

AQUATIC FUNGI OF ICELAND:
UNIFLAGELLATE SPECIES

T. W. JOHNSON, Jr.

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Aquatic fungi of Iceland: Uniflagellate species

T. W. JOHNSON, Jr.

Department of Botany, Duke University, Durham, North Carolina, U. S. A.

Abstract. This is an account of the morphology and taxonomy of 45 species of uniflagellate aquatic (zoösporic) fungi collected in Iceland. These fungi are distributed in three orders, Chytridiales, Blastocladales, and Hyphochytriales, and in 21 genera of 10 families. No new taxa are proposed, and emphasis is on morphological variation in recognizable species or species complexes. Some taxa are only tentatively identified or provisionally assigned, but their taxonomy is fully discussed. Notes on the occurrence of aquatic fungi in Iceland are included as is an account of methods for collecting, culturing, and preserving specimens.

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INTRODUCTION

Among slightly over eight hundred species of fungi known to occur in Iceland, Larsen (1932) listed nine taxa (*Synchytrium* and *Phy-soderma*) ordinarily classed among the uniflagellate groups of the aquatic Phycomycetes. Apparently no further reports of aquatic fungi in Iceland appeared until 1960. At that time Höhnk published a note on the recovery of sixteen species with uniflagellate planonts.

In early 1964 I began a survey of the aquatic (zoösporic) fungi in Iceland. For the most part, the "freshwater" species were emphasized. From time to time, segments of the study were published, treating either general portions of the mycoflora (Johnson, 1968, 1973b; Johnson and Howard, 1968; Howard and Johnson, 1969) or specific taxa (Johnson, 1966; 1969a, b; 1971; 1972; 1973a; Johnson and Howard, 1972). In this and a companion account of some biflagellate species, an investigation involving over 11,000 collections is concluded. Previously published material is not repeated except where brief reference is necessary or pertinent taxonomic changes are made.

In keeping with other accounts of the aquatic mycoflora of Iceland, I am providing discussions and illustrations where these adjuncts are necessary to transmit species concepts. Formal descriptions of most taxa are excluded, since these are readily available in other sources (Sparrow, 1960, notably).

Because recognition of taxa often turns on ephemeral characteristics or ones absent in a particular state of development, it was impossible to identify all specimens. This problem was partially overcome by propagating individuals in culture and characterizing developmental stages. Some fungi did not yield to such treatment, and consequently specimens either were assigned names provisionally, or were left unnamed. Reference to them is in-

cluded, however, to present a complete account.

I have not proposed new species, although arguments could be made to justify new taxa. The variability existing among segments of the aquatic mycoflora in Iceland dictates extreme caution in this regard, and some species would have to be based on only a few specimens, or on ones known only from gross culture. I prefer merely to describe as fully as possible those fungi not readily accommodated in established taxa, and future studies perhaps may then properly identify these plants without the hindrance of an accompanying clutter of names.

The flora of aquatic fungi in Iceland is not as rich as that of tropical and temperate regions. A striking feature of the flora — its uniqueness, in fact — is the array of forms or variants (races or strains, perhaps) of species. These make identification difficult, but their occurrence is of singular importance to taxonomy.

With few exceptions, the taxa included in this account are represented by preserved specimens in the collections of the Museum of Natural History, Reykjavik. Pertinent data on substratum and source are included with the specimens.

Because the fungi themselves were often refractory toward growth in pure or unifungal culture, it was impractical to quantify all observational data. In the formal descriptions (and in some other instances) the numbers in parentheses represent the 70% median of 200 measurements or counts in at least five preparations. Wherever possible (exceptions are noted), the characterizations of fungi were prepared from observations on gross, unifungal, or pure cultures of specimens grown on the appropriate substrates in 40 ml of sterile, charcoal-filtered, distilled water or (in Iceland) sterile tap water, and incubated at 23–25°C. Preparations containing active planonts were

killed by inverting them over the fumes of 1% osmic acid for 1 minute; the spores were then measured.

OCCURRENCE

Nearly any habitat in Iceland — some exceptions are barren lava, soil immediately adjacent to hot springs, shallow pools of standing water where bacterial growth is exceptionally high and sandy areas without vegetation — harbors some aquatic fungi. Certain habitat types contain a wider variety of species than do others. Generally where there is ground cover, or emergent or shallowly submersed vegetation, aquatic fungi are sure to exist. The most diversified flora occurs in these habitats: marshy areas populated by grasses, sedges, mosses and horsetails; moss-filled depressions (particularly of *Sphagnum* or *Rhacomitrium*) in low, wet spots; ponds or streams populated heavily by waterfowl and fish (the soils and waters of the rearing ponds in the fish hatchery at Kollafjörður contain some species of fungi not found in any other habitat in the country); agricultural soils, and soils and drainage water from pastures (“tún”) and barnyards (“hlaðvarpi”). Thus, where there are substantial accumulations of organic matter, there are abundant populations.

Some aquatic fungi occur naturally on organic substrates in aquatic habitats. Algae (*Spirogyra* spp. and *Zygnema* spp., very often) constitute suitable substrates. Species also occur on other aquatic fungi, on the soft tissues of angiosperms, on pollen of local species of *Salix* and *Betula*, on the exuviae of chironomids (in Mývatn, for example, in great seasonal abundance) and on eggs, embryos and adults of microscopic, aquatic invertebrates.

While periodically wetted and dried habitats generally harbor a richer mycoflora than do constantly waterlogged ones, there seem to be no seasonal occurrences of aquatic fungi in Iceland. Similarly, I found no distributional patterns related to soil types, and except in agricultural soils, few species were recovered be-

low 3–5 cm. Silty soil from the bottom of pools or ponds (such as at the eastern entrance to Heidmörk, and Ellidavatn and its tributaries) harbors few species in contrast to wet soils at the waterline or under shoreline vegetation.

Many species are widely distributed in Iceland, and the results of far-ranging sampling excursions often yield little in the way of undiscovered forms. Intensive collecting in a particular locality (even in one previously sampled) is more likely to add to knowledge of the flora than is extending into unsampled areas.

COLLECTION

Certain aquatic fungi are found by directly examining algae, eggs and other developmental stages of aquatic invertebrates, and the soft tissues of phanerogams. There are culture methods for collecting fungi from such substrates, but there is no substitute for direct microscopic searches though collections of aquatic plants and animals and debris. An indirect way of collecting aquatic fungi, however, is to “seed” soil and water samples with a variety of bits of organic matter — the process familiarly known as baiting.

Samples of soil or water, the latter preferably mixed with adjacent sediments or organic debris, are collected either in disposable containers (such as “Whirl-Pacs” or plastic food bags) or in bottles or vials that can be surface-sterilized. A container holding 25 ml of water and debris gives an adequate wet sample for baiting. If soil is collected, such a container half-filled is adequate for one sample. Collections of water can be stored for 12–18 hours, and wet or moist soils may be kept unbaited for 36–48 hours before the fungal population is noticeably affected. Air-dried soils can be stored for many weeks or months, and still, on baiting, yield some aquatic fungi. The diversity of the flora in any sample is substantially reduced as storage lengthens; there is a resulting uniformity (and sparseness) in species that survive.

Some types of bait — hempseed, grass leaves, chitinous or keratinized materials — may be put into the vials for collecting water before taking them to the field. In this manner, some fungi may become established on the bait while in transit. Lens paper and pollen, for example, are baits which must be floated on the surface of water in the culture dishes, hence these substrates cannot be used in this fashion. Organic matter should be incorporated into the samples. For this reason, soil at the water's edge (or just below the surface) is stirred up vigorously before samples are taken. Soil taken within 1 cm of the surface usually contains substantial amounts of organic debris.

Water samples are put into sterile (glass or plastic) Petri dishes, and sterile water added to bring the culture dishes 2/3 full. Soil samples (no more than about 5–8 grams of each) are similarly treated. The soil is stirred gently to mix it thoroughly with water before bait is added. Gross cultures are usually diluted with sterile, charcoal-filtered, distilled water, but the exceptional purity of cold tap water in Iceland makes distillation followed by filtering through a chelating agent unnecessary.

Organic substrates of various kinds are added to the gross cultures. The baits most certain to support growth in the majority of samples are hempseed (*Cannabis sativa* L.), cast snakeskin, roach wings (*Periplaneta* spp.), lens paper, boiled cellophane, bleached, boiled grass leaves, human hair, and pollen (*Pinus* spp.). In any serious sampling program where maximum yield is a goal, untreated human skin, shrimp exoskeleton (see Karling, 1945, for preparation method), whale baleen (boiled to remove residual salt), horse hoof shavings, termite wings, onion skin, and boiled, filamentous green algae can be used as well. Some attention must be given to the preparation and use of baits.

Whole hempseeds are boiled vigorously for 1–2 minutes to soften the seed coat, and then are cut transversely into halves. The cut seeds are air dried (1½–1 hour), placed on filter paper in a Petri dish, and are autoclaved for

8–12 minutes at 121°C. Two or three halves are floated cut surface down on the gross culture water, or are submerged. Within 4–6 days, growth sufficient for transfer or isolation has taken place. Colonies are removed from the gross culture, washed vigorously in a stream of tap water (from a “squeeze bottle”), and placed in fresh, sterile water. Such cultures must be refrigerated if they are to be kept for several days; they soon are fouled by large populations of bacteria and protozoa if left at room temperature. Fouling may be to some degree limited by using water containing 0.01% potassium tellurite as a bacterial suppressant.

Gymnosperm or angiosperm pollen may be used, but that from species of *Pinus* is universally best. The pollen is collected fresh from shedding trees and autoclaved at 121°C for five minutes. Once sterilized, the grains are suitable as bait for several years if kept dry. The pollen is sprinkled lightly (twice the amount adhering to a dry dissecting needle dipped fully into pollen) on the gross culture water surface. Clumps of pollen — and that accumulating at the meniscus — tend to be invaded by filamentous fungi (*Pythium* spp. notoriously). Pollen used as bait in samples from marine habitats should be examined 48 hours after seeding into gross culture. Pollen in soil and freshwater cultures is examined 4–7 days after seeding.

