted, or contorted antheridial branches (and oögonial stalks), and enlarged, often prolonged and irregular, straight, curved, dichotomously or unequally branched, relatively sparse wall ornamentations.

The oögonia produced by colonies of *Aphanomyces stellatus* 2154 grown in tap water formed wall ornamentations (Figs. 38–40) that were at once recognizably different from those of *Aphanomyces* 7533 grown under identical culture conditions. When a simple culture manipulation was performed, however, individuals of the two taxa formed nearly identical types of wall markings. Thus, it would seem that *Aphanomyces* 7533 with its cylindrical, nearly truncate ornamentations shows a closer structural alliance to *A. stellatus* than to either *A. scaber* or *A. irregulare*.

The foregoing account of morphology and structural variability in the three species of *Aphanomyces* — *scaber*, *irregulare*, *stellatus* — neither provides a dependable scheme for identifying these species with confidence, nor solves any problems surrounding their supposed close relationship. Certainly the limits of these species have had to be broadened prominently to admit the Iceland plants, and there are still numerous specimens at hand that defy identification.

A very real difficulty encountered in the study of Iceland’s representatives of *Aphanomyces* in general (and the species with ornamented oögonia in particular) has been their failure to respond to isolation and culture. Snakeskin and roach wing baits have been especially useful in collecting specimens, but the fungi so obtained have often not yielded

even to attempts at simple unifungal culture. To sort out species on the basis of plants growing in gross culture alone is futile, and any binomials attached to such individuals are highly provisional indeed.

On the basis of the meager information at hand, it would appear that the decision by Howard, *et. al.* (1970) to link *Aphanomyces irregulare* with deBary's *A. scaber* as a synonym did not solve the taxonomic questions surrounding these two species. A host of *scaber*- or *irregulare*-like forms that have come to light need to be analyzed before a final decision is made. On the other hand, present evidence suggests that *A. stellatus* — even if my Iceland specimens (isolates 2892 and 7533, in particular) are admitted to it — is a valid and recognizable taxon distinguishable from the members of the *A. scaber* and *A. irregulare* complex.

Aphanomyces sp. 2894 (Figs. 87–93)

Sporangium filamentous, isodiametric, of various lengths; segmenting directly from the apex of vegetative hyphae; 4–11 μ in diameter. Encysted planonts 9–11 μ in diameter; cysts papillate at emergence of secondary planonts. Oögonium lateral or terminal; broadly obovate or obpyriform to laterally expanded or bulged and somewhat angular; no spherical ones observed; 22–(28–33)—39 μ long by 18–(21–29)—34 μ in diameter. Oögonial wall smooth, thin, unpitted. Oögonial stalks of various lengths; straight, curved, bent, occasionally moderately twisted or irregular. Antheridial branches predominantly dichinous, infrequently monochinous; simple or branched. Antheridial cells small, clavate, curved or straight; attached apically or laterally to the oögonial wall; fertilization tubes occasionally present and persisting. Oöspore single, spherical, thick-walled; containing a large, centric or slightly eccentric oil body; not filling the oögonium; 13–(15–18)—23 μ in diameter, germination not observed. On roach wing, soil under *Equisetum arvense*, Vaglaskógur, 16 August 1970 (Herb. No. 2894).

The plants in the single collection were transferred readily to roach wing bait to form unifungal cultures, but the organism would not grow on any agar media (Johnson, 1973a) or on other types of bait. The degree of its variability is therefore unknown, and for this reason the fungus remains unnamed.

The characteristics of *Aphanomyces* sp. 2894 are, with three or four chief exceptions, not far removed from those of *A. laevis* (Scott, 1961). The spore cysts are papillate (Fig. 93) in the unnamed species, but are consistently poroid (Fig. 86) in *A. laevis*. Whether the nature of the cyst opening will prove to be an important taxonomic criterion remains to be seen. Scott thought it to be a prominent feature, and included it as one of the characteristics in the descriptions of species. The oöspores of *Aphanomyces* sp. 2894 are certainly smaller than those of *A. laevis*, and predominant oögonium shape clearly separates the two as does the small size (in *Aphanomyces* 2894) of the antheridial cells.

While *Aphanomyces* 2894 may not be allied properly to *A. laevis*, its characteristics show even less affinity to any other known species in the genus. If the nonsymmetrical nature of the oögonium and the distinctly aplerotic nature of the oöspores should prove to be persistent features of this *Aphanomyces*, it should then be set off with its own binomial. Additional specimens, propagated in various culture conditions to determine ranges of variation, need to be characterized thoroughly before a binomial is applied.

Aphanomyces sp. 6422 (Figs. 15–25)

Sporangium filamentous, isodiametric, of various lengths; segmenting from the apex of vegetative hyphae; 5–9 μ in diameter. Encysted planonts 7–9 μ in diameter; cysts poroid at emergence of the secondary planonts. Oögonium lateral, rarely terminal; predominantly pyriform or spherical, infrequently bulged laterally (asymmetrical); 14–(17–22)—33 μ in diameter. Oögonial wall smooth, thin unpitted. Oögonial stalks of various lengths;

simple or once-branched; usually curved or sinuous, and often irregular. Antheridial branches usually absent; when present, simple or once-branched, irregular, often cutting off a terminal cell without prior attachment to the oögonium wall; androgynous or monoclinal. Antheridial cells, when produced, evidently nonfunctional; clavate or expanded; fertilization tubes not observed. Oöspore single, spherical, relatively thin-walled; containing a large, conspicuous, eccentric oil globule; not filling the oögonium; 11–(15–18)–27 μ in diameter; germination not observed. On hair (bait) in soil from sheep pen, farm east of Fell, 4 September 1972 (Herb. No. 6422).

Unifungal cultures were propagated, and the organism characterized from growth on human hair (pretreated; Johnson, 1973a) in 20 ml of sterile tap water containing 0.01% potassium tellurite (incubation at 23–25° C).

With respect to the substratum on which it occurred in gross culture, this unnamed *Aphanomyces* seems to be allied to *A. keratinophilus*. However, the scarcity of antheridial branches in *Aphanomyces* sp. 6422 makes this suspected alliance much less certain. The oögonia and oöspores of this *Aphanomyces* are noticeably smaller than those usually (Okubo and Kobayasi, 1955; Seymour and Johnson, 1973b) produced by *A. keratinophilus*. In size, these structures approach what has been described (page 16, figs. 13, 14) as a form of *A. keratinophilus*. Some of the oögonia in *Aphanomyces* sp. 6422 are asymmetrical (Fig. 17), recalling a similar type in *Aphanomyces* sp. 2894. The presence of functional antheridia in the latter would seem to separate the two taxa rather effectively.

A prominent feature of *Aphanomyces* sp. 6422, and one not heretofore reported for any member of the genus, is that of the supposedly nonfunctional antheridial cells (Figs. 15, 16, 18, 21). The few antheridial cells that were seen in the various cultures were unmistakably filled with cytoplasm, even when the cell was attached to an oögonium contain-

ing a fully formed oöspore. In other water molds, of course, the antheridial cell, if it functions in the sexual process, discharges its cytoplasm, and then appears as an empty cell. Antheridial cells do appear to be cut off by a septum from branches that do not attach directly to an oögonium (Fig. 16), another apparently unique feature of this fungus.

Aphanomyces sp. 6422 will have to be characterized from pure cultures (and in a variety of environmental conditions) before it can be identified with any degree of confidence. As the fungus is currently understood, it is set off from *A. keratinophilus* solely on the basis of its antheridial apparatus.

BREVILEGNIA

Fungi belonging to this genus are surprisingly common in Iceland, even though the actual number of species seems small. *Brevilegnia unisperma* var. *montana* Coker and Braxton, *B. minutandra* Höhnk, *B. parvispora* Höhnk, *B. bispora* Couch, and some as yet unnamed representatives have been recovered (Johnson, et al., 1973; Johnson, 1974). Specimens of *Brevilegnia* usually do not appear in gross culture of Iceland soils and waters as rapidly as do other Saprolegniaceae. Often no water molds have developed on hempseed in gross cultures incubated for 2 or 3 weeks. These cultures should not be discarded as they are likely to yield the slowly-growing *Brevilegnias* with prolonged incubation.

There is at hand a specimen of a *Brevilegnia*, collected on human hair (bait), and several individuals on hempseed, that have been identified provisionally with *B. unisperma* var. *unisperma* Coker and Braxton (Coker, 1927). None of these fungi could be isolated, and none had irregular oögonia such as are usually associated with this species. It may be recalled, however, that Milanez and Bencke (1968) reported a *B. unisperma* var. *unisperma* isolate in which the oögonia were seldom irregular. The Iceland specimens might be more properly identified

with *B. bispora*. As the secondary sporangia were rare in the plants, and were not studied adequately, it is impossible to be certain of the spore discharge patterns in these various representatives of the genus. The mechanism of discharge, whether brevilegnoid exclusively, or brevilegnoid and achlyoid, still remains an important criterion needed to separate the *B. bispora* complex (Johnson, 1974) from the varieties of *B. unispërma*.

DICTYUCHUS

The mating strains of the heterothallic *Dictyuchus monosporus* Leitgeb, and the parthenogenetic strain "N" described by Couch (1936) have been reported once from Iceland (Howard, *et al.*, 1970). The latter is Nagai's (1931) *D. anomalus*.

Dictyuchus anomalus Nagai (Figs. 153–155)

A variant of this species has now been recovered (Herb. No. 3741) in Iceland. The fungus retains the chief character of *Dictyuchus anomalus*, namely, the absence of antheridia, but there are some features of the Iceland form that digress from the circumscription given by Nagai (1931).

The empty planont cysts of isolate 3741 (Figs. 153, 154) are angular, and the resulting sporangium is the true-net type. This is a broadened view of Couch's (1931) concept of the true-net sporangium since it ignores the presence of the sporangium wall as a diagnostic feature of the condition. The uncertainties existing over the interpretation of the structure of a true-net versus a false-net sporangium are reviewed elsewhere (Johnson, 1951). Padgett (communication) provides much enlightening insight into this matter also.

A prominent and not previously known feature of *Dictyuchus anomalus* (as I interpret the species from isolate 3741) is its occasional production (Fig. 155) of glomeruli (loosely- or compactly-branched oögonial stalks bearing several oögonia). In a few instances also in this variant of *D. anomalus* the oögonia are irregularly thickened on the

inner surface. Neither of these two structural features is sufficiently frequent to be of any taxonomic value beyond indicating degrees of variation in the species.

Johnson (1951) concluded that *Dictyuchus anomalus* was very likely a valid species that should not remain synonymous with Leitgeb's (1869) *D. monosporus*. He also called attention to the very close structural similarity between Nagai's species and Couch's (1931) *D. missouriensis*. Whether *D. anomalus* and *D. missouriensis* should be combined under one binomial is impossible to decide from any characterization of Iceland specimens of *Dictyuchus*. The fact that parthenogenetic fungi having characteristics consistent with those of *D. anomalus* have appeared in various parts of the world (Couch, 1936; Johnson, 1951; Howard, *et al.*, 1970) argues strongly for its recognition as a valid taxon. Convincing evidence to support or refute this view should be sought in wide-ranging compatibility studies between *D. anomalus* and the mating strains of *D. monosporus*. Padgett's (communication) discovery that sporangia with achlyoid discharge can be induced in *D. anomalus* will be of immense value in settling species limits within the genus.

Dictyuchus carpophorus Zopf
(Figs. 156–159)

Zopf's species was isolated from four samples (Herb. No. 1773, 3425, 3600, 3930), though at the time of isolation the specimens were thought to be *Dictyuchus pseudodictyon* Coker and Braxton (Couch, 1931). *Dictyuchus carpophorus* has, of course, long been (Couch, 1936; Coker and Matthews, 1937) considered to be a synonym of *D. monosporus*.

While Zopf (1893) described *Dictyuchus carpophorus* at length, he did not include certain characterizations that are now viewed as critical ones taxonomically. He clearly illustrated diclinous and monoclinous antheridial branches for his plant, and these structural features alone exclude his species from syno-

nymy with the heterothallic *D. monosporus*. Kobayasi and Konno (1971) report and illustrate androgynous antheridia for a fungus they identified as *D. monosporus*. Their specimen, obviously homothallic, must also be excluded from alliance with heterothallic species; it may perhaps be allied with *D. pseudodictyon* (*sensu* Coker, in Couch, 1931) or with *D. carpophorus*.

Dictyuchus carpophorus and *D. pseudodictyon* (*Dictyuchus* sp. of Coker and Braxton, 1926) are certainly very closely related, and may, indeed, prove to be indistinguishable from one another. *Dictyuchus pseudodictyon*, *sensu* Johnson, *et al.* (1951), is known to produce both false- and true-net sporangia (Johnson, 1951). The Iceland plants likewise form these two types of sporangia.

Precisely what limits circumscribe *D. pseudodictyon* remains an open question (Seymour, communication). Johnson's (1951) *Dictyuchus* 521 was subsequently (Johnson, *et al.*, 1951) identified as *D. pseudodictyon*, and the description of *Dictyuchus* 521 taken as that of the named species. This circumscription, if accepted as that of *D. pseudodictyon*, separates that species adequately from *D. carpophorus*. Seymour (communication) maintains that *Dictyuchus* 521 has been incorrectly identified, and deserves a new binomial.

Three fungi (Herb. No. 1452, 3411, 3585) from Iceland have been identified with *Dictyuchus* 521 (which would require that they be named *D. pseudodictyon* in conformity with the decision reached by Johnson and his associates in 1951). These isolates, however, have less profusely branched antheridial filaments than is the case in *D. pseudodictyon* (as that species is interpreted by Johnson, *et al.*, 1951). Clearly, these three isolates of *Dictyuchus* 521 approach *D. carpophorus* equally as strongly as they do the original (and more restrictive) concept of *D. pseudodictyon*.

Pending an evaluation of Seymour's ultimate disposition of *Dictyuchus* 521, I am

not formally proposing that *D. pseudodictyon* and *D. carpophorus* are synonymous species. Should future evidence overwhelmingly support the view that *Dictyuchus* 521 is not representative of *D. pseudodictyon*, the limits of this latter species will revert to those more restrictive ones recognized by Coker and Braxton. In such an instance there is little to be said for maintaining *D. pseudodictyon* separate from *D. carpophorus*.

The characteristics of the Iceland specimens are ample evidence that *Dictyuchus carpophorus* cannot continue to reside as a synonym of a heterothallic species. Zopf's species is therefore reinstated irrespective of whether or not it will in time be shown to include *D. pseudodictyon*.

SAPROLEGNIA

Ten species of this genus found in Iceland were treated in a reasonably detailed fashion elsewhere (Howard, *et al.*, 1970). Two additional species have been recovered in this country.

Saprolegnia furcata Maurizio (Figs. 160–162)

This fungus is apparently rather rare, and has only been found in water samples generously mixed with decaying vegetation from mossy, bog-like areas. The species is easily recognized by the spherical to pyriform, smooth-walled oögonia that are often borne on coiled stalks. Monoclinous antheridial branches are equally as abundant as androgynous ones (Seymour, 1970).

Saprolegnia parasitica Coker

Species of *Achlya* occur on dead or diseased fish (fry or fingerlings) in the Kollafjörður hatchery, but only one *Saprolegnia* (Herb. No. 3177) has been isolated from this substratum. Because the fungus produced only sporangia and gemmae, its identity as *S. parasitica* has had to be based largely on habitat. Seymour (1970) commented that the identification of all fish-inhabiting, nonoögonial species of *Saprolegnia* as *S. parasitica* had to be viewed with skepticism.

THRAUSTOTHECA

Thraustotheca clavata (deBary) Humphrey
(Figs. 163–166)

This easily recognized species is by no means common in Iceland. With three exceptions, it has been collected most often at Kollafjörður, in soil, debris, and water from the edges of rearing ponds. Aside from the very stout, short, clavate to broad-cylindrical sporangia, this species may be recognized by its exclusively declinous antheridial branches. These filaments are very often branched abundantly (Fig. 166) even when not applied directly to any adjacent oogonium.

Thraustochytriaceae

Fungi in this family are easily recovered on heat-sterilized pine pollen from sea water, marine muds and sands, and from the surfaces of thallose marine algae. Samples are placed in sterile Petri plates, and sufficient sterile seawater added to bring the content half-full. Pollen is then sprinkled generously on the surface of the gross culture water, and the dishes incubated at room temperature. Within 3–5 days the cultures usually yield thraustochytriaceous fungi.

Members of the Thraustochytriaceae are relatively easy to isolate, and several media (Gaertner, 1970a) have been used by various investigators. The formulations devised by Booth and Miller (1968), Goldstein (1963a, 1963b), and Goldstein and Belsky (1964) give consistently the best results, particularly if 0.1% potassium tellurite is added as a bacterial suppressant (Willoughby, 1958) prior to sterilization.

SCHIZOCHYTRIUM

This genus should not be retained in the family Thraustochytriaceae as Sparrow (1968b) remarks. Pending a thorough analysis of that family to determine taxon limits, however, continued temporary assignment of the genus here is advisable.