Snakeskin, roach wings, and human hair are most effective as baits if pretreated in soil extract. Approximately 100 g of garden soil are mixed into one liter of tap water and stirred or shaken occasionally during a period of 6–8 hours. The water is then filtered through cheesecloth and absorbent cotton, then through Whatman No. 42 paper, and the filtrate reconstituted to one liter. The unsterile soil extract is poured into Petri plates. Large pieces of snakeskin (not the ventral portion), whole roach wings, and masses of human hair (blond hair, from a child 10 weeks old or less is far superior to ether-defatted hair) are floated on this soil extract. The bait is incubated in contact with the soil extract for

2–3 days at room temperature, washed in a stream of tap water, and autoclaved (121°C for ten minutes) on filter paper in Petri plates. Two or three small strips (2–3 mm wide, 4–10 mm long) of the snakeskin or of roach wing are floated on the surface of gross cultures, but will usually serve submerged as well. Pieces of hair 1–2 cm long are sprinkled lightly over the surface. Cultures should be examined at 14 days, and thereafter at weekly intervals up to 6 weeks.

Several cellulosic substrates are easily obtainable, and should be used in any regular sampling program. The preparation and use of five of the commonest sources are described in the following paragraphs.

Strips of lens paper 4–6 mm wide are autoclaved for 5 minutes (121°C) on a disc of filter paper in a Petri plate. The sterile strips are cut into 4–6 mm lengths, and floated on the surface of the culture water. Sunken pieces can be discarded since fungi will not develop on these.

Any of the common lawn grasses in Iceland are suitable for leaf bait. Leaves of any convenient length are boiled in tap water for 10 minutes, allowed to cool, and the water poured off. The leaves are then boiled gently in 100% ethyl alcohol for five minutes, and again allowed to cool to room temperature. Subsequently, the leaves are transferred to fresh tap water, boiled an additional ten minutes, removed, cut into 10 mm lengths, and autoclaved wet at 121°C for 10 minutes. The sterile leaf sections may be air dried and stored for later use, or used wet. Two sections of leaf — one floated, one submerged — are generally sufficient in any gross culture.

Waterproof or nonwaterproofed cellophane have been variously recommended. Better yields are obtained with waterproof cellophane (gently boiled to disrupt but not to remove the waterproof “coating”) floated on the culture water than from a nonwaterproof product that sinks. Convenient sized strips of cellophane (from any commercial packaging) are held by forceps onto the surface of gently boiling water for 2–4 minutes. The strips are then

cut into squares (4–5 mm on a side), and autoclaved at 121°C for five minutes. Fungi usually appear on cellophane within 10–15 days of incubation, though baits that have not been invaded during this time should be held in gross culture for an additional 2–3 weeks.

Two other cellulosic substrates may be used in place of or in addition to the foregoing. Strips of onion epidermis are peeled from the “inner” surface of scale leaves in the bulb, put in water in Petri plates, and autoclaved (10 minutes, 121°C). Pieces of the stripped epidermis are floated on the surface of gross culture in water. Unfortunately, the thin epidermal cells are subject to rapid decomposition in the gross cultures. Small mats of filamentous green algae are occasionally of some value as cellulosic bait, particularly in water samples containing decaying algae and other vegetable matter. The algae should be collected at the peak of their development before they become encrusted with diatoms and other organisms. Filaments of *Spirogyra*, *Cladophora*, *Oedogonium*, *Ulothrix*, *Zygnema*, and *Mougeotia* are most suitable; plants of *Melosira* seldom are satisfactory. Masses of filaments are boiled gently in tap water for five minutes, autoclaved in tap water (121°C for five minutes), and, when cool, placed in the gross culture dishes. The disadvantages of boiled algae, of course, are that they sink in the culture water, become encrusted with debris and various secondary organisms during incubation, and are difficult to find in the culture dishes and to examine.

Specialized substrates — human skin and termite wings, notably — are used directly in gross cultures without prior treatment other than sterilization. Whole termite wings or 2–3 small pieces (*ca.* 3 mm square) of skin are floated on the culture water. Because these substrates are readily attacked by bacteria, they are not generally useful if the cultures are to be incubated longer than 3–4 weeks.

Unless the bits of substrate (pollen excluded) have softened appreciably in gross culture, they should be washed thoroughly in a stream of tap water from a squeeze bottle before being ex-

mined. Gentle washing seldom removes any of the fungi from the baits, but it does flush away many of the fouling organisms. The rather unique structure of roach wings, however, makes them troublesome to wash after incubation. In roach wings, "upper" and "lower" chitinous layers are separated by a clear, amorphous substance which swells appreciably during the soaking that accompanies incubation. It is on this "middle layer," however, that fungi most often develop, and washing may dislodge this layer and the thalli on it. In making wet mounts for observation, particular care must be taken not to remove the inner layer inadvertently.

Whether it is more practical, in terms of yield, to use a single bait type in each gross culture, or to mix the types of substrates has not been determined. The nature of the substratum could dictate which course is followed. Some baits foul very quickly, and adding other types to dishes simply compounds this problem. I routinely use no more than two types of bait in any culture. If two kinds are used, they are of quite different make-up: hempseed and hair, cellophane and snakeskin, roach wing and lens paper, for example. Pollen is best used alone in gross cultures. It is the substratum least likely to become decomposed, but the grains often adhere to other baits, interfere with viewing, and are difficult to remove.

Certain types of bait may be placed directly into aquatic environments in the field and harvested after 3–6 weeks submergence. Hempseeds, surface sterilized by short-time autoclaving (121°C for 5 minutes), are placed in small, perforated aluminum containers (commonly called "tea balls"). These are secured to a line and anchored in a stream, pond, or lake. Some fungi inhabit submerged twigs and fruits, and these organisms, likewise, can be "trapped." Twigs are cut from local willow, birch, or ash species in a length sufficient to include current and some previous-year's woody growth. The twigs are autoclaved (121°C for 5 minutes), and enclosed (in groups of 3–6) in small, cylindrical baskets made of ordinary window screen. These "traps" are

anchored in suitable aquatic habitats, and harvested after 2–3 months submergence. Screen wire baskets are also fashioned to hold rosaceous fruits such as apples or rose hips, or the fruits of the local ornamental *Sorbus* (*Sorbus aucuparia*). Firm apples or the ash fruits are washed carefully in ether to remove the cutin (rose hips do not need this treatment), placed in the baskets and submerged. One apple per basket, or 3 or 4 rose hips or fruits of *Sorbus* are adequate. Members of the *Blastocladales*, *Leptomitales*, *Saprolegniales*, and *Peronosporales* occur on such soft and woody substrates in 5–9 weeks during the summer months. Species of *Monoblepharidales*, common on submerged woody twigs elsewhere, have not thus far been found in Iceland.

Aquatic fungi themselves, in particular the water molds. Pythiums, and some *Phlyctidiales* are parasitized occasionally by other fungi collected in gross culture. Specimens of any fungi should be examined for endo- and epibiotic parasites.

ISOLATION AND CULTURE

Although most aquatic fungi have not been cultured, great strides in developing suitable techniques have been made since about 1950. However, a single, all-purpose medium or method for isolation and culture does not exist. Emerson (1950) and Sparrow (1960) should be consulted for most major techniques.

Of the many medium formulations created by various investigators, three are particularly suitable. Emerson's (1941) YPSS agar, either $\frac{1}{2}$ or $\frac{1}{4}$ strength, is by far the best general purpose medium when 0.01% potassium tellurite (Willoughby, 1958) is added as a bacterial suppressant before autoclaving. The medium devised by Fuller, *et al.* (1964) for the isolation of marine *Phycomycetes* is with two modifications especially useful for isolating fungi from chitinous or keratinic baits in gross culture. The medium is made up with cold tap water rather than seawater, and 0.01% potassium tellurite is

substituted for penicillin and streptomycin. Cornmeal agar (Difco, dehydrated) is the best medium (Johnson, 1956; Seymour, 1970) for isolating water molds and Pythiums.

Methods for isolating nonfilamentous aquatic fungi into pure culture are mainly modifications of techniques described by Couch (1939) and Stanier (1942). Planonts from sporulating sporangia are picked from cultures by a loop or micropipette, and streaked on a dilute nutrient medium (such as $\frac{1}{4}$ strength YPSS agar). Single, germinated spores are then located with a low power lens, and transferred aseptically along with a bit of the medium to fresh agar plates or to broth. With proper streaking and the incorporation of bacterial suppressants into the media, pure cultures can be obtained of some species.

Nonfilamentous species often can be propagated in unifungal culture. Single sporangia nearly at the moment of spore discharge are dissected from baits in gross culture. These sporangia are then transferred into a sterile, plastic Petri plate containing 2–3 ml of sterile water with 0.01% potassium tellurite. Sterile bait is added. An alternative method is to sterilize glass slides (dipped in 100% ethyl alcohol and flamed), and place them on a short length of glass rod bent to a "V" shape and set in a sterile Petri plate. Sterile potassium tellurite water (1 ml) is pipetted onto the glass slide, and the dissected sporangium and new bait put into this drop of water. In either method, the substratum is removed after 48 hours, transferred to a plate containing about 40 ml of sterile tellurite water, and additional pieces of sterile bait are added.

Unifungal cultures of the chitinophilic or keratinophilic fungi can best be prepared in sterile soil extract (see p. 00 for method of preparation) water incorporating 0.01% potassium tellurite. After the soil is extracted, the filtrate is reconstituted to 1 liter and diluted 1:1 or 1:5 with tap water. The potassium tellurite is then added, and the solution is autoclaved (121°C for 15 minutes).

The chance of developing unifungal cultures on chitinous or keratinized substrates is

measurably improved by two simple treatments. The gross culture bait from which sporangia are to be dissected must be washed thoroughly and vigorously in a stream of sterile tap water. Those bits of substratum to be added to soil extract-potassium tellurite water cultures containing individual sporangia should be preincubated in contact with non-sterile soil extract at room temperature for 2–3 days (see p. 00 for method of preparation). It is highly unlikely that thalli from spores of any aquatic fungi in the soil extract can develop within the short incubation time that the substratum is in contact with it. These pre-treated substrates are in any case sterilized before use.

PRESERVATION

Short of maintaining viable, pure cultures, there is no fully satisfactory way of preserving specimens of aquatic "*Phycomycetes*." Preserving fluids invariably distort cell contents, and may shrink or collapse reproductive cells and vegetative parts. Even so, general structural features are usually visible in such preserved specimens.