Schizochytrium aggregatum Goldstein and Belsky (Figs. 236–237)

This species is by far the most common of the “thraustochytriaceous” fungi to occur on pollen baited in dishes of thallose algae, and less so in sediments. The fungus is easily recognized by its unique growth pattern: an epiendobiotic thallus that divides into diads, triads, or tetrads to form large clusters of sporangia. From these sporangia the planonts escape through an irregular fissure in the wall (Goldstein and Belsky, 1964). Booth and Miller (1969) have shown that planonts can be released from sporangia in the monad stage.

See also, remarks under *Thraustochytrium* (?)*aggregatum*.

THRAUSTOCHYTRIUM

The very rapid development in the 1960s in knowledge of *Thraustochytrium* led to the description of ten species in addition to the one first described by Sparrow in 1936 (*T. proliferum*). Unfortunately, a few of these species are remarkably similar to one another, and investigators (Booth and Miller, 1968; Konno, 1972) have questioned the validity of some named entities.

Eight of the described species of *Thraustochytrium* have been isolated from coastal habitats in Iceland, but at least one of these is a highly dubious identification. Plants identified with the remaining three species have been seen in the various collections from time to time, but are excluded from consideration because they have not been isolated.

Gaertner (1968) was the first to report thraustochytriaceous fungi from waters and sediments off Iceland, although he actually used few samples in his determinations. The *Thraustochytrium* sp. reported by Johnson (1968) as a possible variant of *T. proliferum* has not been again recovered, and remains unidentified.

Thraustochytrium (?)*aggregatum* Ulken
(Figs. 234, 235)

Small, spherical or subspherical sporangia

clustered on the substratum (Fig. 234) in rather sparse numbers have been identified as *Thraustochytrium aggregatum* (Ulken, 1965). It is exceedingly difficult to distinguish nonsporulating thalli of this species from small sporangia of *T. aureum* (Fig. 222), and several collections of Ulken's species are consequently suspect.

The method of sporangium formation — by cleavage of an enlarging sporangium initial (Gaertner, 1972a) — is evidently a critical characteristic for the identification of *Thraustochytrium aggregatum*. In this pattern of thallus development, most sporangia in an aggregate are the result of cleavage from other, previously-formed ones. Usually such aggregates are tetrads. I have not been able to follow successively the described manner of sporangial origin in any of my collections alleged to be this species.

Whether the sporangia of *Thraustochytrium aggregatum* are single or in aggregate clusters, they have precisely the same discharge pattern (Gaertner, 1972b): the release of fully motile spores through a pore-like orifice. The mechanism in *T. aureum* Goldstein is similar, save that in Goldstein's species the sporangium usually possesses a basal proliferation rudiment visible at discharge (see discussion, next species). It should be noted that Gaertner had illustrated planont discharge for *T. aggregatum* in quite a different fashion: release of motile spores upon deliquescence of the sporangium wall. In my specimens, planont discharge was rare, but when it occurred, the motile cells were released through a large, irregular fissure in the sporangium wall. Such a mechanism clearly points to the affinity of my material to *Schizochytrium aggregatum*, and not to *T. aggregatum*. In a very few instances, more than half of the sporangium wall was ruptured as the discharge process began. Such cases, of course, approached the mechanism of release through dissolution that Gaertner, for example, attributed to *T. aggregatum*.

An analysis of the structure and behavior of my Iceland plants suggests that they are

very likely not specimens of *Thraustochytrium aggregatum*. Moreover, the past interpretations of this species show considerable conflict at rather critical points as to the actual structure of the fungi that have been identified with Ulken's species. My specimens are provisionally allied to *T. aggregatum* for two reasons. First, the aggregate and individual sporangia are larger than those usually encountered in *Schizochytrium aggregatum*. Second, the aggregates contain noticeably fewer thalli than do those of the *Schizochytrium* in culture 5–7 days old.

Thraustochytrium aureum Goldstein
(Figs. 221, 222)

Epibiotic, faintly pigmented sporangia (bronze to pale yellow) that were spherical, discharged planonts through a pore dissolved in the wall (Fig. 222), and produced a basal endogenous rudiment from which internal proliferation occurred were identified as this species (Goldstein, 1963a). As Sparrow (1968b) remarks, *Thraustochytrium aureum* has a chytrid-like habit: the sporangium wall persists, a discharge orifice is produced, and the planonts assume motility within the sporangium. Whether this species and a very closely allied one (structurally), *T. motivum* Goldstein (1963b), are truly separate taxa is doubtful.

Thraustochytrium motivum, as originally defined, was supposedly distinguishable from *T. aureum* largely (if not solely) on the basis of the discharge mechanism. In *T. motivum* the sporangia opened by an irregular fissure in contrast to the poroid orifice formed in *T. aureum*. Both species are alike, certainly, in sporangium shape, persistent wall, endogenous motility of the spores prior to release, and the formation of a basal sporangium rudiment ("proliferation body").

Booth and Miller (1968), investigating a number of isolates of the genus *Thraustochytrium*, concluded that the characteristics used to separate *T. aureum* and *T. motivum* (Goldstein, 1963b) were quite variable, and thus of questionable diagnostic

value. Pigmentation, for example, showed an unmistakable clinal tendency among the isolates, as did the nature of sporangium dehiscence. Booth and Miller chose not to make specific taxonomic changes; they concluded simply that these species were two elements of a single complex. Konno (1969) concurred with this decision, but the evidence, I believe, would support a formal merger of the two species.

Thraustochytrium kinnei Gaertner
(Figs. 223, 224)

There are evidently two types of sporangia produced by this species. In the original account, Gaertner (1967) described a thin-walled form and its spore release pattern. The planonts, motile when freed from the sporangium, were discharged upon dissolution of the confining wall. A basal proliferation rudiment was present at the time of discharge. As late as 1972(b), Gaertner described this pattern as the only one for *Thraustochytrium kinnei*. Discharged sporangia of this thin-walled type (Gaertner, 1967) are suspiciously like those of *T. proliferum*. In that species, however, the spores are nonmotile at discharge (motile in *T. kinnei*).

The second type of discharge, that involving a thick-walled sporangium, was described and illustrated for *Thraustochytrium kinnei* in 1970(b), by Gaertner. In this form of the fungus, the mechanism involved the separation of a thick-walled upper portion of the sporangium (Fig. 223) from a lower, thinner-walled segment. The endogenously formed planonts (fig. 223) were released in a mass from the disintegrating sporangium, floated free (Fig. 224), and then assumed motility. Only this type of discharge pattern was observed in the Iceland specimens. Curiously, the method did not persist in sporangia in culture, and thalli in successively transferred subcultures failed to sporulate at all within three or four "generations". This suggests, of course, that the form with thick-walled sporangia is an aberrant one, and is hardly typical of the species.

Thraustochytrium kinnei remains in need of precise definition.

Thraustochytrium multirudimentale
Goldstein (Fig. 233)

The species is easily recognized by the production of 2–4 basal rudiments in the sporangium (Fig. 233). In each instance of sporangium discharge observed in the specimens at hand, planonts escaped as a slowly moving mass of cells through a large, irregular fissure in the sporangium wall. This appears to be the pattern characteristic of the species (Goldstein, 1963b).

Thraustochytrium pachydermum Scholz
(Figs. 230–232)

Substantial variations occur (Figs. 230, 231) in the thickness of the sporangium wall in the species. Scholz (1958) related this variability to salinity, but in my specimens, variations often occurred in cultures at a single salinity level. The sporangium wall disintegrates (dissolves?) fully to release spores that are latent in assuming motility. There are no basal rudiments, and Konno's report (1969) of this species in which some individuals produced such proliferation bodies is at variance with the generally accepted circumscription of the species.

Thraustochytrium pachydermum has been found by Sparrow (1968a) in an inland saline pool (Death Valley, California). The fungus is evidently common in coastal sands, but I have collected it most often in muddy sediments, or have isolated it from the surfaces of marine thallose algae.

Two other species, *Thraustochytrium roseum* and *T. visurgense*, also have thick-walled sporangia.

Thraustochytrium proliferum Sparrow
(Figs. 217, 218)

This species is not commonly collected on pollen bait in cultures of sea water or marine sediments of Iceland. I have found the fungus occasionally by baiting dishes of sea water containing algae.

As has been reported elsewhere (Sparrow, 1936; Johnson, 1957) the spores are released as nonmotile, somewhat angular cells, through partial deliquescence of the sporangium wall (Fig. 218). The basal endogenous rudiment (proliferating sporangium) in this species is usually larger and more conspicuous prior to planont discharge than in any other *Thraustochytrium* producing such structures.

Thraustochytrium roseum Goldstein
(Figs. 219, 220)

The planonts of Iceland fungi assigned to this species are fully formed (Fig. 219) within the sporangium, and assume motility only after most of the group of cells has been liberated by the disintegration of the thickened sporangium wall (Fig. 220). There is no basal proliferation body (Goldstein, 1963c). In my specimens, at least, a substantial portion of the sporangium wall (Fig. 220) persists after the spores have been released.

Further remarks on this species are found in the account to follow.

Thraustochytrium visurgense Ulken
(Figs. 225–229)

The immature sporangia in the Iceland collections are globose or subglobose, and thin-walled (Figs. 225, 226). The sporangium wall appears to thicken (Fig. 227) coincident with the onset of its dissolution and the emergence of the protoplast (Figs. 227, 228). As the sporangium wall dissolves, the partially released protoplast cleaves into planonts (Figs. 228, 229) that subsequently become motile and swim sluggishly away. In my specimens, only a small, basal remnant of the sporangium wall remains after discharge, and there is no internal proliferation such as is found in some other species in the genus.

The discharge sequence in the Iceland plants follows very closely that figured and described by Gaertner (1972a, b). Ulken (1965), however, had described planont cleavage as occurring within the intact sporangium, and the spores assumed motility at a

much earlier stage in planont emergence than I find in the Iceland material.

Ulken (1965) cited sporangium wall thickness as one of the major characteristics separating her species from the closely allied *Thraustochytrium roseum*. Booth and Miller (1968), in a study of seven isolates in this complex of two species, found some specimens with thin-walled sporangia, and, in fact, by manipulation of culture conditions could induce the plants to respond with various wall thicknesses. They noted also that their isolates discharged planonts either in the fashion of *T. visurgense* or in the manner attributed to *T. roseum*. Pigmentation and the nature of the rhizoidal system, Booth and Miller observed, were also variable and could be modified by culture environment. On the basis of evidence thus accumulated by their extensive analysis of isolates, they concluded that *T. roseum* and *T. visurgense* was a species complex. Of this, they wrote (Booth and Miller, 1968: 495) that *T. visurgense* "... may consequently be considered synonymous with *T. roseum*." A formal proposal was not offered, and Konno did not (1969) accept their conclusion regarding these two species.

The specimens from Iceland add nothing to support the conclusion reached by Booth and Miller. In pine pollen cultures, my specimens did not show the degree of variation noted by these two investigators for their fungi. It should be emphasized, however, that I did not subject my plants to the extensive culture manipulations which they employed. I have maintained *Thraustochytrium visurgense* and *T. roseum* as separate species solely on the basis of planont behavior in my collections: cleaved within the intact sporangium in the latter (Fig. 219), but forming coincidentally with sporangium wall disintegration (Figs. 228, 229) in the former. Admittedly, the evidence from the study by Booth and Miller rather explicitly refutes the value of this characteristic for species separation.

LEPTOMITALES

Leptomitaceae

An *Apodachlya*, provisionally identified as *A. pyrifera* Zopf, was collected earlier (Howard and Johnson, 1969) on pine pollen. It has not again been recovered, and its identity remains unknown.

LEPTOMITUS

Leptomitus lacteus (Roth) Agardh
Figs. 201,202)

This readily recognizable filamentous fungus with the noticeably constricted hyphae (Fig. 202) has been found repeatedly (on hempseed bait) in water and debris from rearing and holding ponds at Kollafjörður. Large, whitish masses of the hyphae of this fungus may also occur at the edge of some fish ponds, on obviously decaying grass leaves.

Rhipidiaceae

SAPROMYCES

Sapromyces sp. (Fig. 195)

Known from one collection (Herb. No. 1770) on an apple submerged near Öxará (Thingvallavatn). No sexual apparatus was evident on any of the specimens, though the whorls of apically positioned sporangia (Fig. 195) mark the fungus as a member of this genus. The substratum suggests that the fungus is *Sapromyces elongatus* (Cornu) Coker, but this is conjecture only.

RHIPIDIUM

Rhipidium americanum Thaxter (Fig. 194)

Rhipidium americanum is not common in Iceland, and is apparently sporadic in its occurrence. Apple traps (Sparrow, 1960; Johnson, 1973a) placed in a suitable location one year (as, for example, in the deep streams north of Thingvallavatn) may support luxurious growth of this species. Fruits submerged in the same locality in the following year may well be barren of this fungus. The pustules composed of plants of *R. americanum* are often hidden by dense mats of hyphae of *Pythium* species (or, in some cases, by filaments of *Achlya radiosa*) also growing profusely on submerged apples.

The individual plants of this species are exceptionally variable in the general aspect of the basal cell. While this portion of the thallus is generally thick and stout (Fig. 194), some thalli merely consist of a slender, branched or unbranched, hypha-like basal cell.

Some plants of *Rhipidium americanum* can be mistaken for those of *Araiospora* (Sparrow, 1960) unless care is taken to determine the structure of the oöspores. In *R. americanum* the oöspores are areolate in surface view (stellate in optical section), but in *Araiospora* species the oöspore is provided peripherally with a cellular envelope. *Rhipidium* species do not produce ornamented sporangia as do fungi assigned to *Araiospora*.

LAGENIDIALES

Olpidiopsidaceae

Höhnk (1960) reported *Petersenia irregularis* (Constantineanu) Sparrow (see Sparrow, 1960), and *Olpidiopsis pythii* (Butler) Karling from samples in southwestern Iceland. Neither has again been recovered. The *Petersenia* mentioned by Johnson (1968) likewise has not appeared in any collections, and is therefore an unconfirmed report of a member of this genus. A treatment of several species of *Olpidiopsis* from Iceland was published (Johnson) in 1972; three species had earlier been recovered (Johnson, 1968; Johnson and Howard, 1968).

OLPIDIOPSIS

Olpidiopsis fusiformis Cornu (Figs. 172–174)

In 1972, I reported as a member of the *Olpidiopsis achlyae*-*O. fusiformis* complex a fungus that produced ellipsoidal or cylindrical, spiny, warted, or slightly papillate sporangia. The oval or ellipsoidal resting spores of this fungus were sparingly ornamented, and were occasionally accompanied by ornamented companion cells. *Olpidiopsis fusiformis*, it was noted (Johnson, 1972), was not known to produce warted or papillate sporangia, nor did it form ornamented companion cells. On the basis of the plants at hand, I could not identify the specimens

other than to relate them to the *O. achlyae-O. fusiformis* complex. McLarty's (1941) *O. achlyae* occasionally produced resting spores with a fibrillar, serrate, or undulant wall; this feature alone appeared to be (Johnson, 1972) the only one separating this species from *O. fusiformis*. It may be recalled that McLarty (1941) was unsure of the identity of his *O. achlyae* since he pointed out that it might be referable to *O. fusiformis*. Both fungi, of course, invade only species of *Achlya* so far as is known.

On several occasions I have found endobiotic thalli of an *Olpidiopsis* in *Achlya americana* and in an unidentified *Achlya* (with eccentric oöspores). Some characteristics of these specimens of *Olpidiopsis* digress sharply from those of the fungus reported earlier (Johnson, 1972) as a member of the *O. achlyae-O. fusiformis* group.

In some infected hyphae the very abundant sporangia are small — 20—(31—44)—57 μ long by 16—(22—29)—39 μ in diameter — and ellipsoidal, ovoid, or nearly spherical (Fig. 172). Small, densely spiny, nearly spherical resting spores with smooth-walled companion cells accompanied the small sporangia in my material (Fig. 172). No such sporangia or resting spores were found among the specimens reported earlier in the *O. achlyae-O. fusiformis* complex (Johnson, 1972).

Other infected hyphae of *Achlya* contained very large, cylindrical to ellipsoidal, smooth-walled sporangia (Fig. 173): 130—(228—270)—340 μ long by 41—(55—66)—83 μ in diameter. Accompanying these sporangia were subspherical to broadly ovoid, densely spiny resting spores (Fig. 174) indistinguishable from those found in association with the small sporangia (Fig. 172). These resting spores were also provided with smooth-walled companion cells (Fig. 174).

From his specimens, Shanor (1939) illustrated small ellipsoidal sporangia, referred them to *Olpidiopsis minor* Fischer, and then reduced this species to synonymy with Cornu's *O. fusiformis*. The small sporangia (Fig. 172) I find in *Achlyas* from Iceland are

identical (in general aspect, at least) to the individuals Shanor identified with *O. minor*. Shanor's illustrations (1939) of *O. fusiformis* show large, ellipsoidal sporangia, some smooth-walled and some ornamented. My specimens in *Achlya americana* (Fig. 173) have smooth sporangia; the fungi reported earlier (Johnson, 1972) as *O. achlyae-O. fusiformis* possessed ornamented sporangia.