Lactophenol (Amann's) solution, with a stain is a suitable mounting medium (Sparrow, 1960, describes an alternate medium of 10% glycerine and eosin). Lactophenol is a solution of 1 part phenol, 39 parts glycerin, 1 part lactic acid, and 9 parts distilled water. To this may be added a small amount of cotton blue, eosin, or acid fuchsin, the amount depending upon the stain intensity desired in the final product. A duplicate set of specimens, one in the mounting medium with cotton blue, and one with acid fuchsin provides a contrast of dark and light staining of the same structural features.

Specimens are mounted directly into a small drop of the mounting medium on a slide, positioned (or teased apart with needles if filamentous), and a circular cover glass added. The preparation is then allowed to dry for 2–3 days and a heavy coating of clear (or "natural shade") fingernail polish is applied to the cover

glass edge and slide (ringed). After the first coat dries, a second heavy application is made. Such slides must be stored flat. If properly sealed, these slides will last for many years.

Large developments of specimens or whole colonies may also be preserved in 70% alcohol. Small, 1 dram vials with tightly fitting lids ("snap-cap" brands) are suitable containers.

SYSTEMATIC ACCOUNT

Three orders of unflagellate fungi are represented in the Icelandic mycoflora: *Chytridiales*, *Blastocladales*, and *Hyphochytriales*. In the first of these, individuals are distributed in seven families (Sparrow, 1960: 120, 121).

CHYTRIDIALES

Olpidiaceae

Several species of *Olpidium*, and two of *Rozella* are known in Iceland (Johnson, 1966, 1969a; Howard and Johnson, 1969). Barr's remarks (1971) on the relationship of *Olpidium* to *Entophlyctis* should be consulted, and Booth's (1971c) account of variation in *Entophlyctis* is especially appropriate.

ROZELLA

Rozella sp. (Fig. 4, 5)

This unnamed member of the polysporangiate series (Sparrow, 1960) invaded an unidentified watermold, inducing segmentation of the host hyphae into terminal and intercalary, catenulate, ovoid, fusiform, dolioform, or cylindrical sporangia (generally 40–70 μ long). The small, ovoid to ellipsoidal planonts (Fig. 5) escaped through one or two small exit papillae. Subspherical to spherical, hyaline, smooth-walled, immature resting spores, 16–20 μ in diameter, accompanied some sporangia (Fig. 5). Until mature resting spores are found, this fungus cannot be properly identified.

The *Rozella* would not infect these species (colonies 7–12 days old): *Achlya flagellata* Coker, *A. colorata* Pringsheim, *A. papillosa* Humphrey, *A. treleaseana* (Humphrey) Kauffman, *Aphanomyces keratinophilus* (Ookubo & Kobayasi) Seymour & Johnson, *Brevilegnia unispërma* var. *montana* Coker & Braxton,

Saprolegnia ferax (Gruith.) Thuret, *S. asterophora* deBary, or *S. torulosa* deBary. The *Rozella* invaded *A. americana* Humphrey (a form with very large oögonia containing 18–25 oöspores) on one occasion, but could not then be carried over into subculture in its new host.

Synchytriaceae

Species of *Synchytrium*, the largest genus of the family, have been found in Iceland (Larsen, 1923). So far as is known, the family is further represented in this country only by the following taxon.

MICROMYCES

Micromyces zygogonii Dangeard (Figs. 6–8)

Micromyces zygogonii occurred in *Mougeotia* at Lagarfoss, Kollafjörður, Laugarvatn, and in a roadside pool east of Vogar. In all collections, most of the invaded cells were hypertrophied (Figs. 6, 7). Considerable variation existed in the density and length of the spines on the prosorus (Figs. 6–8). The collection of *Micromyces* reported by Johnson and Howard (1968) is Dangeard's species.

Phlyctidiaceae

Several species in this family are already known in Iceland (Höhnk, 1960; Johnson, 1968; Johnson and Howard, 1968; Howard and Johnson, 1969). The provisionally identified *Blyttiomycetes* on *Closterium* (Johnson and Howard, 1968) has not been recovered again, nor has *Podochytrium clavatum* Pfitzer appeared in any additional samples of algae (Johnson and Howard 1968). The fungus that Howard and Johnson (1968) tentatively allied with

P. cornutum Sparrow was found again (in 1972) on *Melosira*, but in such scanty numbers that accurate identification was not possible. Canter (1970) contends that the 1968 report of Sparrow's species is incorrect, and the illustrations she provides of *P. cornutum* certainly support her view.

PHLYCTIDIUM

The identification by Johnson and Howard (1968) of Sparrow's *Phlyctidium olla* remains unconfirmed by examination of additional specimens. *Phlyctidium anatropum* (Braun) Rabenhorst occurs in Iceland (Johnson, 1972; Höhnk, 1960), as does *P. brebissonii* (Dangeard) Sparrow (Howard, 1968), and *P. mycetophagum* Karling (Johnson and Howard, 1972). Howard (1968) has also found other species of *Phlyctidium* (he did not name them), and has proposed reassigning *Rhizophydium braunii* (Dangeard) Fischer to *Phlyctidium*. No chytrids similar to the one on which he based this decision have appeared in any subsequent collections.

Phlyctidium tenue Sparrow (Fig. 9–13)

Alliance of a chytrid occurring on *Zygnema* sp. (Herb. No. 3302, 3306) with Sparrow's species is done with reservation. That the specimens are of a *Phlyctidium* is established by the tubular nature of the endobiotic system (variously designated as a rhizoid or ahaustorium).

The rudimentary sporangium is a globose, subglobose, or hemispherical enlargement of an encysted planont (Fig. 9), but it lacks a prominent discharge tube or papilla. Planonts are formed endogenously, and emerge rapidly through a large, lateral pore (Fig. 11). As discharge proceeds, that portion of the wall opposite the pore collapses (Fig. 11), and the empty sporangium takes on a distinctly pyriform, turbinate, or napiform (Figs. 12, 13) aspect. Usually the collapsed basal portion of the emptied sporangium is slightly wrinkled, and occasionally shows very fine striations. The globose sporangia are 12–(15–18)–28 μ in diameter; subglobose or hemispherical ones are

16–(21–27)–34 μ in diameter by 8–(10–12)–15 μ high. There were no resting spores.

The Iceland specimens are like *Phlyctidium tenue* (Sparrow, 1952) in sporangium shape and size, and they occur on a species of *Zygnema* as does his fungus. There are noteworthy differences between Sparrow's species and my specimens. Planonts of *P. tenue* as described by Sparrow emerge through an apical orifice rather than a lateral one (Fig. 11). Further, the plants from Iceland lack the thickened basal wall characteristic of *P. tenue*.

In *Phlyctidium tenue* and in my specimens as well, the sporangia collapse after discharge, and it is on this basis that I align my collection with that species. Should the fungus again be recovered, it must be cultured, transferred if possible to other algae, and again characterized. The results might show it to be incorrectly named as it is now assigned. Certainly the characteristics of a large, lateral orifice coupled with basal collapsing of the sporangium are without parallel among other species of the genus.

Phlyctidium sp. 1 (Figs. 14–17)

Sporangium sessile; erect, generally oblong-ellipsoidal, occasionally depressed-globose or broadly obovate; smooth-walled; exit papilla absent; 11–(13–16)–20 μ high by 8–(10–12)–15 μ in diameter. Endobiotic system slender, cylindrical, peg-like. Planonts posteriorly uniflagellate; spherical, 2.5–4.5 μ in diameter; escaping through a large, apical orifice or one or two subapical pores dissolved in the sporangial wall.

On *Rhizophydium* sp. on snakeskin bait in soil from barnyard, farm on Ellidavatnsvegur, east of Hafnarfjörður, 30 May 1971 (Herb. No. 3051).

With the exception of *Phlyctidium mycetophagum* Karling and the doubtfully valid *P. dangeardii* Serbinow, species of *Phlyctidium* occur on algae. Karling's *Phlyctidium* invades a wide range of fungi, among which are *Rhizophydium* species. The similarity in host suggests that the fungus from Iceland might be *P. mycetophagum*, but the sporan-

gia of *Phlyctidium* sp. 1 are obviously very different from those of Karling's species. The small, apical papilla on the sporangium of (?)*P. dangeardii* (and absence of information on the nature of the endobiotic system in that fungus) prevents identification of the Iceland material with Serbinow's species.

The broad, apical discharge pore of *Phlyctidium* sp. 1 seems to be a reasonably constant feature. Small sporangia of Sparrow's *P. megastomum* resemble those of *Phlyctidium* sp. 1 but in my material these cells are not urceolate after discharge. Additionally, the spores of *P. megastomum* enlarge during the time they are motile, and this feature obviously sets it off from the Iceland fungus even if host (*Anabaena flos-aquae* for *P. megastomum*) is ignored.

None of the known species of *Phlyctidium* accomodates this one on *Rhizophydium*. The specimens in the one collection are very sparse, and it would be unwise to identify the species without additional material. Certainly nothing is known of the plant's degree of variability (but see also discussion under the species following).

Some sporangia have adjacent to them (Fig. 17) small, spherical, thick-walled cells attached to the *Rhizophydium* by a tubular endobiotic system. Whether or not these are resting spores of the *Phlyctidium* remains to be determined by culture work.

Phlyctidium sp. 2 (Figs. 261–271)

Sporangium sessile, erect; oval, ovoid, dolioform, or broadly ellipsoidal prior to discharge; ovoid, broadly ellipsoidal or (rarely) urceolate after planont release; smooth-walled; producing an apical (rarely subapical), broad, inconspicuous exit papilla; 9–(10–13)–16 μ high by 7–(9–11)–14 μ in diameter. Endobiotic system slender, inconspicuous, thread- or peg-like. Planonts few, endogenously formed; posteriorly uniflagellate; spherical, but becoming ovoid on release; 3–4 μ in diameter; escaping through a broad exit pore dissolved in the sporangium wall, and swimming at once.

On *Rhizophlyctis* sp. on human skin (bait) in soil at edge of drainage stream below barn-

yard, farm on Ellidavatnsvegur, east of Hafnarfjörður, 30 May 1971 (Herb. No. 3052).

The resemblance of this chytrid (Fig. 261) to *Phlyctidium* sp. 1 (Fig. 16) is at once apparent but the sporangia of *Phlyctidium* sp. 2 are smaller than those of the former, and, of course, occur on a different host. The sporangia of this *Phlyctidium* on *Rhizophlyctis* are generally ovoid in contrast to the ellipsoidal ones of *Phlyctidium* sp. 1 on *Rhizophydium*. Occasionally on the host there are small (7–10 μ diameter), spherical, thick-walled cells (Fig. 267) adjacent to the sporangia of the *Phlyctidium*. These may or may not be resting spores of this fungus, but their likeness to the cells accompanying sporangia of *Phlyctidium* sp. 1 (Fig. 17) is certainly striking.

Phlyctidium sp. 1 and sp. 2 may, in fact, prove to be manifestation of the same species, with the slight differences in morphology and size being a response to dissimilar substrates. Neither could be cultured (nor carried through gross culture techniques to propagate them on additional bait). Accordingly, their true relationship and identities remain unknown.

Willoughby's (1962) *Chytriomycetes* sp. 2 on *Rhizophydium elyensis* Sparrow has sporangia within the size range of *Phlyctidium* sp. 2. The empty sporangia of Willoughby's plants (he did not see planont discharge) are urceolate, whereas those among the Iceland specimens are rarely so. However, Willoughby illustrates resting spores for *Chytriomycetes* sp. 2 that are indistinguishable from the spherical cells I find associated with sporangia of *Phlyctidium* sp. 2. One of the resting spores figured by Willoughby clearly has a phlyctidiaceous endobiotic system. Whether or not *Phlyctidium* sp. 2 and the *Chytriomycetes* are the same taxon — as circumstantial evidence would suggest — must await the results of culture and cross-inoculation studies, and the discovery of the discharge mechanism in Willoughby's species.

SEPTOSPERMA

Septosperma anomala (Couch) Whiffen ex Seymour (Figs. 19–24)

Four collections of this species have been made. In two (Herb. Nos. 53, 2444), the specimens occurred on a monocentric chytrid having roughened, verrucose, bullate, or warted sporangia. The immature epibiotic sporangia of the host are conspicuously or faintly ornamented (Figs 23, 24), and are sometimes slightly irregular. The rhizoidal system is sparingly branched and nonapophysate.

The fungus with roughened, verrucose sporangia (Figs. 144, 146–149) assigned provisionally to *Phlyctochytrium* resembles this host for *Septosperma anomala*. The *Phlyctochytrium*, however, is apophysate. Willoughby's (1961) "monocentric sp. 2" is also very suggestive of this host for *S. anomala*. In the absence of sporulating thalli the host fungus remains unidentified. Because none of the sporangia had prolonged exit tubes, I am inclined to favor assignment to *Rhizophyidium* rather than to *Rhizidiomyces*. Mature sporangia will have to be discovered to settle identification.

In two other collections this *Septosperma* also occurred on a *Rhizophyidium* whose size, shape and smooth-wall condition recall *R. pollinis-pini*. This host likewise did not mature, hence is unidentified.

Neither Couch (1932) — who first described *Septosperma anomala* (as *Phlyctidium anomalum*) — nor Whiffen (1942) observed spore discharge in the species. Canter (1949) saw planonts of *S. anomala*, but did not describe their emergence. The spores of *S. spinosa* Willoughby (1965) are released through one or two orifices. I followed planont discharge from sporangia among my specimens. The planonts are cleaved endogenously (Fig. 20) as polygonal units, emerge through an apical pore (Fig. 21), cluster briefly there, and then rapidly dart away (Fig. 22). The pattern in *S. anomala* thus differs slightly from that in *S. rhizophidii* where the planonts swim directly on emergence.

I have not seen the full extent of the endobiotic system in *Septosperma anomala*. Indications are that the endobiotic portion is a very short, peg- or thread-like process. Both

Couch (1932) and Canter (1949) describe the system as bulbous or discoid. It should be emphasized that *S. anomala* produces "stalked" sporangia (Fig. 24) and resting spores (Fig. 23) as well as sessile ones. The endobiotic portion of these stalked thalli is certainly thread-like. In this regard, *S. anomala* parallels *S. rhizophidii* and *S. spinosa*, which also form stipitate thalli.

Septosperma rhizophidii (Couch) Whiffen ex Seymour (Fig. 18)

This species has been found twice (Herb. Nos. 1914 and 1998) on an unidentified *Rhizophyidium* growing on snakeskin bait floated in 20 ml water cultures of pasture soils from Heimaey (26 June 1967).

As Seymour (1971) notes, *Septosperma rhizophidii* invades immature sporangia very readily. Indeed, none of the sporangia of the *Rhizophyidium* from Heimaey matured sufficiently to form spore initials.

Seymour (1971) gave an extensive account of thallus development in *Septosperma rhizophidii*, validating the genus (Whiffen, 1942) and its species. Insofar as I can judge from my material, *S. rhizophidii* differs from *S. anomala* only in sporangium size and shape, and in resting spore size. Seymour, who was the first to describe planont discharge in *S. rhizophidii*, noted that these cells swim away immediately on release.

Booth (1969) collected *S. rhizophidii* on *Rhizophyidium chytriomycetis* Karling from soil subject to periodic salt spray or tidal waters.

PHLYCTOCHYTRIUM

Several species have already been reported (Johnson, 1968, 1969; Johnson and Howard, 1968). Höhnk (1960) has also found three species which I have not recovered: *Phlyctochytrium chaetiferum* Karling, *P. laterale* Sparrow, and *P. proliferum* Ingold. Neither the unidentified marine *Phlyctochytrium* with ornamented sporangia (Johnson and Howard, 1968) nor the *Phlyctochytrium*-like fungus with the prominent, tapering discharge

tube reminiscent of *Rhizidiomyces apophysatus* Zopf (Howard and Johnson, 1969; Johnson 1969b) have again been collected. The *Phlyctochytrium* sp. illustrated by me (1969b: Figs. 20, 21) is *Chytridiomyces vallesiacus* Persiel (Johnson, 1971). Remarks on the identity of Howard's (1968) *P. islandicum* (a *nomen nudum*) are to be found in an account of hyperparasitism of an *Achlya* (Johnson and Howard, 1972).

Phlyctochytrium aureliae Ajello (Fig. 25–33)

One of the most striking of the members of the genus with ornamented sporangia, this species is relatively common on roach and termite wings, snakeskin, and pollen (baits). The latter is an unusual substratum for the fungus, but Booth (1971b) has also collected it on pollen.

The most common form of *Phlyctochytrium aureliae* in Iceland is that with prominent, bipartite, scattered teeth (Figs. 25–30). In none of the several collections does this form display the broad range of variation in sporangial ornamentation that Booth (1971b) found in his "*Rhizophydium* sp. — *Phlyctochytrium aurilae* (sic) complex." Certainly the polypartite enations that he illustrates are unlike any of the ornamentations on my plants.

The second form of Ajello's species (Figs. 31–33) was found twice on pollen (in one instance accompanied by *Phlyctochytrium reinboldtae* Persiel). This variant had short, broad, bipartite enations and short spines that were often few in number and were scattered widely on the surface of the sporangium (Fig. 33). The scarcity of prominent spines hardly seems taxonomically important in view of variants already admitted to this species.

Phlyctochytrium lagenaria (Schenk) Domjan (Figs. 41–52)

This species was found on nine occasions on *Spirogyra crassa* and *Spirogyra* sp., but in only three localities: Laugarvatn, Raudavatn and Ellidavatn. In three instances the zygospores of *Spirogyra* were also invaded by a *Lagenidium*. While the *Phlyctochytrium* would not grow

on artificial media, it transferred readily to boiled mats of *Spirogyra* sp. The subsequent account of sporangium morphology is based on these unifungal cultures. Since the species is evidently poorly known from only two previous collections (see Sparrow, 1960), some details on the structure of the Iceland plants seem warranted.

The epibiotic, inoperculate sporangia are sessile, spherical to subspherical, or ovoid (only very infrequently depressed-globose; Fig. 46, in part), and possess a broad, shallow, apical (Fig. 51) or subapical (Figs. 41, 42) exit papilla. At maturity (containing well-defined spore initials) the sporangia are 7–(10–14)–23 μ in diameter. The endobiotic system is a large and bulbous (Fig. 42), turbinate (Figs. 44, 45, 46 in part) or narrow and strap- or taproot-like (Figs. 43, 52) apophysis 3–12 μ in diameter, and has sparingly branched rhizoids.

The substratum is penetrated by a small, needle-like tube or peg (Fig. 47). This apparatus enlarges (Fig. 49) into an apophysis with rhizoids (Fig. 48) usually before the settled planont (Fig. 47) begins to develop into the sporangium. Near the time of sporulation, the sporangium rudiment (Fig. 43) develops a conspicuous exit papilla (Fig. 42). Planonts form endogenously (Fig. 51), and escape in a gelatinous matrix as the exit papilla dissolves (Fig. 52). The matrix does not surround the emerging spore mass fully and the planonts swim away shortly after release. The planonts are ovoid, 2.5–3.5 μ long by 2–3 μ in diameter, and have a single, posterior flagellum 10–16 μ long.

Emptied sporangia display a broad, apical or subapical, slightly raised orifice (Figs. 44, 46 in part), and a slight thickening (Fig. 44) of the wall at the site of this opening. Soon after discharge, the sporangia collapse (Fig. 45).

This species is an inoperculate counterpart of *Chytridium lagenaria* Schenk. Howard (1968) found what is unquestionably the operculate *Chytridium* on filaments of *Cladophora* from Thingvallavatn. Subsequent collections in the same locality failed to turn up this species.

Howard and Johnson (1969) reported this species, but neither characterized nor illustrated it. The uncertainties of identification encountered among the multiporous species of *Phlyctochytrium* are prominent with the species.

The sporangium of *Phlyctochytrium papillatum* is presumably to be recognized chiefly by the 3–4 well-defined, elevated discharge tubes (Sparrow, 1952). *Phlyctochytrium reinboldtae*, however, also found on pollen bait, often has only a few prominent papillae (compare Figs. 35, 37). The discharge papillae of *P. papillatum* are cylindrical or broadly conical, and each terminates in a hyaline, broad and shallow, gelatinous plug (Figs. 35, 36). By contrast, those of *P. reinboldtae* are narrowly conical, and each ends in a small plug that imparts a mammiform aspect to the discharge apparatus (Fig. 40, for example). If, as could well be the case, Barr's (1970a) specimens were indeed *P. reinboldtae*, then separating this species from *P. papillatum* on the basis of papilla structure is no longer possible. Some of the photographs presented by Barr (1970a: figs. 6–8, for example) are of *P. reinboldtae* sporangia that are indistinguishable from those of Sparrow's species.