The *Olpidiopsis* in *Achlya americana* and in the eccentric-egged *Achlya* is obviously more closely allied to Shanor's (1939) concept of *O. fusiformis* than was the specimen (in a nonsexual *Achlya*) I assigned earlier (Johnson, 1972) to the *O. achlyae-O. fusiformis* group. Either *O. fusiformis* is an exceptionally variable fungus, or it is in reality a species complex that, as it is now understood (Shanor, 1939), includes more than one taxon. The problem of correct identification cannot be solved until proper culture techniques are devised. Two-member cultures consisting of host plant and parasite propagated from single spores will provide the only condition under which the morphology of these individuals of *Olpidiopsis* can be accurately characterized.

Olpidiopsis (?) *saprolegniae* var. *saprolegniae* (Braun) Cornu (Figs. 169—171)

Plants in one collection (Herb. No. 6144) of *Saprolegnia ferax* (Gruith.) Thuret were invaded by an *Olpidiopsis* with exceptionally variable resting spore wall markings. The sporangial characteristics of the parasite were comparable in all respects to those generally found expressed by *O. saprolegniae* var. *saprolegniae*.

The resting spores (Figs. 169—171) of the *Olpidiopsis* were spherical to broadly ovoid, and 26—(40—58)—74 μ in diameter. One or two spherical or subspherical, hyaline, thin-walled companion cells, 13—(16—20)—29 μ in diameter, accompanied the resting spores. Some resting spores were provided with slender spines (Fig. 170) that were often curved (Fig. 171). Others in the same hypertrophied hyphal tip had small, inconspicuous spines

(Fig. 170, top) or were provided with a minutely serrate wall (Fig. 171, top). In still other instances, resting spores with a serrate wall (Fig. 169, top) were accompanied by ones with only scattered patches of minute serrations (Fig. 169, lower).

Although resting spores with minute serrations occur in the same hyphal tip with those having distinct spines, the possibility of two species of *Olpidiopsis* being involved cannot be ruled out. Single spore, two-member cultures will have to be prepared and studied to provide accurate characterization of the fungus. Those resting spores having long, slender spines are, of course, quite characteristic of the usual circumscription (Sparrow, 1960) of *O. saprolegnia* var. *saprolegniae*.

In 1972 I collected several specimens (from five localities) of *Saprolegnia ferax* infected by an *Olpidiopsis*. The parasite was initially identified as *O. luxurians* Barrett (Sparrow, 1960; Shanor, 1939; Barrett, 1912) because of the nature of its resting spore wall ornamentations. These structures were small, broad, sharply pointed spines 2.2–3.5 μ long. Those resting spores covered by the very short spines were identical to those figured by Barrett and Shanor for *O. luxurians*. Shanor (1940) verified Barrett's contention that *O. luxurians* was limited to species of *Aphanomyces*. This being the case, I am forced to conclude that the thalli in *S. ferax* cannot be identified as those of *O. luxurians*. Nevertheless, the occurrence in a *Saprolegnia* of resting spores indistinguishable from those of Barrett's species raises some doubt about the alleged restriction of *O. luxurians* to *Aphanomyces*.

Olpidiopsis sp. (Figs. 167, 168)

An unnamed *Olpidiopsis* in the hyphae of a non-ooogonial *Achlya* and in *Saprolegnia turfosa* (Minden) Gäumann was reported by me in 1972. The fungi in these two water molds did not survive subculturing, but their gross morphology was similar enough to consider them the same species despite the differences in host. An *Olpidiopsis* has again been col-

lected (Herb. No. 3135) in *S. turfosa*. The characteristics of this endobiotic fungus agree in all respects with those of the specimens in the earlier collection (Johnson, 1972) with one exception. In specimen 3135 the resting spore ornamentations are broad, shallow, and truncate (Fig. 168); the resting spore wall of the individuals found previously (Johnson, 1972: figs. 15, 16) was wavy or undulant.

Two species of *Olpidiopsis* may, in fact, occur in *Saprolegnia turfosa*. This possibility remains to be explored and settled by observations on properly cultured material.

Sirolpidiaceae

Pontisma lagenidioides Petersen and *Sirolpidium bryopsisidis* (deBruyne) Petersen were found once, in algae, in Iceland's coastal waters (Johnson, 1968). Later, two additional species, *P. lobata* (Petersen) Sparrow and *P. pollagaster* (Petersen) Sparrow, were also reported (Johnson and Howard, 1968). None of these species has appeared in any subsequent collections.

Lagenidiaceae

Representatives of two genera, *Lagenidium* Schenk and *Myzocyttium* Schenk, have been reported from Iceland (Johnson, 1968; Johnson and Howard, 1968).

MYZOCYTTIUM

Myzocyttium proliferum Schenk was found (Johnson and Howard, 1968) in *Spirogyra*. The plants in this collection differed from Schenk's species in one feature only, namely, the occasional production of two discharge tubes. A single discharge tube is characteristic of the species.

Specimens in a second collection (Herb. No. 3593) of *Myzocyttium proliferum*, also in *Spirogyra*, have somewhat longer sporangia than previous descriptive matter indicates is characteristic of the species. Each sporangium has but a single discharge tube.

LAGENIDIUM

The one species previously reported (John-

son, 1968) from Iceland was provisionally allied with *Lagenidium pythii* Whiffen, but not specifically identified as such. A non-öogonial *Lagenidium* has appeared in a second *Pythium* sp. (filamentous sporangium group), but could not be identified. Some additional species of *Lagenidium* (none with a sexual apparatus) have been collected in the soft parts of mites and on termite wings used as bait. In the absence of öogonia and antheridia, these fungi could not be identified, and none yielded to attempts at culturing either on agar media or on additional bait. In one gross culture (No. 3005) baited with termite wings, I found spherical resting spores (9–14 μ in diameter) associated with lagenidiaceous sporangia. Fungi from this bait could not be cultured, and there is no way to be certain that the sporangia and resting spores were of a single species.

Lagenidium (?) *destruens* Sparrow
(Figs. 185, 186)

Thallus intramatrical, tubular and irregular with lobes or short branches; 8–(12–19)–27 μ in diameter; cytoplasm containing numerous irregular refractive inclusions; converting into sporangia by segmentation. Sporangia cylindrical to irregular, lobed, or branched; forming a single cylindrical to broadly or narrowly conical discharge tube; 18–(26–38)–66 μ long by 8–(12–19)–27 μ in diameter. Planonts reniform; exogenously formed in a thin, delicate vesicle; 10–(11–13)–14 x 4–(7)–9 μ in diameter. Sexual apparatus unknown.

The fungus characterized in the foregoing description caused hypertrophy in specimens of a nonöogonial *Saprolegnia* sp. (Herb. No. 1944, 5729, 6479, 8715). Sterile hempseed was added to potassium tellurite water (0.01%) in dishes containing infected, sporulating colonies of the watermold and the *Lagenidium*. The resulting new colonies of the *Saprolegnia* were uninfected. Infected hyphae were planted on various nutrient agars, and subsequently the host was transferred to hempseed in water, but again only uninfected plants developed.

Short of the fact that the *Lagenidium* causes hypertrophy of invaded plants, there is little to ally it to Sparrow's (1950) species. The thallus of *L. destruens* evidently converts at maturity before sporulation into a single sporangium. Single thalli of the Iceland plants, by contrast, develop into several sporangia. In *L. destruens* the planonts cleave exogenously in the absence of a vesicle, but an enveloping, vesicular structure is clearly visible (Fig. 186) in the specimens from Iceland. Thick-walled resting spores are formed by *L. destruens*, but neither resting spores nor a sexual apparatus were present in any thalli in my collections.

Because the thallus of the *Lagenidium* in *Saprolegnia* sp. forms more than one sporangium at maturity, its proper identity with *L. destruens* is doubtful. The discovery of resting spores in future collections of the Iceland fungus might shed light on the matter of identification. Certainly nothing would be gained by creating a new benomial based on a plant that has not been fully characterized.

Lagenidium entophytum (Pringsheim) Zopf
(Figs. 175–178)

This species has appeared in three collections of *Spirogyra*, all from the same general locality in Iceland. Some characteristics of the fungi I have found are in disagreement with the usual circumscription (Sparrow, 1960) of the species.

The öospores of the Iceland plants are sometimes subspherical (Fig. 175) and measure 11–(13–17)–21 μ long by 8–(10–12)–15 μ in diameter. Only spherical öospores have been reported (Sparrow, 1960; Karling, 1942) for *Lagenidium entophytum*. While the öospores produced by my specimens lie loosely in an irregular (or lobed) tubular segment of the thallus (Fig. 175), they are warted as often as they are dentate. Only öospores of the latter type have heretofore been reported for the species. More than one discharge tube (Fig. 176) can be produced by the fungus at hand, but in such instances only one appears to function in discharge. Karling (1942)

reports multiple tubes for *L. entophytum*, while Sparrow's (1960) description accords to the species a single discharge tube.

The discharge tube in *Lagenidium entophytum* is described (Sparrow, 1960) as being constricted at the point of its passage through the host wall and locally swollen. My specimens lack this feature, and Zopf's account (1884) seems to indicate that this characteristic is an inconstant one. I find the exit tubes in the Iceland specimens to be more irregular and twisted (Figs. 177, 178) than is evidently (Zopf, 1884; Sparrow, 1960) characteristic of the species. In none of the instances of planont cleavage (Figs. 177, 178) by my plants was a vesicle produced. Other investigators have expressed some doubt that a vesicle is formed (at least generally) in *L. entophytum*.

Lagenidium (?)*humanum* Karling

A *Lagenidium* that is possibly Karling's species was collected once (Herb. No. 11713) on human skin (bait) in a sample of water and debris from a coastal bog area. The water level in this bog fluctuates with the rise and fall of the adjacent tidal waters, but there is no mixing of salt and freshwater at the surface. The peripheral vegetation (mosses, grass, and some ferns) is terrestrial in character.

The few sparse thalli on the bait in gross culture consisted of branched or lobed sporangial segments each with a single, sometimes sinuous discharge tube. In general aspect and size, the sporangia were remarkably like those described by Karling (1947). At discharge the protoplast cleaved external to the exit orifice to form planonts in a vesicle. There were no resting spores or any evidence of a sexual apparatus.

I was unable to propagate the fungus and thereby separate it from accompanying chytrids and a filamentous watermold on the same bits of substratum. Accordingly, its identity with Karling's species is entirely provisional. Clusters of sporangia planted on YPSS agar (with potassium tellurite) failed to grow further, and planonts streaked on the agar

surface did not germinate. Karling (1947) propagated *Lagenidium humanum* on peptone-dextrose-yeast extract agar, but the fungus from Iceland would not grow on a similar medium.

Lagenidium pygmaeum Zopf
(Figs. 179--184)

It is likely that this species is very common in marshy soils and in pasture lands in Iceland. The fungus can be identified in pollen only when it sporulates, and complete characterization of the species can be made only from cultured specimens. In pollen, the immature or discharged sporangia (Figs. 179, 180, 183) are remarkably like those of certain species of *Olpidium* (Johnson, 1969), and can be easily mistaken for those of *Entophlyctis conervae-glomeratae* (Cienowski) Sparrow which also occurs in pollen (Johnson, 1973a).

Lagenidium pygmaeum can be grown in unifungal culture, in pollen, by a successive transfer and replicating technique. A pollen grain showing a sporangium with an intact extramatrical vesicle (in which spore units are in the process of cleaving) is separated from gross culture and transferred to a drop of potassium tellurite soil extract (see discussion of *Achlya debaryana* for the method of preparation) on a glass slide. Heat-sterilized pollen is then sprinkled onto this drop of water, and the slide is incubated in a damp chamber for five days. Individual grains of pollen containing sporangia showing the vesicular, lagenidiaceous type of discharge are removed from this slide culture, and transferred to soil extract — potassium tellurite water on additional slides (one grain per drop). These slides are also incubated for five days, and the process repeated for a third time.

From the third set of slide cultures, an individual pollen grain containing sporangia is transferred to 1 ml of sterile soil extract-potassium tellurite in the bottom of a sterile, plastic Petri plate. Sterile pollen is seeded heavily on the surface of the water, and 24--

36 hours later, 20 ml of sterile soil extract is poured into the dish. Within 3–5 days, heavy growth of the *Lagenidium* can be expected.

Lagenidium rabenhorstii Zopf
(Figs. 187, 188)

Collected once, in *Spirogyra* sp. (Herb. No. 3086), near the eastern entrance to Heidmörk. The characteristics of the fungus agree rather closely with those given in the description by Sparrow (1960). In all observed instances of protoplast discharge from the sporangium a vesicle was formed.

Lagenidium sp. (Figs. 189–191)

Thallus long, cylindrical, hypha-like, sinuous or curved, generally without lobes or irregularities, but often prolonged into extensions that become sporangium discharge tubes. Sporangia produced by segmentation of the thallus; cylindrical, straight, curved, or slightly irregular; separated from each other by a conspicuous constriction; producing one terminal, eccentric or centric discharge tube, this being usually long and curved or sinuous, and often merely an extended portion of the end of sporangium, and projecting slightly beyond the host wall but not constricted as it passes through the wall; 15–(25–38)–47 μ long (exclusive of any terminal exit tube) by 5–10–(14)–23 μ in diameter. Planons reniform; formed in a vesicle at the orifice of a discharge tube; 6–9 μ long by 4–6 μ in diameter. Male gametangium sporangium-like, or crook-necked; fertilization tube present but evidently not persisting. Female gametangium broadly dolioform or expanded centrally, occasionally irregular or broadly fusiform; intercalary; 20–30 μ in diameter at widest point. Oöspore single; lying loosely in the female gametangium; spherical, wall thick and provided with short, broad spines; cytoplasm containing a centric or eccentric globule; 17–26 μ in diameter; germination not observed.

In *Ulothrix* sp., pool at east entrance to Heidmörk, 27 August 1971 (Herb. No. 3088).

Only one rather sparse collection has been

made of this *Lagenidium*, and the fungus has not again appeared in any subsequent collections from Heidmörk or any other site where *Ulothrix* species occur. Although the plants were reasonably well characterized, nothing is known of their variability hence I have chosen not to apply a binomial.

The general configuration of the sexual apparatus (Figs. 189, 190) of this *Lagenidium* very closely resembles that of *L. rabenhorstii* (Fig. 187). The oöspores are ornamented, however, and thus contrast prominently with the smooth-walled ones produced by Zopf's species. Sporangium shape (Figs. 189, 191) in this *Lagenidium* in *Ulothrix* also digresses from that in *L. rabenhorstii*. The sporangia in the unnamed *Lagenidium* are more elongate and more slender than those of *L. rabenhorstii*, and are not as irregular (compare Figs. 187, 189).

None of the species of *Lagenidium* known to occur in algae would appear to accommodate this one from Iceland. Characterization of additional, more abundant material is needed before the fungus can be identified properly. Perhaps this *Lagenidium* is best considered as a form of *L. rabenhorstii* with ornamented oöspores. This possible disposition cannot be proposed formally until something is known of the stability of the ornamentations.

PERONOSPORALES

Pythiaceae

Several species of *Pythium* have been reported from Iceland (Höhnk, 1960; Howard, 1968; Johnson, 1971). Howard (1968) also collected a *Pythiogeton* on pollen bait. He did not name the species, and no representatives of the genus have again appeared in any of the collections. Höhnk (1960) collected *Pythiogeton ramosum* Minden in Greenland, but failed to find it in samples from Iceland.

PYTHIUM

Members of this genus are particularly

common in Iceland, but the majority of its representatives lack a sexual apparatus and therefore cannot be identified as particular species. Johnson's (1971) account of the genus in Iceland included all species previously known to occur in this country, with one exception. Höhnk (1960) reported — without description or illustrations — *Pythium hypogynum* (Middleton, 1943).

Pythium echinulatum Matthews
(Figs. 196–200)

One specimen, referred to this species with reservation, has been collected (Johnson, 1971) in Iceland. Two additional collections (Herb. No. 7764, 9057) of a *Pythium* much like the earlier plant have been made. These fungi were characterized in hempseed culture (40 ml sterile tap water, 25° C incubation). Their structure is such that they, too, can only be provisionally allied with Matthews' species. Moreover, the two isolates (7764 and 9057) have features in common with several other members of the genus with ornamented oogonia. The chief characteristics of these two isolates are incorporated in the following description.

Sporangium spherical to subspherical, rarely broadly cylindrical; terminal, rarely intercalary, not catenulate; producing a single, terminal, subterminal or (rarely) lateral discharge tube of variable length; 11–(16–23)–37 μ in diameter. Oogonium lateral, occasionally terminal; spherical, infrequently ovoid or broadly and bluntly ellipsoidal; wall sparsely or densely ornamented with narrowly or broadly conical, bluntly rounded papillae or with short or long, slender, sharply pointed spines; ornamentations 3–(5–7)–13 μ long; 12–(18–22)–31 μ in diameter, exclusive of the ornamentations. Antheridial branches usually formed; androgynous or monoclinal; slender, slightly irregular, rarely branched; antheridial cell small, slightly expanded, straight or bent, laterally or apically appressed. Oospores 1–(1)–2; generally aplerotic, but occasionally plerotic; containing a large, spherical, eccentric oil droplet and a small,

subspherical refractive body; 10–(14–17)–19 μ in diameter; germination not observed.