Although *Phlyctochytrium synchytrii* Kohler (see Sparrow, 1960) has not appeared in any of my collections, it has been found on pollen elsewhere. Booth's (1971a) illustrations of *P. synchytrii* leave little doubt of the remarkable similarity between the sporangia of Kohler's species and those of *P. papillatum*. Curiously, the one notable characteristic of *P. synchytrii* — planont discharge through sessile pores rather than papillae — seems ignored in subsequent accounts. Booth (1971), for example, refers to "... papillar dissolution ..." in characterizing planont escape in *P. synchytrii*.

Phlyctochytrium papillatum is rather variable. Sporangia of plants collected by Howard and Johnson (1969) were no more than 19 μ in diameter. In my material (Herb. Nos. 1159, 1883, 3411) the sporangia (exclusive of the discharge papillae) are 16–(28–32)–38 μ

in diam., a predominant size noticeably larger than Sparrow recorded. Nearly one-half of the sporangia in my collections have 7–9 discharge papillae. Howard (1968) reported a form of this species in which the papillae are short (3 μ long, maximum) and narrow (2.5 μ in diameter). I have found on pine pollen resting spores ornamented like those attributed to *P. papillatum*, but never in association with sporangia of this same species.

For the present, *Phlyctochytrium papillatum* is maintained as a distinct species among the other morphologically similar fungi also oomultiporous taxa of the genus. The species should be cultured extensively, however, to determine its limits, for it plainly approaches other morphologically similar fungi also occurring on pine pollen.

Phlyctochytrium planicorne Atkinson (Figs. 53–69)

Inoperculate, apophysate, epiendobiotic fungi identified as this species are common in Iceland, and at least a few sporangia (mixed with *Rhizophyidium* species) are usually found on pollen seeded in wet soil samples from marshy areas. *Phlyctochytrium planicorne* occurs only on pollen here, and could not be transferred to boiled *Spirogyra*, cellophane strips, or onion bulb epidermis. However, I have propagated it in unifungal culture (see Isolation and Culture) from plants in one collection (Herb. No. 10303). There is some uncertainty about the identification of the plants from Iceland.

The hyaline sporangia, often somewhat flattened basally, are broadly ellipsoidal or broadly ovoid (Figs. 55, 57), but occasionally are nearly spherical (Fig. 56, in part). They vary considerably in size: 8–(11–16)–31 μ high, inclusive of the apical projections, and 6–(10–14)–22 μ in diameter. Positioned at the apex are 3–(4)–6 short, blunt, incurved, tapering projections (Figs. 54–57). These projections may be short and knob-like (Fig. 53), but they are always in a single row surrounding the discharge pore (Figs. 54, 66).

A spherical, subspherical, or turbinate apop-

hysis, 3–(5–7)–11 μ in diameter, subtends the sporangium. Stout rhizoidal branches originate at the apophysis, but the full extent of the endobiotic system has not been seen.

Spherical, epibiotic resting spores occur within ornamented cells indistinguishable from the sporangia (Figs. 67–69). The mature(?) resting spores – 8–(10–12)–15 μ in diameter – are thick-walled, possess a peripheral sphere of faintly refractive bodies, and may (Fig. 68) or may not (Fig. 69) fill the enclosing cell. The endobiotic portion is apophysate and rhizoidal. Successive stages in development or germination of the resting spores were not seen. These cells are, however, identical to the ones first described by Umphlett and Holland (1960).

A slender, thread-like penetration “peg” from a settled planont (Fig. 59) initiates invasion of the substratum. The penetration apparatus enlarges (Figs. 60, 61) into the apophysis and its attendant rhizoids, while the planont itself expands (Figs. 62–64) into a sporangial rudiment. The apical projections result from localized apical growth of the developing sporangium (Fig. 65). Spherical, endogenously-formed planonts, 3–4 μ in diameter, escape singly and rapidly at the dissolution of an apical orifice (Fig. 66). Motile cells contain one or two refractive bodies, are often ovoid to broadly ellipsoidal, and have a long (26–30 μ) posterior flagellum. There is no enveloping matrix or vesicle.

In size and shape of the sporangium and apophysis, and in their inoperculate discharge, the specimens at hand are accommodated easily within the limits of *Phlyctochytrium planicorne* (Sparrow, 1960). The obvious difference, of course, is in the nature of the sporangium ornamentations. Sparrow (1960) illustrates them unmistakably as sharply-pointed teeth or spines, and refers to their highly refractive nature. The one illustration provided by Atkinson (1909: fig. 7) is woefully inadequate in depicting the sporangial ornamentations, but there can be no doubt from the descriptive matter that he judged the processes to be dentate. In my plants, on the

contrary, the ornamentations are blunt, and, though noticeably refractive at the tip, are merely digitate, tapering extensions of the sporangium wall.

The *Phlyctochytrium magnum* described by Linder (1947) has blunt, digitate wall ornamentations. In Linder's species, however, the projections are arranged in four pairs. From a collection in the Canadian Eastern Arctic, Linder reported the questionably assigned *Rhizophydium digitatum* Scherffel. The sporangia of this fungus were 9 μ in diameter – a size obviously close to *P. planicorne* – but there were five blunt projections on the sporangia. As Linder was unsure of the nature of what appeared to be a bulbous endobiotic system, he could not assign the specimens confidently to *Rhizophydium*. He suggested that the fungus might be placed in *Phlyctochytrium* if there was in fact an intramatrical vesicle and the sporangia were inoperculate. The one figure accompanying Linder's account (1947: pl. 13, fig. G) of *R. digitatum* is indistinguishable from the general aspect displayed by the immature thalli of *P. planicorne*. The same might well be said for his *P. magnum*. As the preserved specimens were sparse (each in a single collection of *Zygnema*), neither of these fungi reported by Linder is well-known. Both could be viewed as extreme forms of *P. planicorne*.

Willoughby (1961: text fig. 4) illustrates ornamentations on some specimens of *Phlyctochytrium planicorne*. One of the variations shown is very similar to the blunt, incurved ones on sporangia in my plants. In an early stage of sporangium maturation, a fungus provisionally identified by Booth (1971b) as *P. dentiferum*, has blunt projections quite like those on the Iceland specimens. The *P. planicorne* figured (as *Phlyctochytrium* sp.) by Willoughby (1962: text fig. 4h) has spiny ornamentations. Konno (1972: pl. 3, fig. F) illustrates the sporangia of *P. planicorne* (on *Spirogyra*) with four acute projections, but Kobayasi, *et al.* (1971) show blunt and pointed ornamentations. The fungus (on pollen) described by Kobayasi and Konno

as *Chytridium corniculatum* (Kobayasi, *et al.*, 1971) has 2–4 blunt projections on its sporangia. As these ornamentations are figured by the authors, they are undeniably like those on his *Phlyctochytrium* from Iceland. Their chytrid is operculate and nonapophysate. It should be noted that the reduction by Kobayasi and Konno of *C. cornutum* Braun to synonymy with *C. corniculatum* is possibly unintentional. Certainly their species contrasts sharply with Canter's (1963) characterization of Braun's fungus.

The "usual" substratum for *Phlyctochytrium planicorne* is filamentous algae, although Sparrow has found the fungus on decaying tissue of *Acorus calamus*. Willoughby (1961, 1962) collected this species on cellophane, grass leaves, shrimp exoskeleton, and onion bulb epidermis. That the fungus can also occur on pine pollen is thus not particularly startling.

Whether *Phlyctochytrium planicorne* is in reality a complex of two forms — one with acute, one with blunt projections — or a single, highly variable species with respect to its ornamentations needs careful scrutiny with additional specimens in culture. To include the Iceland plants in Atkinson's species alters its description, but does not make it unrecognizable. The unnamed fungus (on *Spirogyra*, from Raudavatn) reported by Johnson and Howard (1968: 308, species No. 3) is probably his *Phlyctochytrium*. As their specimens are lost there is no way to be certain of this identification.

Phlyctochytrium reinboldtae Persiel (Figs. 37–40)

Conspicuous, mammiform papillae mark this species (but see discussion of *Phlyctochytrium papillatum*). The apex of the exit papilla is closed by a gelatinous plug that dissolves prior to planont emergence.

Howard's specimens (1968) of this species had up to 6 exit papillae; Persiel reported (1959) 1–14 such structures, and I find them to be more numerous (predominantly 6–10) than Howard noted. In Howard's plants,

the apophyses were less than half the diameter recorded for the type, and the planonts emerged to cluster in a mass at the orifice before dispersing. The planonts in my specimens, as in Persiel's, emerge singly through one or more papillae and swim away immediately.

Phlyctochytrium semiglobiferum — *P. africanum* — *Phlyctochytrium* sp. complex (Fig. 70–89)

A number of specimens believed to represent three species with certain prominent features in common were collected on pine pollen in several localities. The structural similarities among these fungi are such that the plants are best considered as a group. Attention is first given to the appearance of the fungi in uni-fungal culture on sterile pollen, in sterile tap water (see Isolation and Culture).

Phlyctochytrium semiglobiferum Uebelmesser (Fig. 70–71) is ostensibly to be recognized by its broad but shallow, hemispherical papillae (Fig. 70). However, this point is not universally agreed upon. Sparrow (1968) reports 10–12 papillae (some other investigators mention no more than 5) and characterizes them as conical structures. A photograph of *P. semiglobiferum* by Booth (1969) shows hemispherical papillae, but an accompanying line drawing depicts conical ones. In a later account (1971b), Booth notes hemispherical papillae for the species. *Phlyctochytrium semiglobiferum* produces turbinate apophyses on pollen according to the original description, but has narrow and elongate ones in agar.

Separation of *Phlyctochytrium semiglobiferum* from *P. palustre* Gaertner (1954) is allegedly possible on two characters: shape of the apophysis and exit papillae. In *P. semiglobiferum* the apophysis is turbinate and the papillae are hemispherical, whereas in Gaertner's species they are spherical and conical, respectively. None of the variations in my experimental plants of *P. semiglobiferum* included individuals with spherical apophyses, but in an enriched medium, specimens produced conical papillae (Fig. 80). Booth (1969) has right-

fully pointed to the uncertainty surrounding attempts to separate these two species.

Small, hyaline, broadly conical, scattered exit papillae (Figs. 73, 74) and branched or unbranched, taproot-like apophyses and coarse rhizoids (Figs. 74, 75) are the features that best seem to characterize *Phlyctochytrium africanum* Gaertner (1954). The illustrations by Booth (1971a) show exit pores that are evidently not on raised papillae. *Phlyctochytrium africanum* is closely allied to *P. acuminatum* Barr (1969) in shape and size of papillae, but Barr's species is nonapophysate. Booth (1971a) in illustrating the fungus he identified as *P. africanum*, shows an endobiotic system of a stout, extensively branched complex of rhizoids. I find similar systems in experimental plants of *P. semiglobiferum* and *P. africanum*. Since the "hourglass-shaped" exit papillae of *P. spectabile* Uebelmesser seem rather distinctive, I am not certain that this species can be linked with *P. africanum* as Booth (1971a) implies. It should be recognized, however, that Booth has also (1971b) illustrated *P. africanum* with short, hyaline papillae.

Phlyctochytrium sp. (Figs. 82–89) defies proper identification. A formal description, drawn from the structure and development of plants in unifungal culture (see Isolation and Culture) on pine pollen in tap water follows.

Sporangium epibiotic, sessile; spherical or subspherical; thin-walled; provided with 1–30 or more small, inconspicuous, broadly conical exit papillae 3–5 μ wide by 2–3 μ high; 18–(29–42)–63 μ in diameter. Endobiotic system consisting of a spherical or subspherical apophysis 4–(9–16)–26 μ in diameter, from which 1–5 stout, sparingly branched rhizoidal axes arise. Planonts posteriorly uniflagellate, endogenously formed: spherical (3–5.5 μ in diameter) but becoming ovoid (6–8 μ long by 3–4 μ in diameter) on release from the sporangium; containing a single, small, posteriorly positioned refractive body; flagellum 18–25 μ long. Resting spores not observed.

The multiplicity of small exit papillae allies this *Phlyctochytrium* chiefly with Barr's

(1970c) *P. arcticum*. The Iceland specimens have globose apophyses, as does Barr's species, but not ones resembling the peg-like structures he also reports. A second difference is in planont structure: a single globule in those of my plants, multiple ones in Barr's. The taxonomic significance of this is yet to be explored.

Although its apophysis is elongate rather than globose, *P. californicum* Barr (1969) also has multiple, slightly raised papillae as does *Phlyctochytrium* sp. In other features there are also parallels: spherical, apophysate sporangia, and planonts with a single globule. Exit papillae in *P. californicum*, however, are more prominently displayed than in this unnamed fungus from Iceland. The growth expressions of *Phlyctochytrium* sp. in a nutrient medium and in soil extract suggest that prominence of papillae is so variable as to be of no taxonomic value.

None of the foregoing identifications of species from Iceland is wholly satisfactory. Barr (1969) and Kazama (1972) have shown that the nature of rhizoids and apophyses is quite variable when the thalli producing them develop in pure culture on agar media. It is equally important in establishing the limits of variation to characterize thalli on pollen in pure culture, since the multiporous species of *Phlyctochytrium* are often collected on and identified from this substratum. To explore to a limited extent the range of variation in the three species from Iceland, I propagated them in pure culture (on pollen) under two environmental conditions.

The fungi were isolated and propagated on 1/2 strength YPSS agar following the method described by Barr (1969). Potassium tellurite (0.01%) rather than neomycin was used as a bacterial suppressant. When pure cultures of the fungi were established on the agar, sporangia were transferred to sterile liquid media and sterile pine pollen was added. Thalli that had developed on this pollen were then characterized.

Pure cultures were also propagated (on pollen) on a soil extract medium (see Isolation and

Culture) and on an enriched soil extract. The enriched soil extract consisted of a reconstituted soil extract filtrate in which was dissolved prior to sterilization 0.3% each of Difco malt extract and peptone, 0.1% Difco yeast extract, and 1.0% glucose.

It was usually possible to see (though faintly) the endobiotic system of thalli on the pollen. However, as a check on these direct observations, I mounted infested pollen in 0.2 N KOH (Barr, 1969) on a glass slide, added a coverslip, and gently ruptured the grains by tapping lightly on the coverglass. Some pollen protoplasts were extruded in this fashion and usually these bore intact apophysis and rhizoids of the particular fungi.

In the soil extract medium, *Phlyctochytrium semiglobiferum* produced sporangia very similar in shape and size (Figs. 78, 79) to those grown in tap water (Fig. 70, 71). The papillae, however, were broadly conical rather than hemispherical. Apophyses were usually globose or turbinate (Fig. 78) like those of the controls (pollen in tap water), but in about 20% of the thalli, they were prominently branched (Fig. 79). Plants in the enriched soil extract showed certain modifications. Each exit papilla displayed a spherical, mucilaginous plug (Fig. 80) that expanded as the planonts emerged to form a rapidly-dissolving matrix. No matrix was associated with discharging sporangia in the control or non-enriched soil extract cultures. The apophyses of the plants in the enriched medium were profusely branched (Figs. 80, 81), and the exit papillae were again broadly conical. Thus, the two features taxonomically decisive in *P. semiglobiferum* were modified.

Sporangia of *Phlyctochytrium africanum* in soil extract culture were indistinguishable from those produced on pollen in tap water (controls, Figs. 73–75). In enriched soil extract, on the other hand, the sporangia formed much more prominent exit papillae than had the control plants, and each papilla terminated in a conspicuous, cylindrical or spherical mucilaginous plug. On some sporangia these plugs were very large, recalling those of *P.*

kniepii Gaertner collected by Booth (1971b). In *P. africanum* as in *P. semiglobiferum* thalli produced in the enriched soil extract developed conspicuously branched apophyses (Fig. 77).

Of the three fungi in this complex of the genus, the most variable one appears to be *Phlyctochytrium* sp. On pollen in unfortified soil extract, the exit papillae were broadly conical and pronounced (Fig. 84, 85), in contrast to the small, barely perceptible ones (Figs. 82, 83) on sporangia in the control cultures. Soil extract had no noticeable effect on the shape of the apophysis or the extent of its rhizoids. In the enriched soil extract, the exit papillae on sporangia of *Phlyctochytrium* sp. were again large and obvious, and additionally each had a hyaline, mucilaginous plug. The apophysis was also noticeably branched (Figs. 87, 88) as was true for the other fungi grown in enriched soil extract.

Specimens of *Phlyctochytrium* sp. in soil extract produced numerous, fairly prominent, conical papillae. Such plants recall those identified by Booth (1969, 1971a) as *P. spectabile*. However, unlike the papillae of *P. spectabile*, those in my specimens (Fig. 84) were neither hemispherical nor evenly spaced. Booth (1971a) reported that *P. palustre* (Gaertner, 1954) produced up to 12 exit papillae on thalli grown in pure culture. This condition, of course, approaches the culture-induced variations in *Phlyctochytrium* sp.

The foregoing results of rather unrefined experimental work do not solve any taxonomic problems surrounding these species of *Phlyctochytrium*, but they do show something of variability to be expected. For example, by a simple culture manipulation the morphology of *Phlyctochytrium* sp. has been modified in such a way that the plants resemble those of *P. africanum*. Barr's observation on the fungi he investigated is particularly pertinent in this regard. He isolated and grew certain chytrids in pure culture, then transferred the species back to pollen. When propagated to maturity the species "... became almost indistinguishable from each other"

(Barr, 1969: 994). The illustrations he provides cogently confirm this statement.

Most investigators of the multiporous, non-ornamented species of *Phlyctochytrium* (Barr, 1970; Booth, 1971a, b; Kazama, 1972) recognize the extreme difficulty encountered in identifying species, and the poorly defined or variable characteristics on which specific determination is based. In a commendable display of caution, Kazama characterized extensively a *Phlyctochytrium* on *Bryopsis plumosa* (Hudson) C. Agardh, but did not attempt to name the fungus. He found the nature of the rhizoidal system, sporangium size, and the number and position of exit papillae to be highly variable. Certainly the results of my unrefined experiments with the three chytrids from Iceland are not at variance with Kazama's conclusions. One has but to compare illustrations and descriptions of various taxa in the genus identified by highly competent investigators (Barr, 1969; Booth, 1971a, b; Willoughby, 1965) to appreciate the latitude allowed in the delimitations of the various species. A broadly fashioned comparative morphological study of the whole spectrum of these multiporous fungi, coupled with bold steps in taxonomic decisions, is obviously necessary.

(?) *Phlyctochytrium* sp. (Figs. 144, 146–149)

A fungus with densely or sparsely roughened, apophysate sporangia has been collected on six occasions (Herb. Nos. 331, 333, 978, 1380, 1579, 1653) on pollen. The apophysis relates the species (not exclusively, of course) to *Phlyctochytrium*, but since planont discharge was not seen, a firm assignment to a particular genus is impossible. The roughened nature of the sporangium wall is like that of the host fungus for *Septosperma anomala*. That organism is possibly a *Rhizophydium* by reason of its nonapophysate, branched rhizoidal system. It is well known, however, that some presumably apophysate fungi are not always provided with such a structure.

A description of the plants follows. Preserved specimens in the collections are collapsed

or freed from the pollen grains and most are unrecognizably distorted by the mounting fluid.

Sporangium epibiotic, sessile or stalked; spherical to subspherical; wall densely or sparingly finely warted or roughened; opening by a large, circular, subapical, lateral, or nearly basal exit pore; frequently collapsing; 14–(21–30)–38 μ in diameter. Apophysis epibiotic, and then cylindrical or broad and tapering, or endobiotic and globose; extended into at least one main rhizoidal branch; 8–14 μ in diameter. Other features unknown.

RHIZOPHYDIUM

Certain of the very commonest species of *Rhizophydium* have already been reported (Johnson, 1968, 1972; Howard and Johnson, 1969; Howard, 1968; Höhnk, 1960) from Iceland, but not necessarily illustrated or described adequately. The doubtfully assigned *Rhizophydium* found by Johnson and Howard (1968) on *Vaucheria* has not been again recovered and therefore remains unidentified.

The accuracy of the report of *R. globosum* by me (Johnson, 1968) and by Howard and Johnson (1969) is in doubt, but in the absence of specimens cannot be confirmed. *Rhizophydium mammillatum* (Braun) Fischer and *R. macrosporum* Karling collected by Höhnk (1960) in Iceland were searched for repeatedly in the same localities visited by him, but without success. Some keratinophilic representatives – *R. keratinophilum* Karling, *R. nodulosum* Karling, *R. condylosum* Karling, and an unnamed variant – are discussed and illustrated elsewhere (Johnson, 1973c).