In antheridial branch origin, the two isolates of *Pythium* digress sharply from *P. echinulatum*; in that species the antheridial apparatus is predominantly hypogynous (Matthews, 1931: pl. 28, figs. 4–6, 8). Matthews' species also has both monoclinal and androgynous branches. The Iceland specimen first reported as this species (Johnson, 1971: p. 528) produced, though uncommonly, some hypogynous antheridial cells, but the androgynous origin predominated. The antheridial branches of *P. mammillatum* Meurs (Johnson, 1971), another member of the series with ornamented oogonia, are androgynous (though monoclinal if attached to an intercalary oogonium). *Pythium artotrogus* (Montague) deBary, recognized as a valid taxon by Matthews (1931), evidently has hypogynous antheridia (Butler's account, in 1907, of the same species is not clear on this point). In Sawada's *P. spinosum* (Middleton, 1943) the antheridial branches are typically monoclinal [though androgynous ones are figured (see Matthews, 1931: pl. 23, figs. 4, 6), and diclinal ones are said to be produced]. *Pythium polypapillatum* (Ito, 1944) has both an androgynous and a hypogynous antheridial apparatus.

The oogonium wall ornamentations of my specimens from Iceland are generally prominent and sharply pointed (Figs. 199, 200), although variations in their shape do occur (Figs. 197, 198). The fungus which I earlier (Johnson, 1971) identified as *P. echinulatum* also produced sharply-pointed spines on the oogonium wall. In *Pythium mammillatum* the ornamentations are short and papillate (Matthews, 1931: pl. 26), or, if long, are blunt at the tip. Blunt, digitate, narrowly-cylindrical ornamentations characterize Sawada's *P. spinosum* (Middleton, 1943). The oogonium wall in *P. artotrogus* is provided with sharply-pointed markings like those of *P. echinulatum*. Bifurcate ornamentations characterize *P. polypapillatum*. The nature of wall ornamentation, it seems clear,

ally the two isolates (7764 and 9057) most readily to *P. echinulatum*.

In the two individuals from Iceland, both aplerotic and plerotic oöspores may be produced, although the aplerotic condition predominates. The oöspores are aplerotic in *Pythium echinulatum*, *P. polypapillatum*, and *P. artotrogus*, and plerotic, on the contrary, in *P. mammillatum* and *P. spinosum*. Matthews (1931), however, has illustrated some aplerotic oöspores for a fungus she identified as Meurs' *P. mammillatum*. My plants from Iceland obviously bridge these two oöspore conditions and connect the two groups of species with one another at least as far as oöspore position in the oögonium is concerned.

The specimen of *Pythium echinulatum* first found in Iceland (Johnson, 1971) had oögonium and oöspores sizes very nearly identical to those recorded by Matthews (1931). The two more recent isolates are also closely allied to *P. echinulatum* in sizes of these two structures. The median oöspore size in my specimens does not diverge prominently from the size reported for *P. mammillatum*, and is well within the range recorded for *P. spinosum* and *P. polypapillatum*. Oögonium size among all these ornamented species does not appear to segregate out any sharply divergent forms.

The best available evidence at the moment for identifying these taxa with ornamented oögonia seems to set *Pythium spinosum* and *P. polypapillatum* apart from the other two species. In the former, the sporangia may be ornamented, and they usually do not produce planonts. In the latter, the sporangia proliferate internally. The earlier Iceland material of *P. mammillatum* and *P. echinulatum* (Johnson, 1971), and the two specimens at hand do not have sporangial characteristics like Sawada's or Ito's species.

As the specimens from Iceland indicate, the distinctions between *Pythium echinulatum* and *P. mammillatum* are far from precise. At the moment, the only characteristic that appears to be useful in identifying the two taxa is that of the wall ornamentation. Specimens

with sharply-pointed spines are assigned to Matthews' species—an arbitrary and not wholly convincing basis for identification.

Pythium sp. (Figs. 204–216)

Sporangium filamentous, short or long, terminal or lateral; not intercalary; 5–11 μ in diameter. Planonts laterally biflagellate; cleaving in a terminal, spherical, evanescent vesicle; 6–8x3–5 μ . Oögonium spherical or pyriform, occasionally ovoid or angular; infrequently cylindrical; lateral or terminal, infrequently intercalary; stalks, when present, straight or curved, usually somewhat irregular, occasionally sympodially branched or forming a glomerulus, infrequently coiled; wall smooth or occasionally provided with 1-several papillate or digitate projections of various lengths, sometimes with one broadly conical ornamentation; spherical or pyriform ones 16–(21–24)—29 μ in diameter, exclusive of wall ornamentations. Antheridial branches, when present, predominantly androgynous, then short and originating close to the oögonium base; infrequently monoclinal; antheridial cell, when formed, irregularly cylindrical, subspherical, or curved and bent, apically or laterally appressed. Oöspore generally 1, rarely 2; aplerotic but sometimes plerotic or nearly so; spherical; thick-walled; containing a small or large, eccentric, spherical oil body, and a subspherical refractive body; 13–(16–19)—21 μ in diameter; germination not observed.

This fungus appeared in four samples, on hempseed—Herb. No. 8545, 8811, 10082, 10157. The foregoing description was derived from a characterization of colonies of a single spore isolate from collection 8811 grown on hempseed in 40 ml of sterile tap water, at 23–25° C.

The laterally-produced oögonia begin as small enlargements at the apex of branches (Fig. 205). Enlargement of the separate initials proceeds rapidly (Fig. 206), and some show the small, lateral protrusions (Fig. 207) that become the wall ornamentations (Fig. 210) in the mature oögonium. The sub-oögonial branches appear very early in the development of the oögonium (Fig. 205), and

proceed to form as the initial enlarges (Figs. 206, 208). Some suboögonial branches become functional (Fig. 212) or non-functional (Fig. 210) antheridia. Other branches remain as short, sympodial laterals that may bear other oögonia (Fig. 211, 213) or simply enlarge into a somewhat expanded, hypha-like extension (Fig. 214) or into a short filament (Fig. 216, right-hand oögonium). In instances where branching occurs early in the formation of the oögonial apparatus, a glomerulus (Fig. 216) is formed.

Other characteristics—aside from sympodial branching and the formation of glomeruli—mark this *Pythium*. Antheridial cells are often not formed, even though an antheridium-like branch is present (Fig. 210). A second feature of note is the production of smooth and ornamented oögonia. Both an aplerotic and plerotic condition exists with respect to the oöspores, but the former type prevails.

This *Pythium* from Iceland is not accommodated in any of the known species of the genus, although it does have some features known to occur also in a few of the named taxa of the genus. *Pythium papillatum* (Matthews, 1928) has both smooth and ornamented oögonia that are not unlike some to be found in the Iceland plants. Matthews' species is definitely plerotic, however, and it lacks antheridial branches. Some suboögonial branches are produced in *P. papillatum*, however, as the figures show (Matthews, 1931: pl. 8), and a comparable situation occurs in my specimens. The androgynous antheridial branches of *P. torulosum* (Coker and Patterson, 1927) recall those in the Iceland fungi, as does the aplerotic condition of the oöspores. The latter individuals lack the prominent toruloid outgrowths of *P. torulosum*. The specimens from Iceland could be allied to *P. irregulare* Buisman (see Matthews, 1931) on the basis of its ornamented oögonia, but Buisman's species produces spherical or pyriform sporangia, and is thus in a very dif-

ferent section of the genus. The androgynous antheridial branches (of near origin) in *P. ultimum* Trow (see Johnson, 1971: figs. 1, 2) are somewhat like those of *Pythium* sp., but the spheroidal sporangia (among other features) of Trow's species prevents the use of this binomial for my plants. The irregularity of hyphae adjacent to the oögonial apparatus and the formation of some androgynous antheridial branches in Serbinow's *P. perniciosum* recall *Pythium* sp. Other features of Serbinow's species (Matthews, 1931) (consistently smooth-walled oögonia, declinuous antheridial branches, to name two) are not matched by my Iceland fungi.

Pythium sp. seems most closely allied to *P. papillatum*, but if so, it is a prominently varied form of that species. Experimental work with additional isolates is obviously needed to determine something of the stability of the characteristics of *Pythium* sp. (and also of *P. papillatum*). In the absence of supporting evidence from such a study, I believe the fungus from Iceland is best left unnamed.

PHYTOPHTHORA

Howard (1968) collected *Phytophthora cryptogea* (Pethybridge and Lafferty, 1919) on submerged twigs of *Fraxinus* sp. (bait) and succeeded in culturing the fungus on agar. This species has not appeared again in subsequent collections.

A *Phytophthora* producing only sporangia (Fig. 203) was found on four occasions on submerged apples. The fungus must remain unidentified until such time as the sexual apparatus is discovered. Neither the nonsexual *P. oryzae* (Ito and Nagai) Waterhouse (1958) or the *Phytophthora* sp. I (*Pythiomorpha* sp. I) of Lund (1934) seem allied to the Iceland plants. The sporangia of *P. oryzae* and Lund's specimens are shorter and more globose than are those of this *Phytophthora* sp. from submerged fruits.

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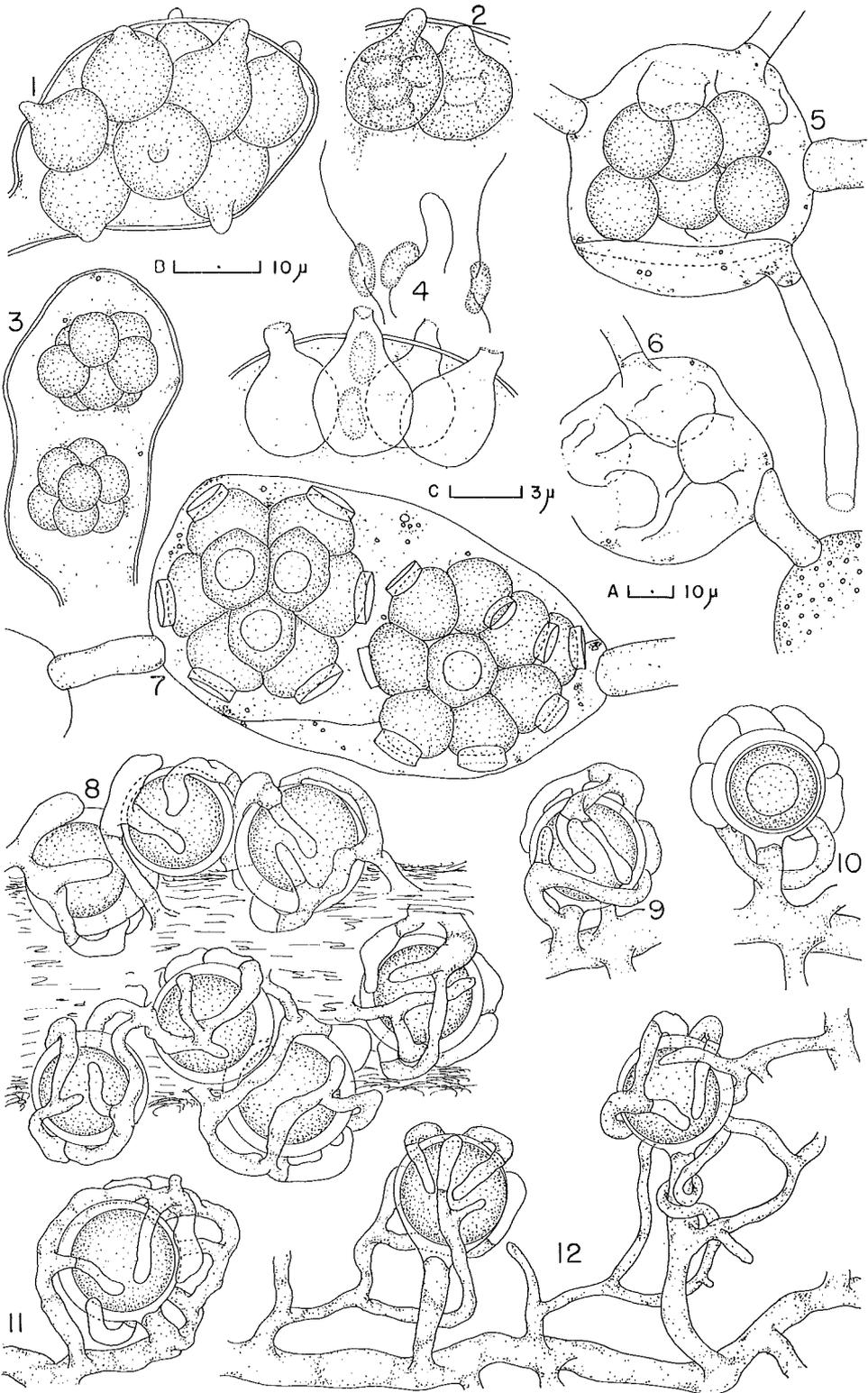
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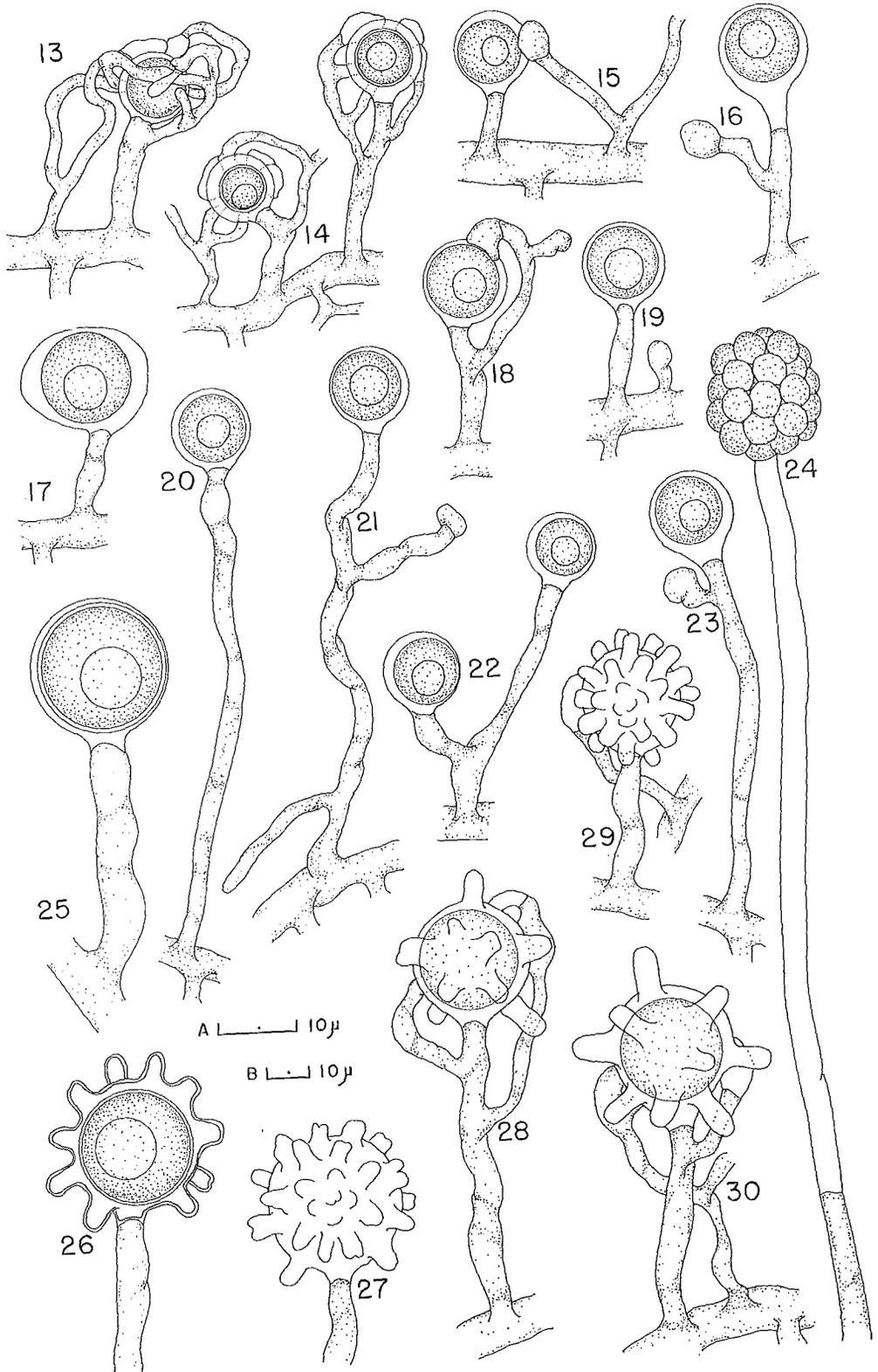
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PLATES AND
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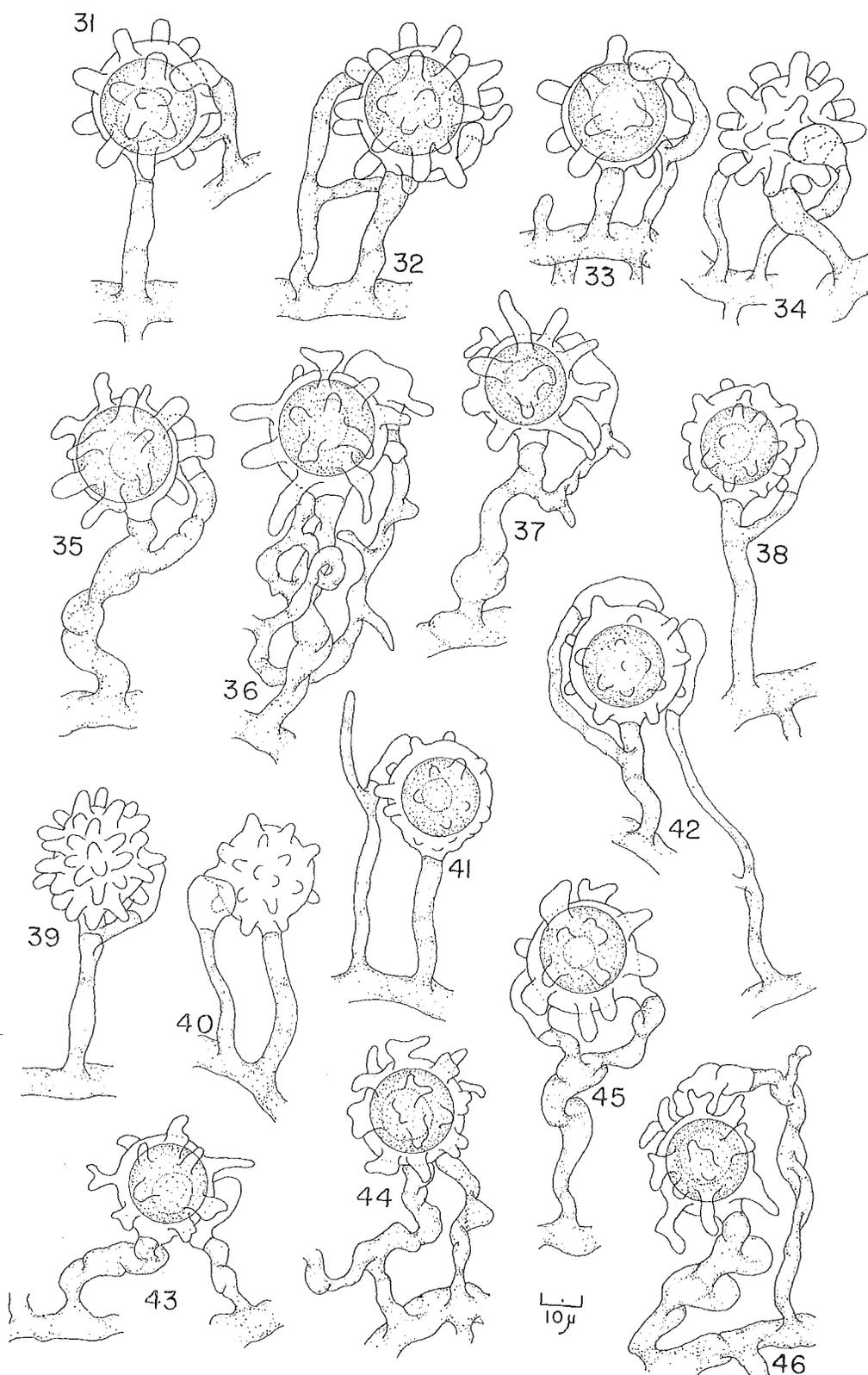
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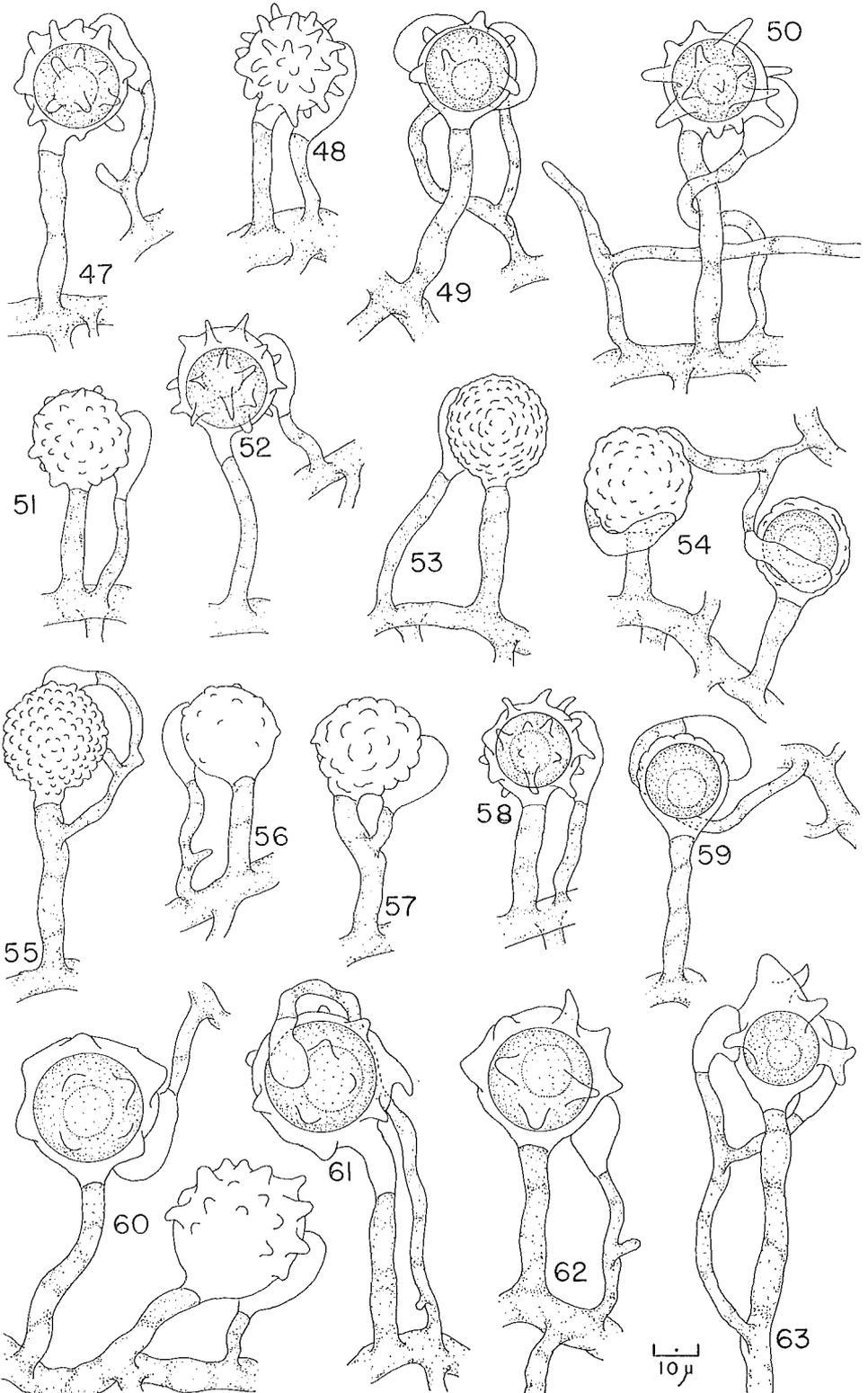
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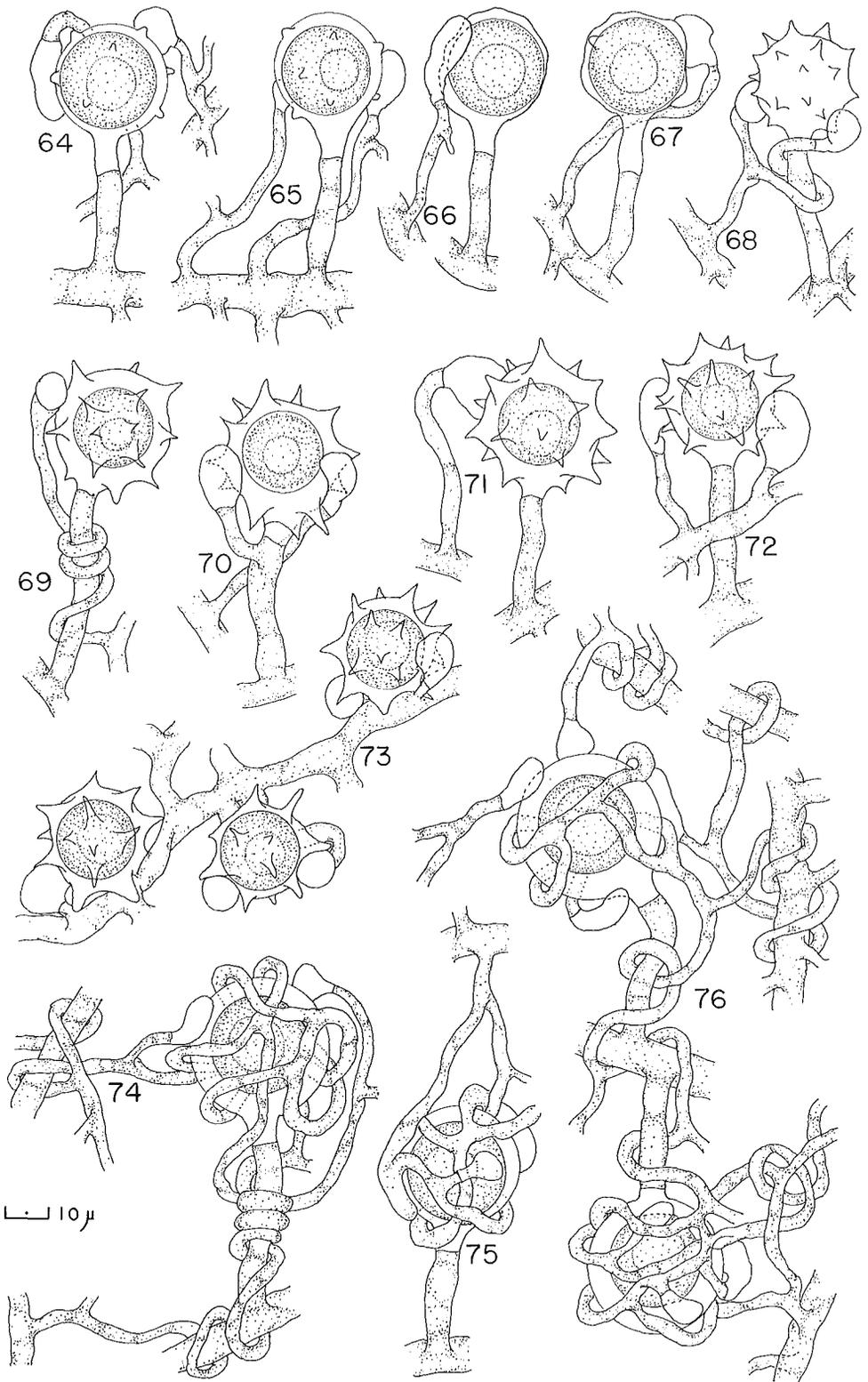
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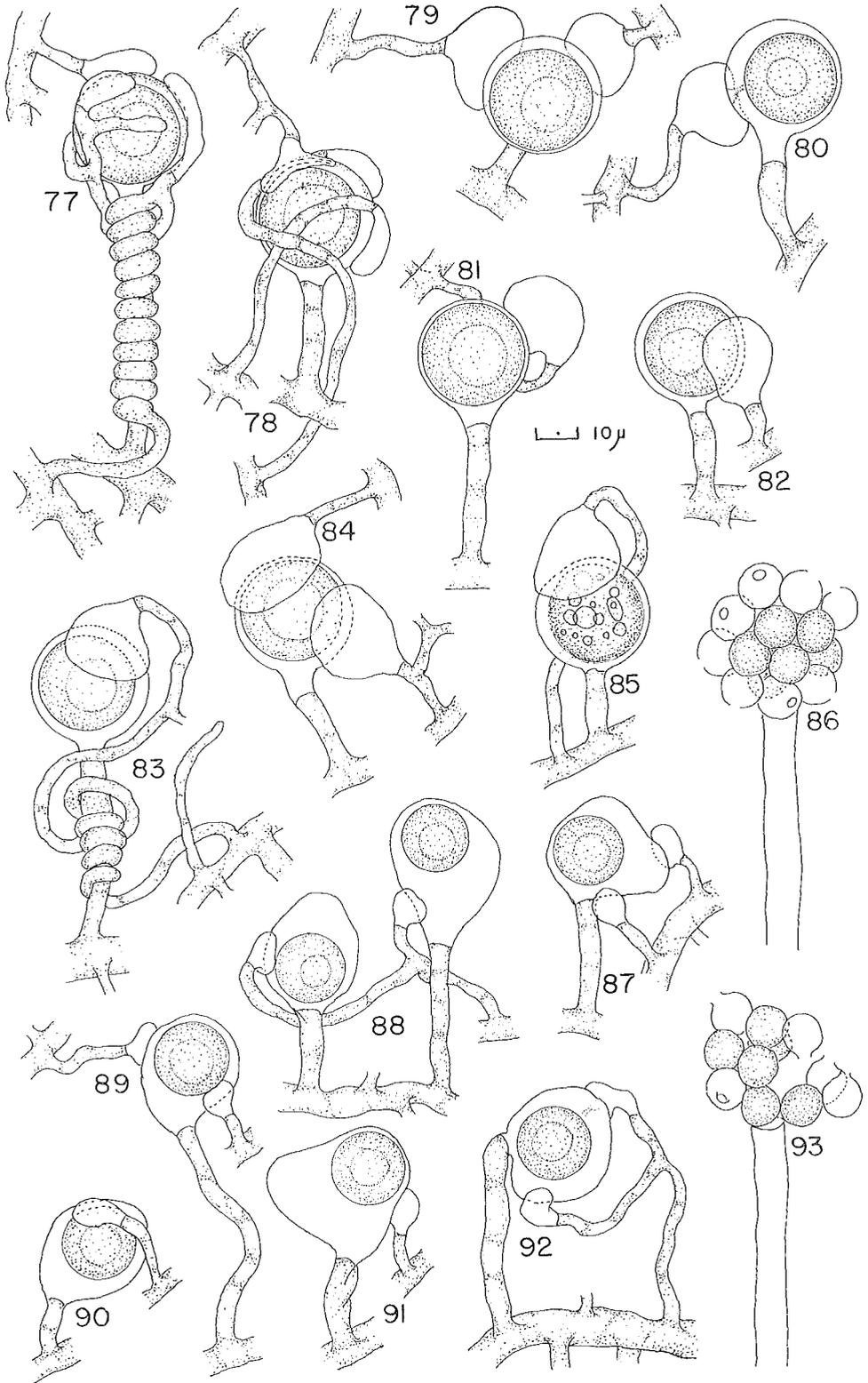
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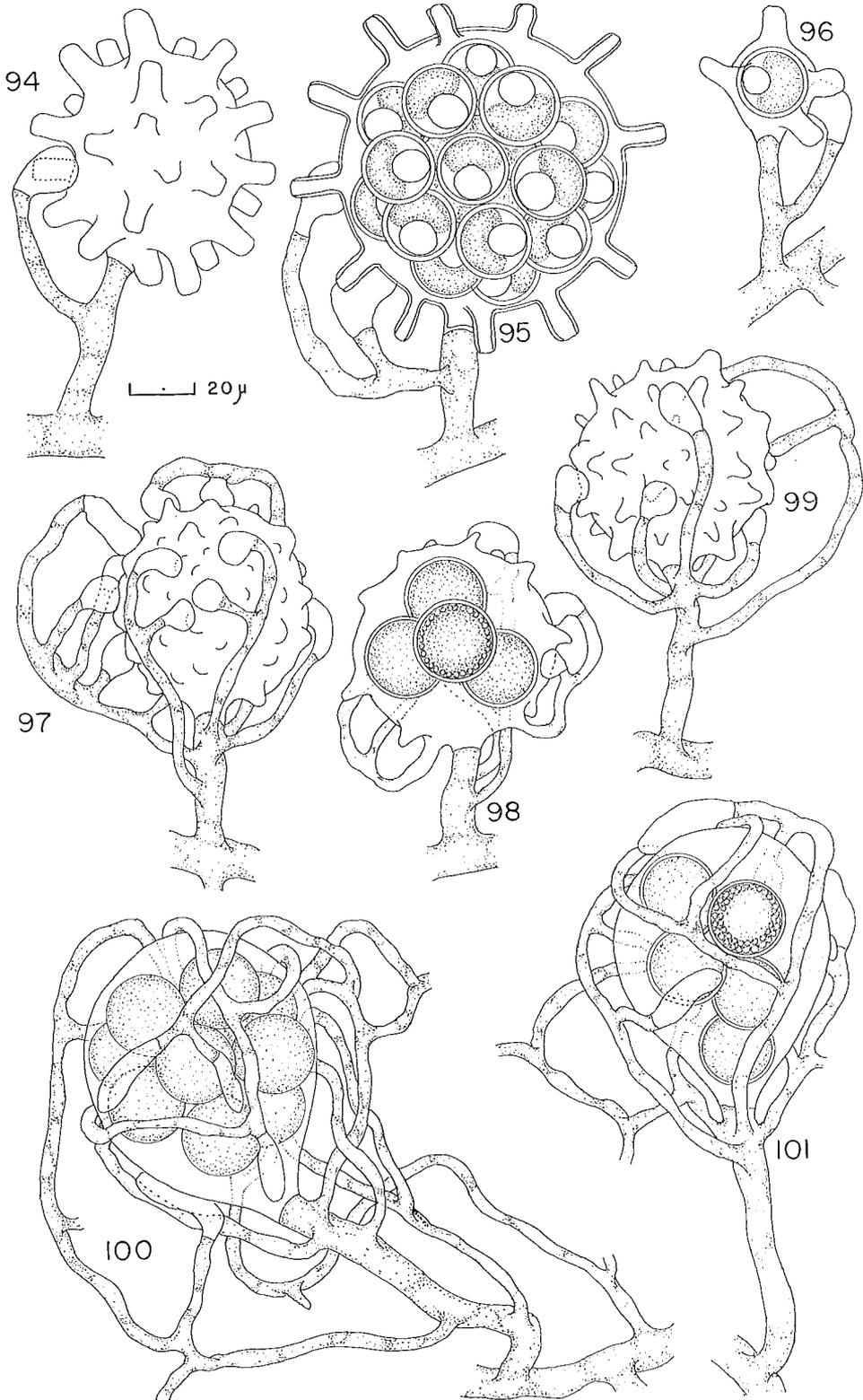
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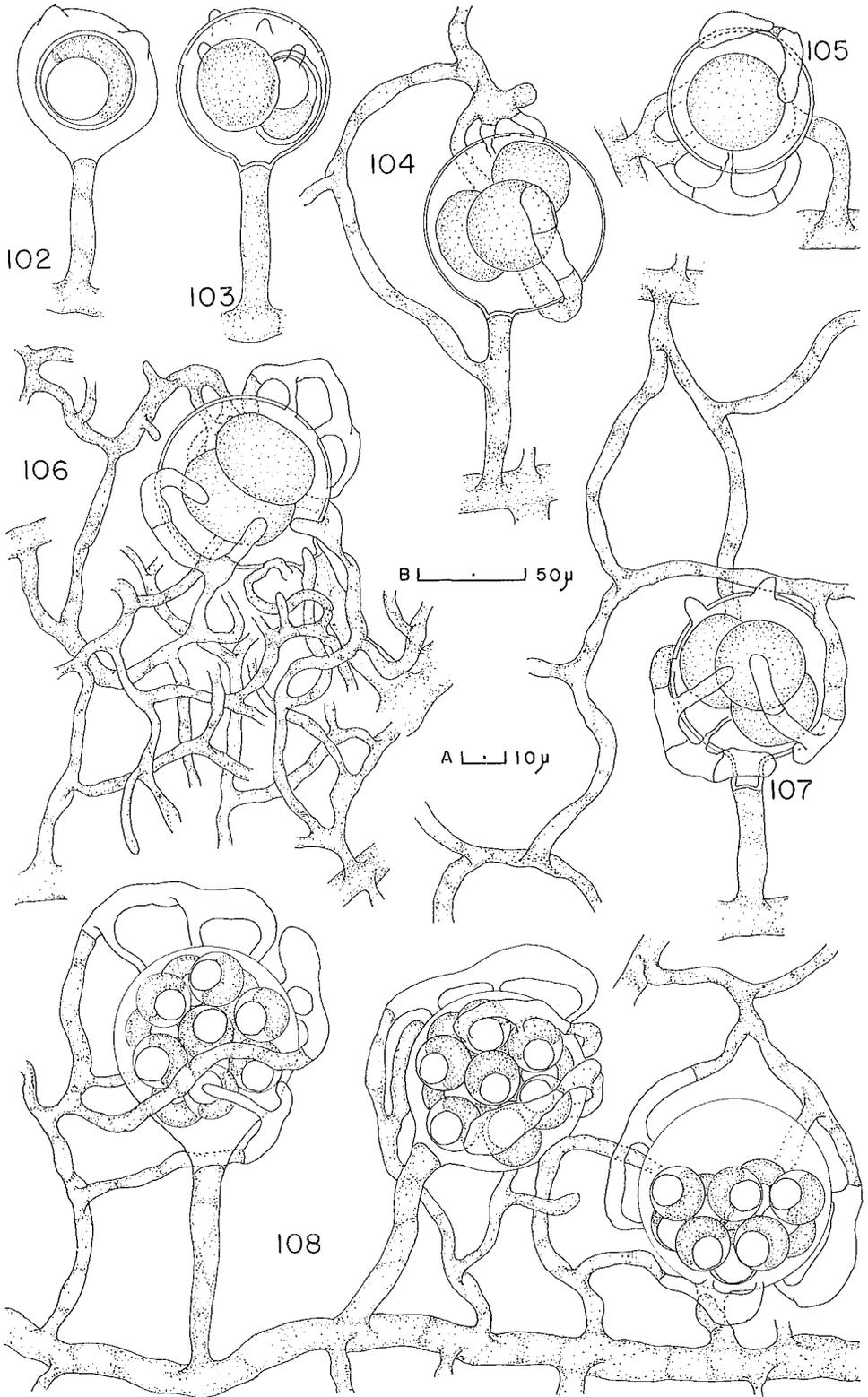
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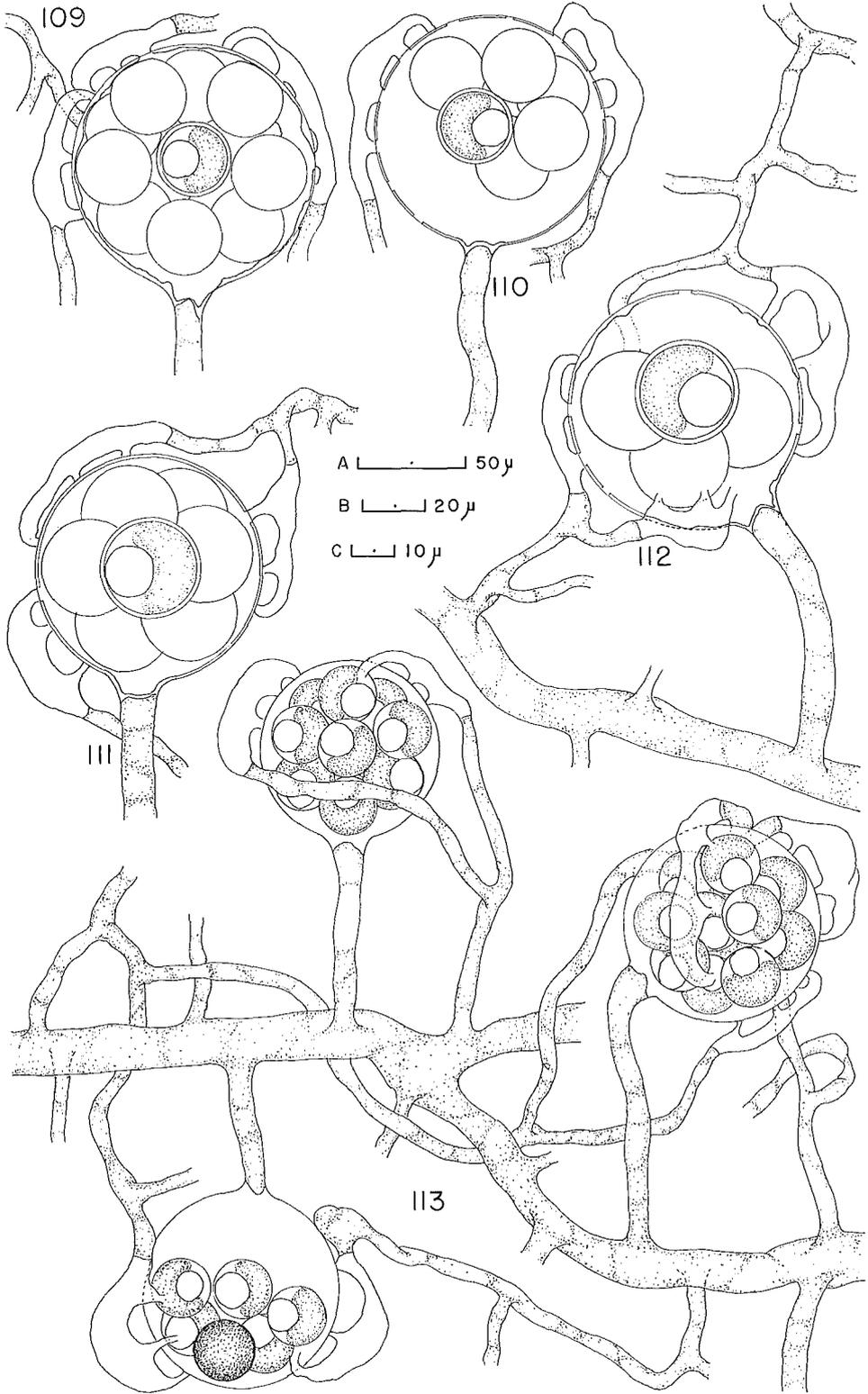
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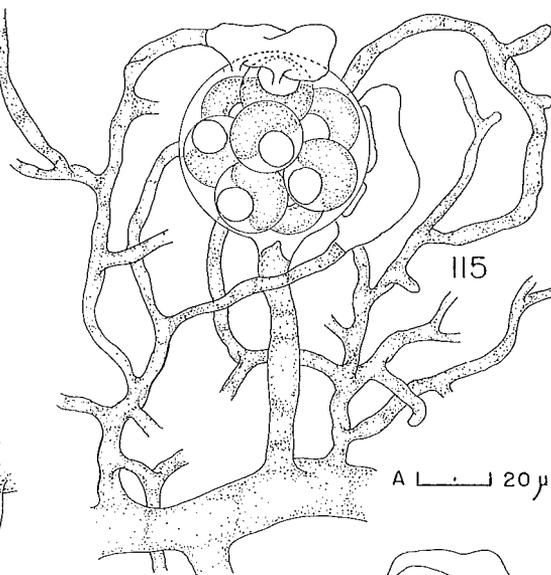
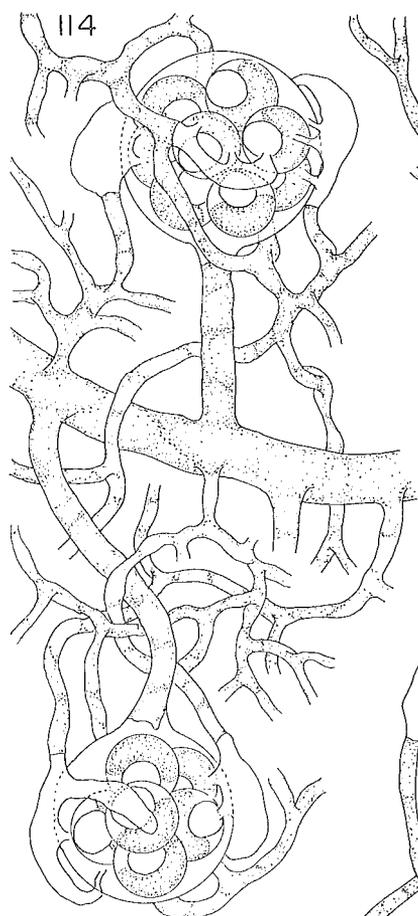
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B 50 μ