Rhizophydium carpophilum (Zopf) Fischer (Fig. 90–93; 94–98)

Howard and Johnson (1969) earlier reported this species, but provided no illustrations or descriptive notes, and did not identify the host. The species has since appeared in two collections on oögonia of *Achlya fla-*

gellata Coker (Herb. Nos. 2227, 8166). A somewhat different *Rhizophyidium* (Figs. 94–98 on *Achlya colorata* Pringsheim (Herb. No. 3238) is provisionally identified as a form of the *R. carpophilum* on *A. flagellata*.

Sporangia of the *Rhizophyidium* on *Achlya flagellata* (Figs. 90–93) are surprisingly uniform in size — 15–22 μ high by 11–16 μ in diameter — and shape (predominantly obturbinate to ovoid). They are sessile (Figs. 90, 92), often clustered (Fig. 93), and prior to planont release exhibit a well-defined, broadly conical and shallow, apical or subapical exit papilla (Fig. 90, 93). The endogenously formed spores are motile (Fig. 92) as they escape, and each possesses a long (25–30 μ), posterior flagellum. Slender, tapering, sparingly-branched rhizoids (Figs. 93) constitute the endobiotic system. Neither of the collections contained resting spores.

The fungus (Figs. 94–98) on *Achlya colorata* differs in several major respects from that on *A. flagellata*, as the following formal description shows.

Sporangium sessile; generally depressed globose to ovoid, occasionally globose or subglobose; thin-walled, smooth, hyaline; producing a single, lateral (usually), subapical, or (rarely) apical, raised exit papilla; 16–(18–27)—31 μ long by 11–(15–21)—27 μ in diameter; spherical ones 23–32 μ in diameter. Rhizoids slender, tapering, sparingly branched. Planonts posteriorly uniflagellate, ovoid; containing a single posterior, refractive globule, and provided with a long (25–28 μ) flagellum; escaping singly through an exit pore dissolved in the discharge papilla, and swimming immediately; 4–5 μ long by 2.5–3 μ in diameter. Resting spores not observed.

On oögonia of *Achlya colorata*, on hempseed, mud from roadside pool near Hella, 11 March 1972 (Herb. No. 3238).

The only undisputed *Rhizophyidium* invading saprolegniaceous fungi is *R. carpophilum*, a species rather well defined and easily recognized. This *Rhizophyidium* on *Achlya colorata* differs from *R. carpophilum* in two particulars.

The fungus on *Achlya colorata* generally has ovoid to depressed-globose sporangia attached laterally to the host wall (Figs. 94, 96, 97). Its exit papillae are usually lateral (Figs. 94, 97). However, there are exceptions. Spherical (or nearly spherical) sporangia (Figs. 95, in part; 98) are also produced. These, each with a single, apical exit papilla, bring to mind the fungus on *A. flagellata*. The rhizoids of this parasite of *A. colorata* are generally more delicate and tenuous than those of *R. carpophilum* on *A. flagellata* (compare Figs. 93 and 94), but some thalli have stout and conspicuous ones (Fig. 95). Planont structure in this fungus on *A. colorata* is similar to that in *R. carpophilum*, and the spore release pattern is identical.

Attempts to transfer the chytrid from *Achlya colorata* to cultures (one- and four-weeks old) of *A. flagellata*, *A. americana*, *A. papillosa*, and *Brevilegnia unisperma* var. *montana* failed. In the absence of any experimental evidence to the contrary, this *Rhizophyidium* seems best accommodated as a doubtful form of *R. carpophilum*. The differences between this chytrid and the one on *Achlya flagellata* do not seem important enough to justify setting aside two taxa.

Rhizophyidium chitinophilum Antikajian (Figs. 257, 258).

Although thalli of *Rhizophyidium* were rather common on chitinous and keratinized baits in soil and water samples, I was able only twice (Herb. Nos. 2950, 3000) to identify *R. chitinophilum* with any certainty. The fungus developed on roach wing, and then only sparsely.

Only spherical or subspherical sporangia each with a single, apical discharge papilla, were formed on the bait, but ovoid and pyriform ones are known to occur in this species, as are sporangia with two exit papillae. The spherical sporangia were 37–80 μ in diameter, a maximum somewhat larger than reported (see Sparrow, 1968) for *Rhizophyidium chitinophilum*. There were no resting spores. The rhizoids were stout at their junction with the

sporangium wall, but tapered rapidly and were richly branched.

Rhizophyidium coronum Hanson (Figs. 118–123)

When its gelatinous sheath or “corona” (Figs. 118, 120, 121) is fully developed, this striking species cannot be confused with any other in the genus. It was most often recovered on lens paper (only once on cellophane) bait in soil samples from grassy tussocks or the edge of intermittently marshy areas. Booth (1971b) and Booth and Barrett (1971) report *Rhizophyidium coronum* on pine pollen.

In unifungal culture on pretreated lens paper (see Isolation and Culture) the stipitate sporangia (Figs. 120, 122) are spherical and produce 1–3 (Figs. 118, 119, 120) large, shallow, dome-like exit papillae. The gelatinous, nonlaminated hull may shred from the sporangium (Fig. 119), and is absent from discharging (Fig. 123) or empty ones (Fig. 122). This nonlaminated condition runs contrary to Hanson’s (1944, 1945b) description of the species and the account by Booth and Barrett (1971), but agrees with the observations by Booth (1971b) and Willoughby (1965). Occasionally, sporangial rudiments or nearly mature sporangia of *Rhizophyidium coronum* will lack the enveloping sheath. In such instances, only size distinguishes this species from others in the genus with globose sporangia. On lens paper the sporangia are 16–(38–47)–62 μ in diameter. In many specimens the exit pores are quite prominent (Fig. 122), and much larger than noted by others: 16–27 μ in diameter. The planonts emerge in a mass, cluster briefly at the orifice, and then assume motility.

Rhizophyidium (?)*echinocystoides* Sparrow (Figs. 124–131)

There are sufficiently noteworthy differences between the characteristics of my specimens and those recorded by Sparrow (1968) to make this a tentative identification. The fungus occurred once (not in a bog sample as Sparrow had found) in my collections (Herb.

No. 2661). I was unable to propagate any of the Iceland plants even in unifungal culture.

On pollen the sporangia are upright (Figs. 127–131), and each has a prominent, hyaline, hemispherical apical exit papilla (Figs. 126, 129) filled with a mucilaginous or gelatinous substance. The endogenously formed planonts (Fig. 126), motile at discharge (Fig. 125), do not escape into a matrix. The thallus produces a branched rhizoidal system with a single main axis (Figs. 126–131). In these characteristics, at least, my specimens agree quite well with the descriptive matter Sparrow has provided. Furthermore, sporangium size in my plants – 18–27 μ high by 12–21 μ in diameter – is within the range recorded by him: 15–25 \times 10–22 μ .

As defined in the original description, *Rhizophyidium echinocystoides* has ovoid sporangia ornamented with numerous, short spines. While broadly ellipsoidal (Fig. 129) to ovoid (Figs. 126, 130) sporangia do occur in the specimens from Iceland, just as Sparrow figured them for his species, some are nearly spherical (Fig. 128) or slightly irregular (Figs. 127, 131) while retaining the general ovoid appearance. There is a regularity in the nature of the echinulations on the sporangia of Sparrow’s fungus which I do not find in the collection at hand. On the contrary, the ornamentations in my specimens are of varying lengths (Figs. 127, 130), and often appear to be somewhat thin and flaccid or flexible (Figs. 125–127) rather than stiff and spine-like as Sparrow illustrates them. Neither the slight differences in sporangium shape nor nature of the ornamentations between Sparrow’s plants and mine have much, if any, taxonomic impact although the description of *R. echinocystoides* must be expanded somewhat to admit the Iceland plants.

Sparrow (1968) described but did not illustrate spherical, epibiotic, spiny resting spores (12–15 μ in diameter) associated with the sporangial thalli of *Rhizophyidium echinocystoides*. Spherical resting spores (Fig. 124) ornamented like the sporangia, and 11–17 μ in diameter, also occur in my collections.

Circumstantial evidence suggests that these are resting spores of the species, but this must be confirmed by culture studies.

In shape, at least, the sporangia of Cejp's (1933) *Rhizophyidium verrucosum* seem to be indistinguishable from those of Sparrow's species. The terminal exit apparatus in *R. verrucosum* is conspicuously prolonged rather than being dome-like or hemispherical as in *R. echinocystoides*. Cejp illustrates wart-like ornamentations for his species.

Rhizophyidium pollinis-pini (Braun Zopf *pro parte* (Figs. 99–104, 115–117)

Among the most ubiquitous of the aquatic fungi, this and the next species should be among the most easily recognized of the chytrids. It is certain, however, that *Rhizophyidium pollinis-pini* and *R. sphaerotheca* have been confused with each other, and with other species as well. Sparrow (1960) limits identification of *R. pollinis-pini* to fungi with spherical, uniporous sporangia (Figs. 99, 102, 104) on pollen and with one exception this is followed here.

Paterson's (1963) revealing culture study of some *Rhizophyidium* species demonstrates the fallibility of giving taxonomic weight to substratum. He did not name the fungi he investigated, but one clearly had the attributes (save one of planont discharge pattern) of *R. pollinis-pini*. This fungus, designated species 2, invaded pine pollen and nematodes as well as algae. Paterson found, however, that species 2 discharged planonts into a vesicle, and this pattern was not modified by manipulating the substrate types. Such a discharge mechanism seems to set off species 2 from *R. pollinis-pini*, though perhaps not irrevocably. In the abundant Iceland material collected from many sites, all of the sporulating plants identified as this species had nonvesicular discharge (Fig. 103).

Mixed with some specimens of *Rhizophyidium pollinis-pini* and *R. sphaerotheca* in gross culture were plants of a *Rhizophyidium* with 2–5 large, shallow, dome-like exit papillae (Figs. 115–117). In some instances,

these large papillae were elevated to such a degree that the sporangium appeared lobed (Fig. 116). Planonts indistinguishable from those of *R. pollinis-pini* emerged through one or more pores at discharge, and moved swiftly away from the exit orifices.