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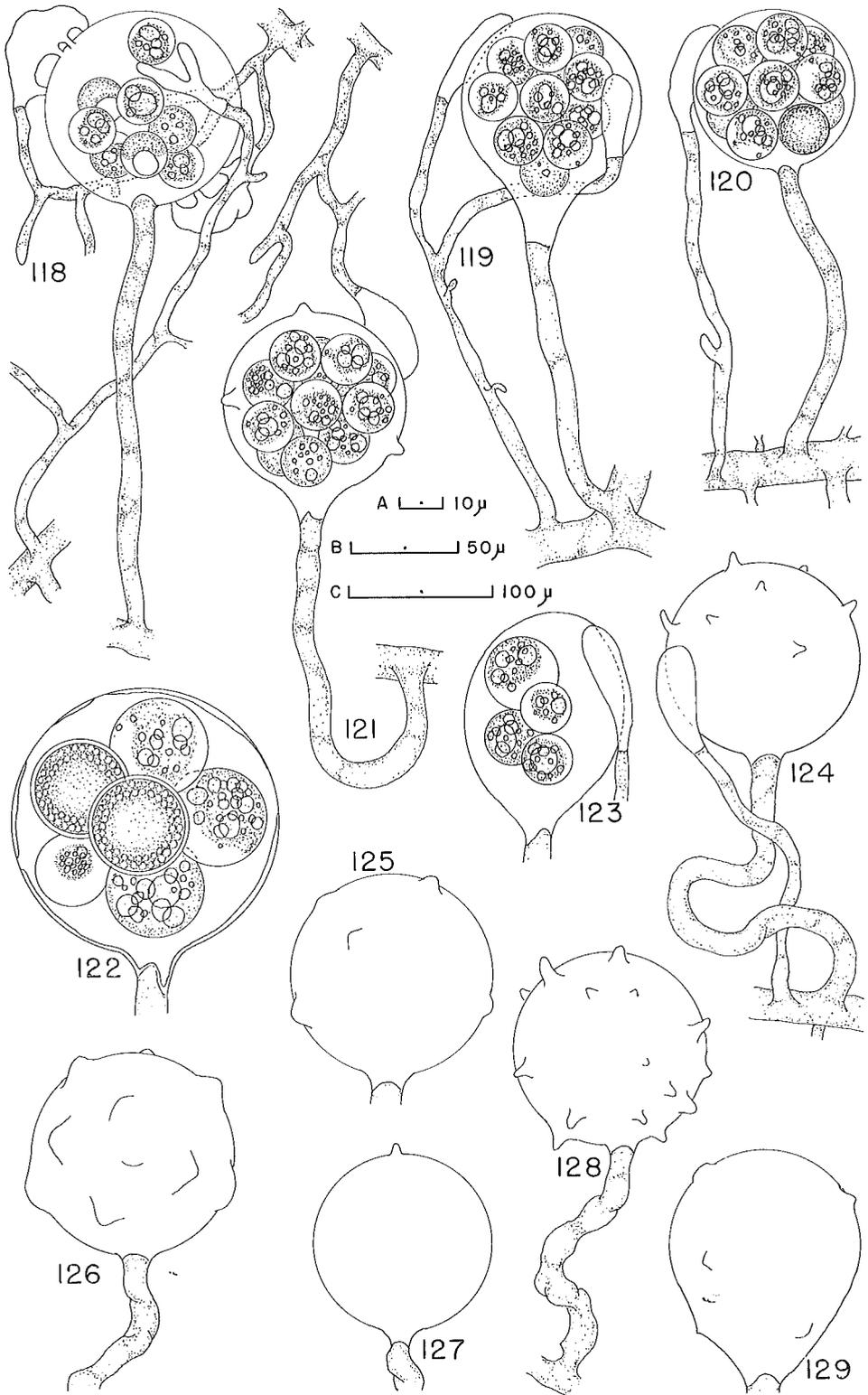
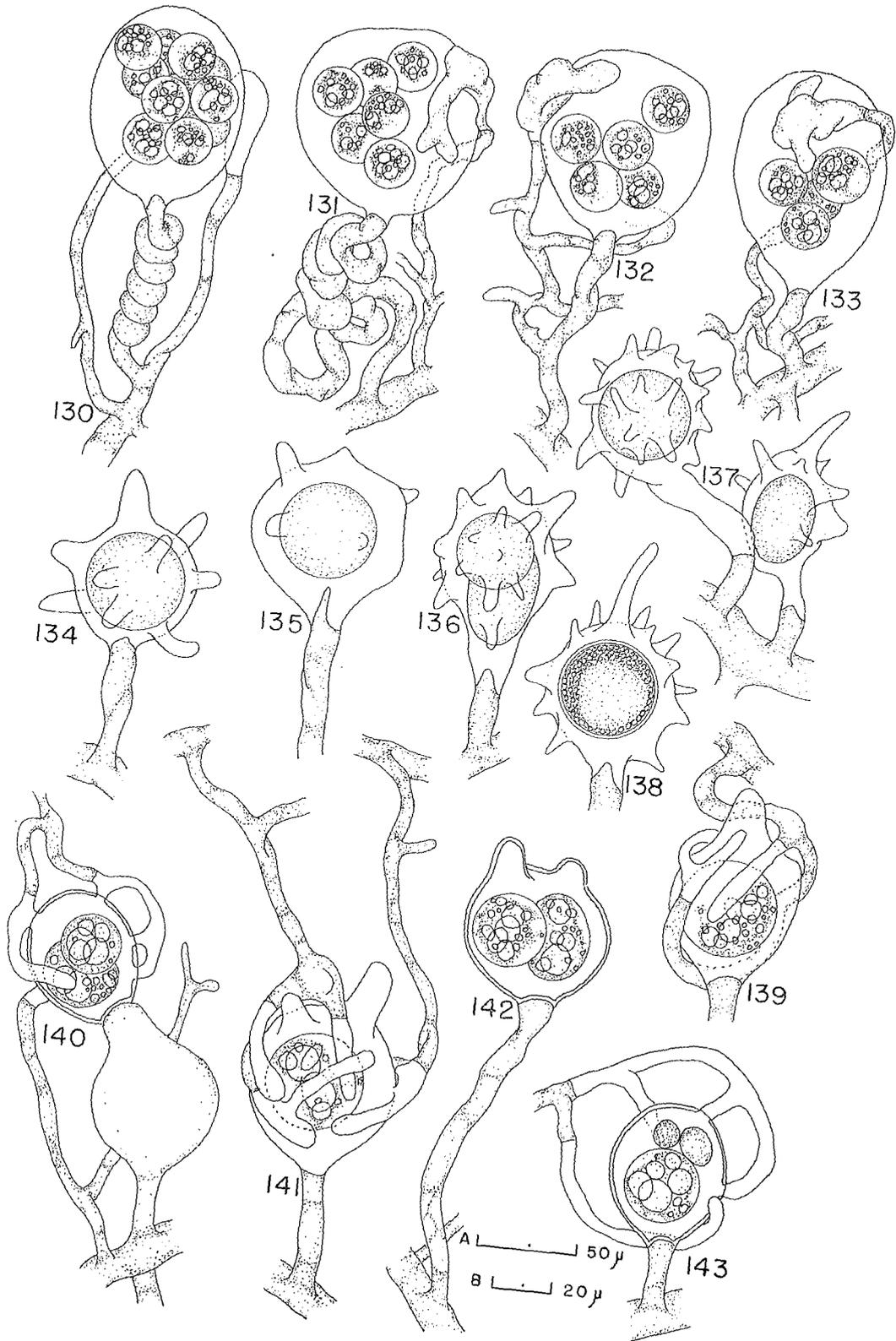
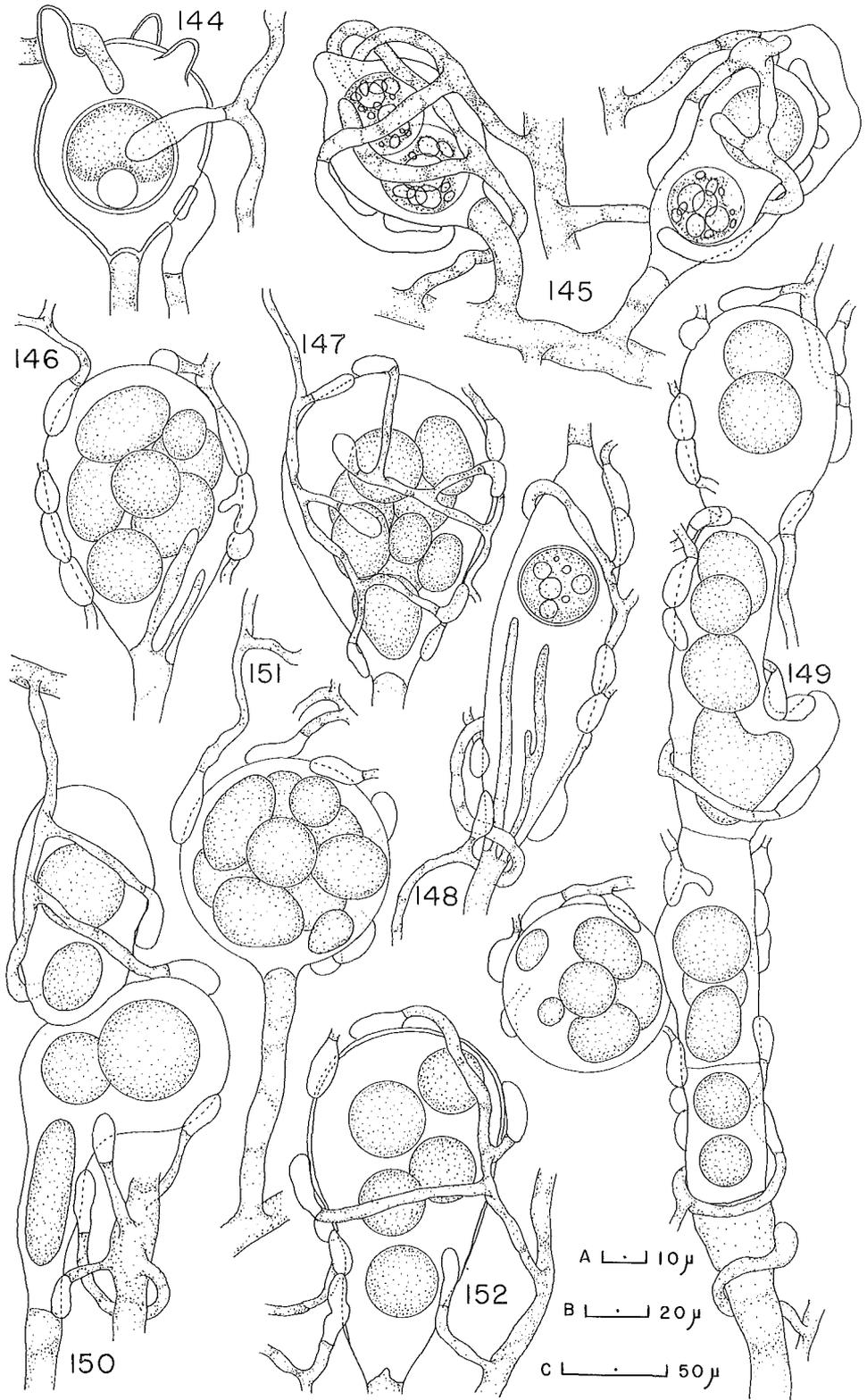


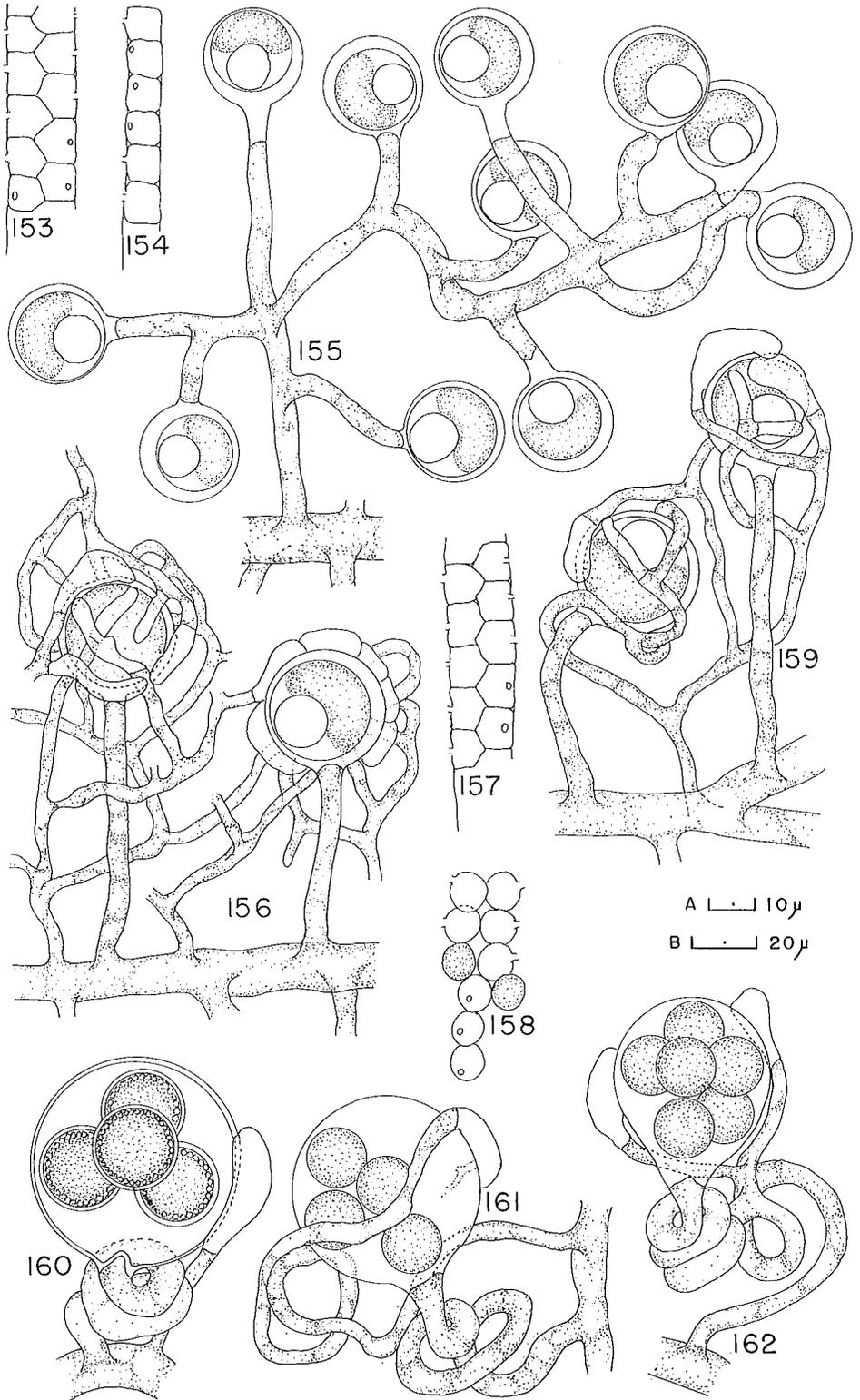
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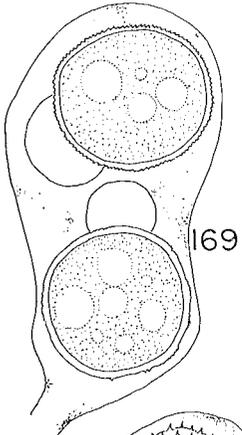
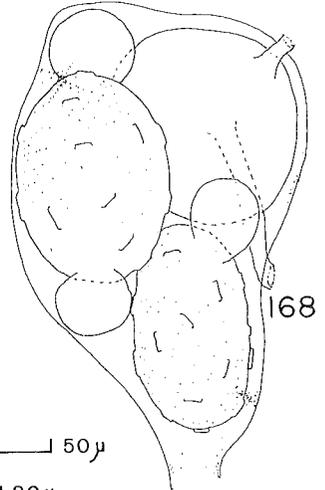
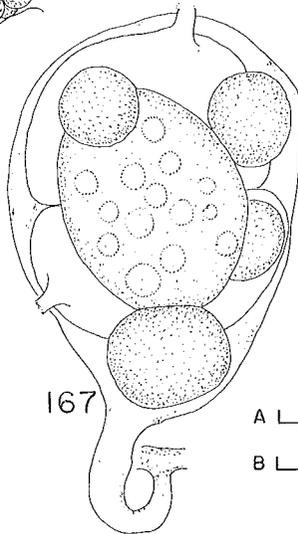
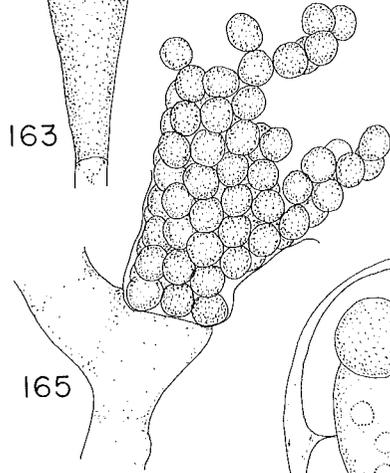
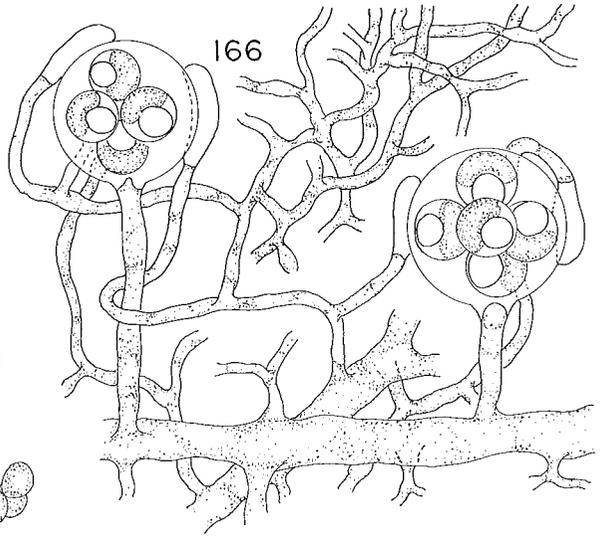
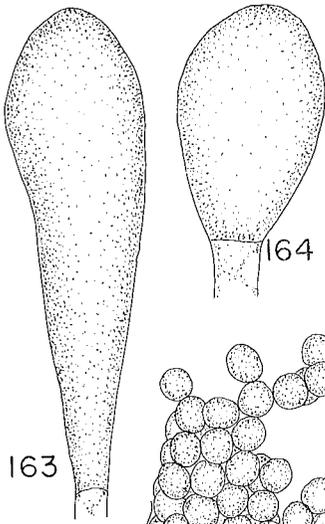
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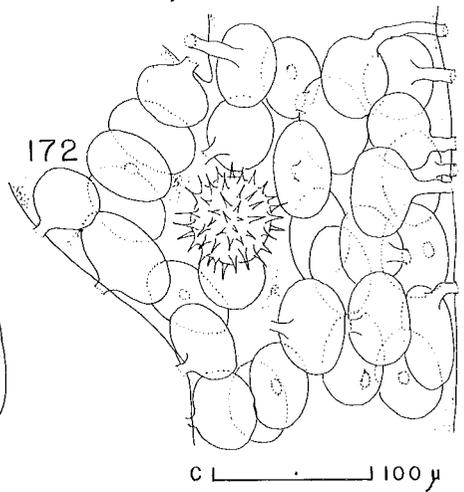
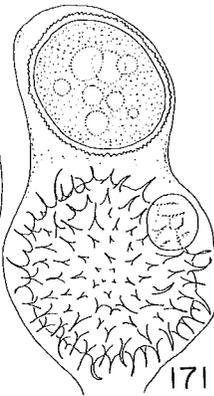
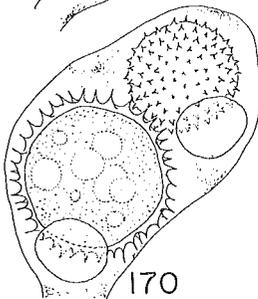
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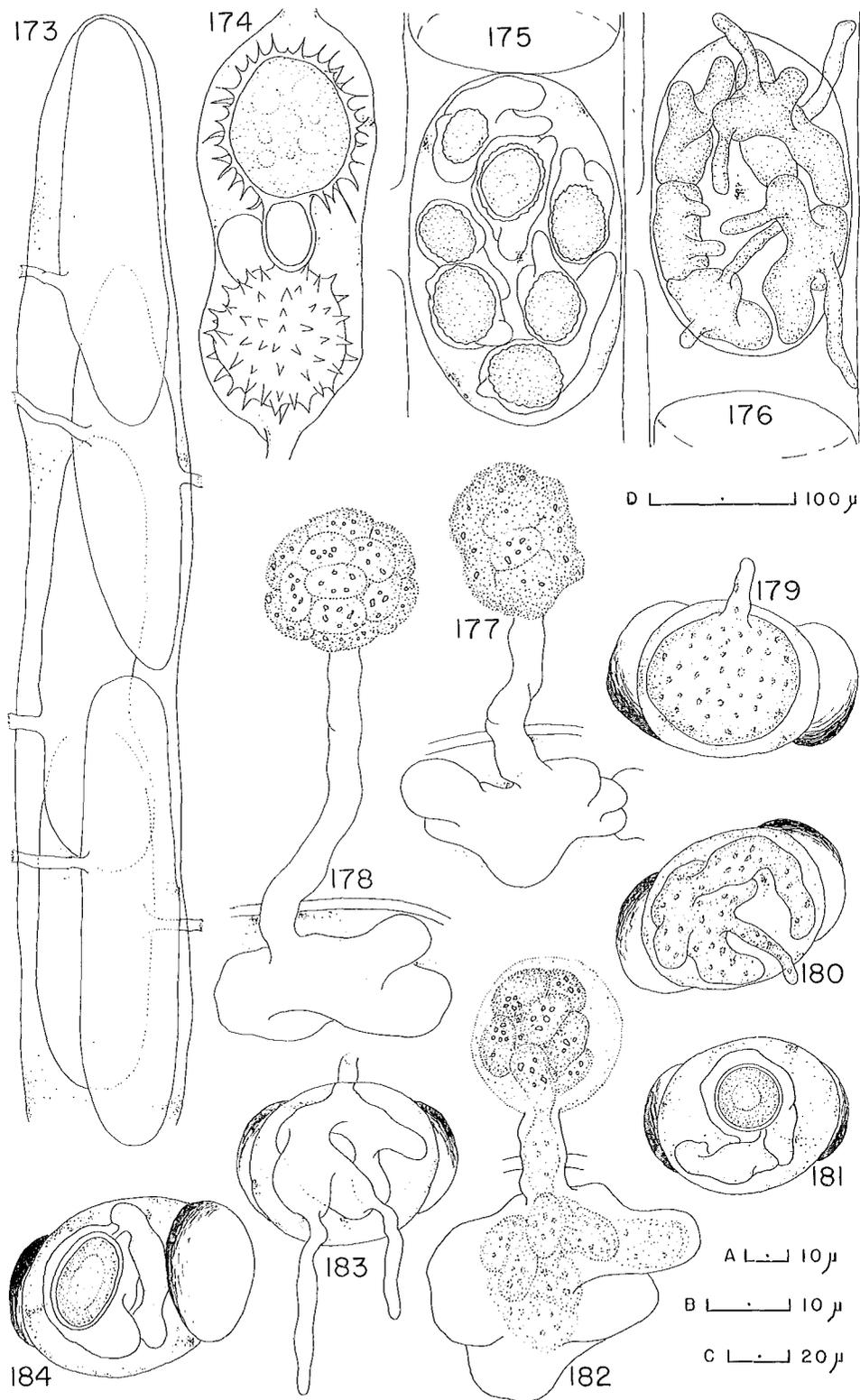


A — 50 μ
B — 20 μ



C — 100 μ

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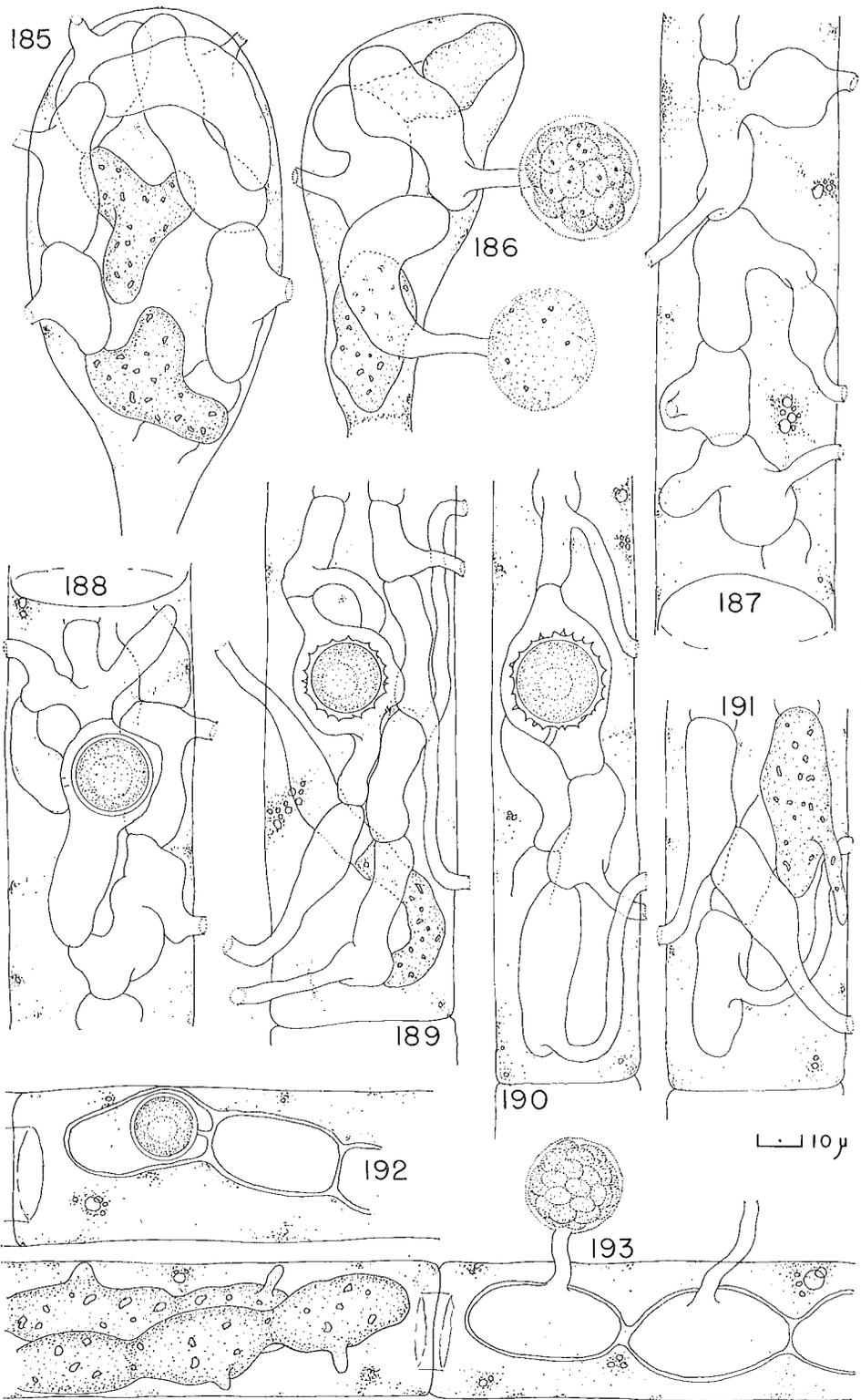
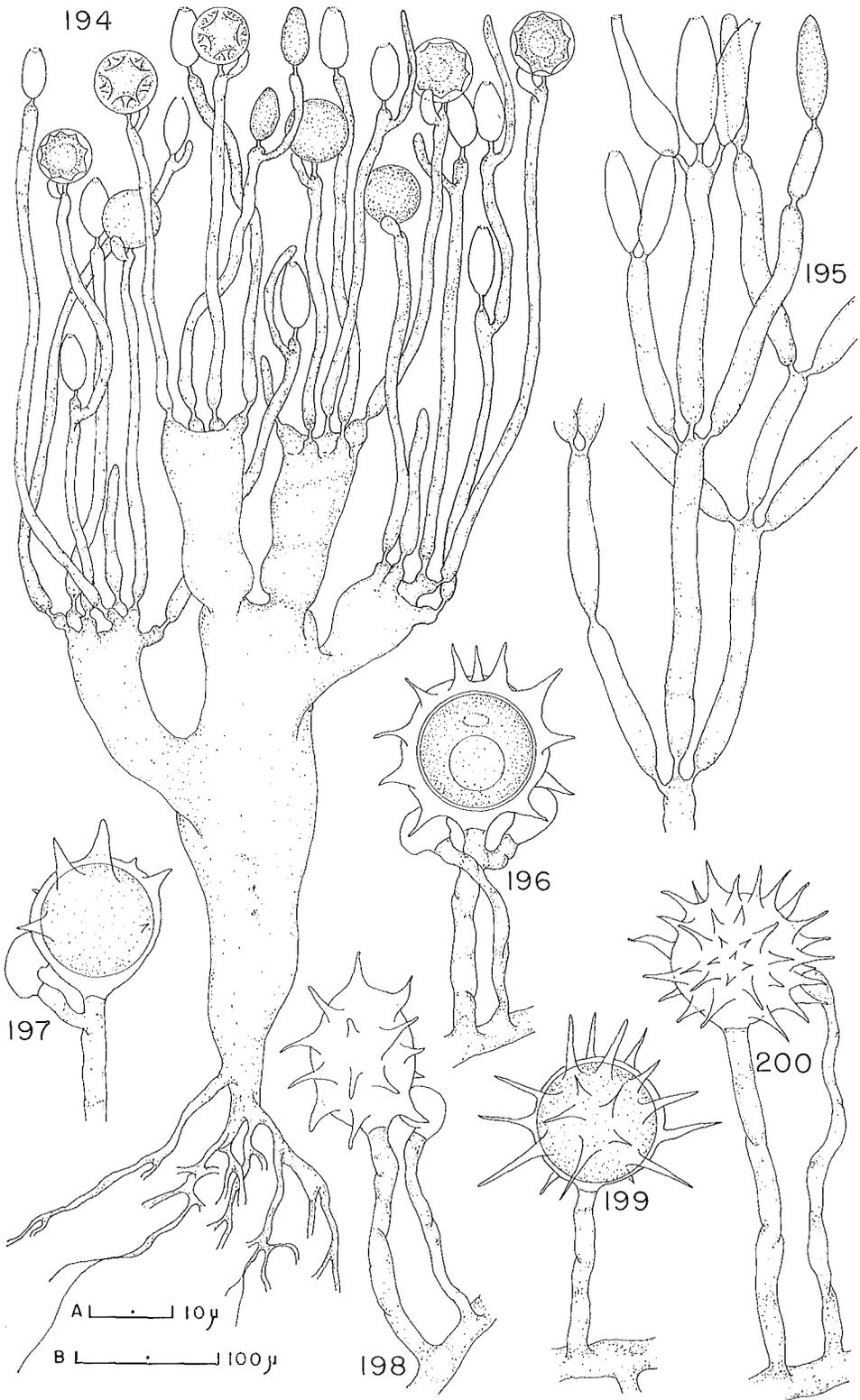
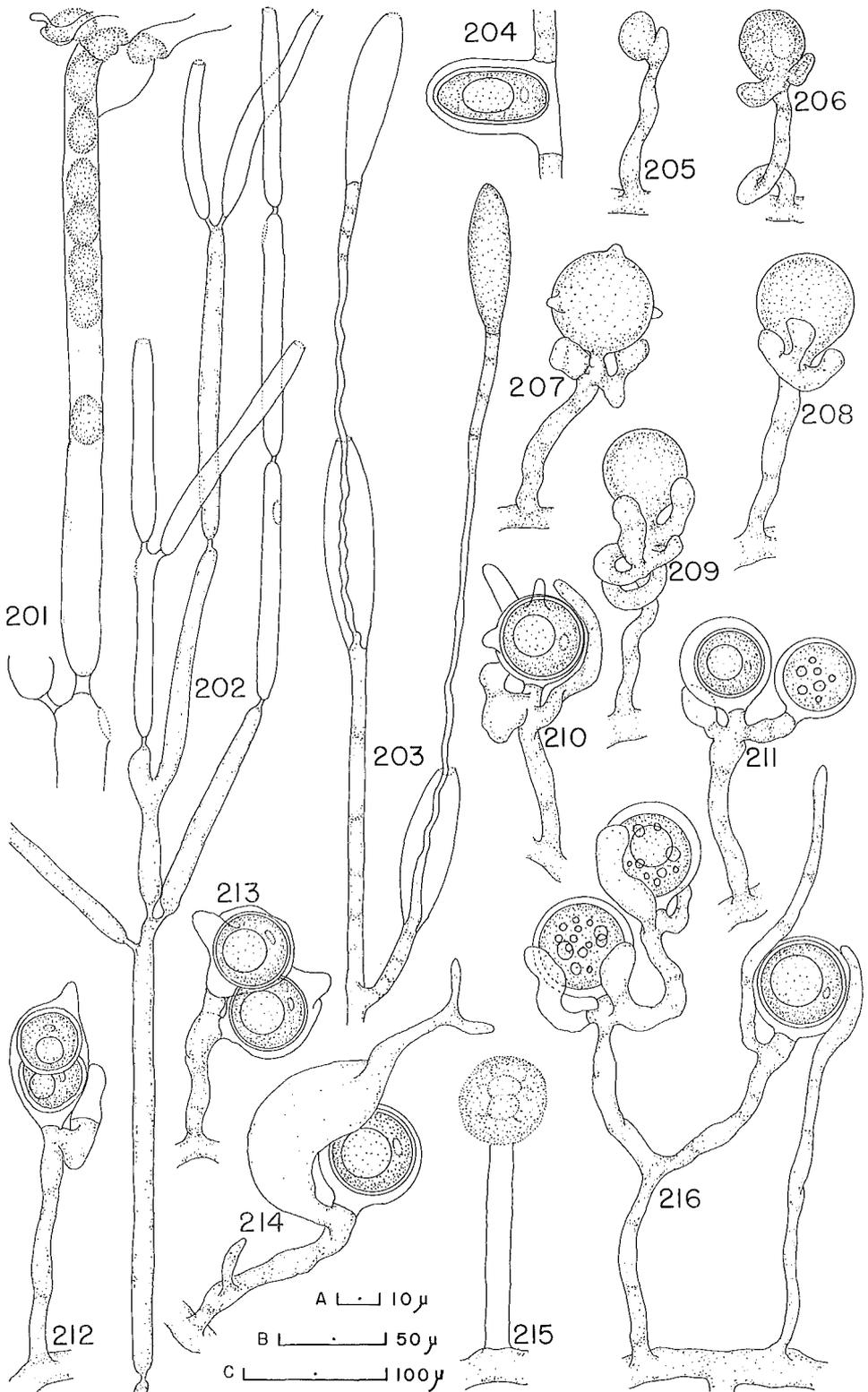


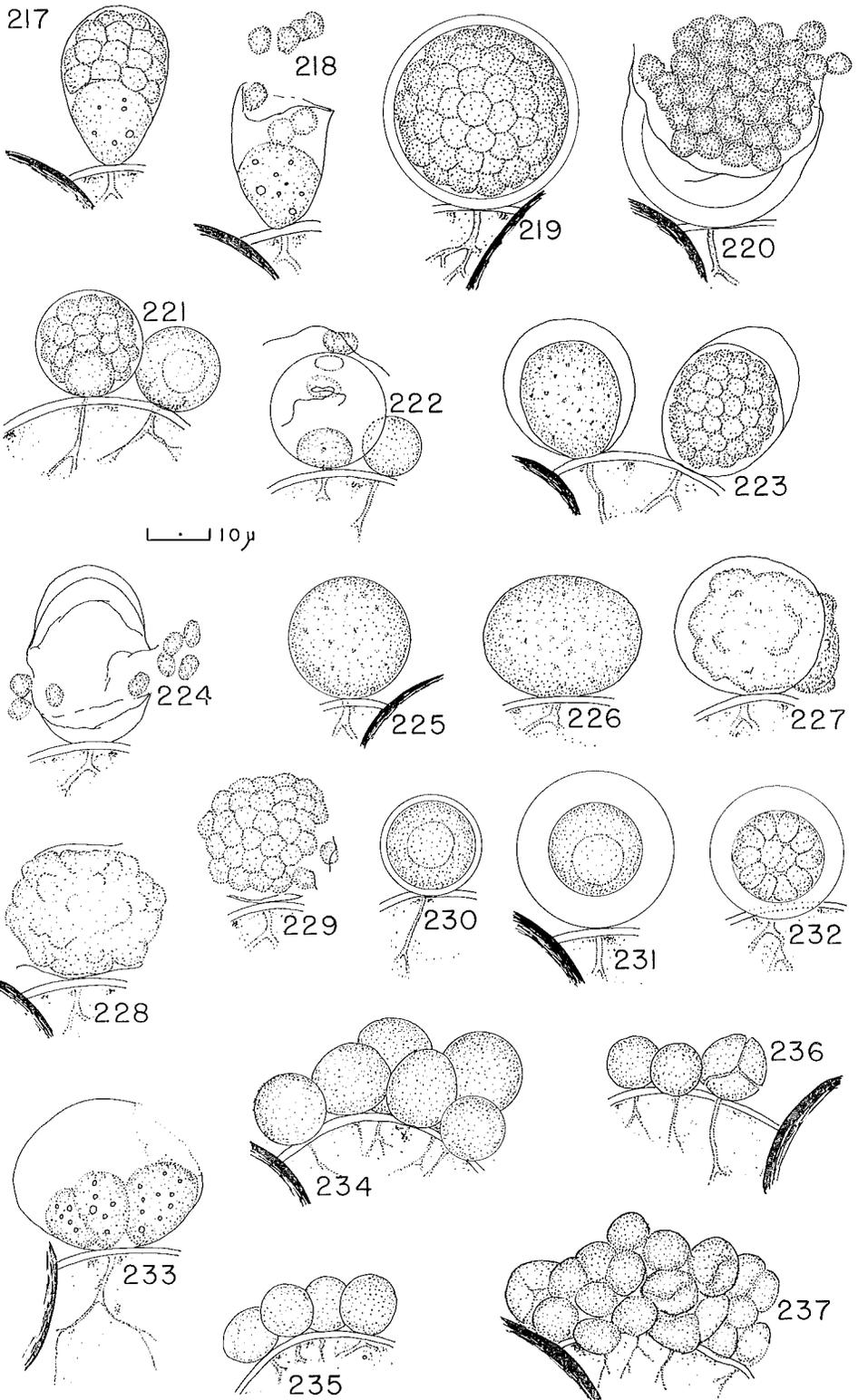
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