The large, shallow exit papillae of this fungus give its sporangia an aspect not far removed from that of *Rhizophyidium coronum*, since it, too, may have multiple exit pores (Fig. 118). Moreover, sporangia of Hanson's species may lack a gelatinous "hull" or sheath. In the *Rhizophyidium* (Figs. 115–117) on pollen, however, the sporangia are substantially smaller (predominantly 16–21 μ in diameter) than those — 38–46 μ in diameter (median 70%) — of *R. coronum*.

The *Rhizophyidium* with large exit papillae would not grow on agar, nor in unifungal culture. The plants probably are incorrectly assigned if kept with *R. pollinis-pini*. In the uncertainties surrounding identification of the *Rhizophyidium* species with globose, non-ornamented sporangia, however, the creation of new taxa is hardly justifiable on characters developed solely in gross culture.

Rhizophyidium sphaerotheca Zopf (Figs. 105–110)

Sparrow (1960) applies this species name to pollen-inhabiting chytrids with branched rhizoids, and spherical or subspherical, multiporous sporangia. *Rhizophyidium globosum* (Braun) Rabenhorst, on algae, evidently has been confused with *R. sphaerotheca*, but a study by Paterson (1963) sheds some light on identification of the two. His *Rhizophyidium* species 1, indistinguishable in my view from *R. sphaerotheca*, was propagated on algae, pollen, and nematodes. Thus the one reason — difference in substratum — for keeping *R. sphaerotheca* separate from *R. globosum* vanishes.

Booth (1969, 1971b) and Miller (1961) collected sporangia of *Rhizophyidium sphaerotheca* that exceeded 22 μ in diameter, a size taken (Sparrow, 1960) as an upper limit to the species. Certainly the sporangia of *R.*

sphaerotheca are usually smaller (Fig. 105) than those of *R. pollinis-pini* (Fig. 100). As noted by others the sporangia of *R. sphaerotheca* have a noticeably double-contoured wall (Figs. 106–110).

The orifice of each exit papilla is plugged with a minute drop of mucilaginous substance (Fig. 108) that evidently gives the shiny aspect to the papillae themselves. In some sporangia (Fig. 106), the exit orifices are conspicuously smaller than the diameter of the planonts and very small sporangia are likely to have a single, broad exit orifice (Fig. 110). The rhizoids of *R. sphaerotheca* are more delicate, tenuous, and abundantly branched than usually are encountered in *R. pollinis-pini*. Paterson's (1963) illustrations of his two unnamed species clearly show such a structural difference. Booth's (1971b) *Rhizophyidium* sp. (No. 48) could be identified with *R. sphaerotheca* since the number of exit papillae in his plants was clearly variable.

Rhizophyidium subangulosum (Braun) Rabenhorst (Figs. 111–114)

Sporangium sessile, thin-walled, smooth, hyaline; at first spherical, then becoming angular as 2–15 prominent, broadly conical exit papillae develop; 14–(18–25)–33 μ in diameter, exclusive of the papillae; inoperculate, non-apophysate. Rhizoids slender, tapering from a prominent main axis, and becoming sparingly branched. Planonts posteriorly uniflagellate; ovoid to broadly ellipsoidal; provided with a posteriorly positioned refractive globule; 2.5–3.5 μ long by 2–3 μ in diameter; flagellum 8–11 μ long; formed endogenously, and escaping singly through one or more exit pores at the dissolution of the exit papillae. Resting spores not observed.

This fungus has been found once: on pine pollen, in a sample of water and organic debris at the edge of Masvatn (Herb. No. 1007). It was propagated in unifungal culture (but grew very sparingly) on sterile pollen in potassium tellurite water. Inasmuch as its identification as *Rhizophyidium subangulosum* is open

to question, a full description of pertinent characteristics is given.

Karling (1968) described *Rhizophyidium angulosum* (on pollen) as a chytrid having some features in common with *R. subangulosum*. However, he demonstrated that his fungus would not invade algae (the substratum most often reported for *R. subangulosum*) and that the planont exit mechanism did not necessarily involve the papilla-like protrusions. The description of *R. subangulosum* by Sparrow (1960) leaves no doubt that planonts emerge through pores dissolved in the prominent papillae. This is the case in my specimens as well (Figs. 112, 114).

The Icelandic plants do not occur in aggregates, but *Rhizophyidium angulosum* has such a growth habit. (The fungus described by Malacalza, 1968, as *R. subangulosum* does produce aggregates of sporangia.) Furthermore, the rhizoids of specimens in my collection are scantily branched (Figs. 111, 113) very much in contrast to the delicate, bush-like, branching pattern in Karling's species. In its endobiotic system, therefore, the fungus from Iceland agrees well with Sparrow's description of *R. subangulosum*.

Previous reports of *Rhizophyidium subangulosum* (see Sparrow, 1960) from pollen are not accompanied by descriptive matter. Thus, whether these earlier collections are of fungi identifiable properly with *R. subangulosum* or with Karling's *R. angulosum* cannot be determined. In any case, the characteristics of the Iceland plants agree most readily with *R. subangulosum* in spite of the occurrence of that species on algae.

Pollen grains infested with the *Rhizophyidium* from Iceland were put in Van Tieghem cells together with filaments of *Oedogonium*, *Spirogyra*, and a filamentous blue-green (*Phormidium*?) but none of the algae was infected. This evidence, however, is too scanty to provide any sound basis for taxonomic conclusions. It is of course possible that the fungi on pollen are neither *R. subangulosum* nor *R. angulosum*. Experimental work (with abun-

dant material) is needed to explore this suggestion.

Rhizophydium sp. (Figs. 132–136)

Sporangium sessile, thin-walled, smooth, hyaline; ampulliform to obturbinate with a flattened base, infrequently depressed globose or ovoid and appressed laterally to the substratum; sometimes slightly irregular, rarely spherical; provided with one apical, hemispherical, refractive exit papilla, and infrequently with a second subapical or lateral one; 18–(24–29)–41 μ in diameter, 14–(20–27)–36 μ high; inoperculate, nonapophysate. Rhizoids long, sparingly branched, their long axis parallel to the long axis of the sporangium. Planonts posteriorly uniflagellate; ovoid; provided with a small, refractive, posteriorly positioned globule; 4–4.5 μ long; formed endogenously, and escaping individually and rapidly swimming away at the dissolution of the exit papilla. Resting spores not observed.

On cellophane (Herb. No. 290) and on lens paper (Herb. No. 292), in soil under mosses, Saudafell, 1 September 1965.

This *Rhizophydium* was isolated into unifungal culture on boiled cellophane, and the foregoing description is compiled from characteristics of the thalli on that substratum. The plants grew only at the edges of the cellophane, and the rhizoids were often obscured by the decomposing bait.

The specimens are not accommodated by any of the known members of the genus (see Sparrow, 1960), nor does there seem to be a counterpart among the unidentified species found by others. In unifungal culture at least, sporangium shape – perhaps the only distinctive feature of this fungus – seems reasonably constant. However, the fungus must be propagated in pure culture if it is to be identified confidently.

ENTOPHLYCTIS

Howard (1968) collected an *Entophlyctis* on pine pollen and while he related his specimens to *confervae-glomeratae*, he did not choose to name them as such. See also, under

Rhizophlyctis rosea, the discussion of *Entophlyctis aurea* Haskins.

Entophlyctis confervae-glomeratae (Cienkowski) Sparrow (Figs. 150–153)

That *Entophlyctis* species occur in pollen grain baits is well established (Barr, 1971; Booth, 1971c), but their precise identity remains obscure (Booth, 1971). Most evidence from propagation of isolates in axenic cultures confirms Sparrow's (1960) suspicion that *E. confervae-glomeratae* is a collective species. Thus, the identification of my specimens with this species is purely a convenience.

The fungus grew in pure culture (technique and medium used by Booth, 1971c), and was successfully reinoculated into sterile pollen. By enlargement of the penetration tube from a settled planont (Fig. 150) the sporangia develop endobiotically. Resting spores are also endobiotic (Fig. 152). In what are evidently older specimens, the delicate rhizoids of the sporangia and resting spores are usually absent (deliquesced?). These thalli are then more like sporangia of *Olpidium* than of *Entophlyctis*. Very probably some specimens identified as species of *Olpidium* in pollen in gross culture are in reality representative of *Entophlyctis*, and the result of Barr's (1971) study leave no doubt on this point. Booth (1971c) has demonstrated that wide ranges of variability can be expected in *Entophlyctis*. It is in any case true that collecting pollen-inhabiting species in this genus is greatly facilitated by culture techniques. Where identification of *Olpidium* species in pollen is not based on specimens in culture (Johnson, 1969a) the results must be open to question.

DIPLOPHLYCTIS

Two species have been reported from Iceland: *Diplophlyctis sexualis* Haskins, and *D. intestina* (Schenk) Schroeter (Howard, 1968; Johnson and Howard, 1968). In the latter account, the substratum was probably misidentified. Neither species has been recovered subsequently.

Diplophlyctis sp. (Figs. 202–207)

Sporangium irregularly subglobose, with 1–3 prominent lobes; wall smooth, thin, hyaline; producing a broad, cylindrical or slightly tapering, often sinuous exit tube 6–15 μ long by 3–8 μ in diameter at its broadest point; 17–23 μ in diameter by 15–33 μ high; inoperculate. Apophysis spherical or subspherical, 5–9 μ in diameter, usually containing 2 or more small, highly refractive bodies; rhizoids broad, moderately branched, tapering abruptly, and originating from one or more points on the apophysis. Planonts posteriorly uniflagellate, spherical; containing a small, conspicuous, refractive body, 4.5–5 μ in diameter; flagellum 28–31 μ long; emerging through a pore dissolved in the tip of the exit tube, and swimming sluggishly. Resting spores spherical to broadly ovoid or ellipsoidal; pale brown; wall thick (up to 3 μ) and densely ornamented with small bullations or verrucose markings; spherical ones 15–26 μ in diameter, ovoid to ellipsoidal ones 16–22 μ in diameter by 21–33 μ high; apophysis spherical to depressed globose, 4–9 μ in diameter and up to 11 μ long; stout rhizoids arising from one or more axes, and becoming moderately branched. Germination not observed.

On cellophane, in pasture soil, farm west of Selfoss, 9 September 1966 (Herb. No. 749) and in pasture soil, farm south of Hveragerdi, 22 October 1972 (Herb. No. 10858).

In both collections, thalli were sparse, and very few mature or discharged sporangia (Figs. 204, 205) were observed. At first the resting spores are thin-walled and hyaline, and contain several refractive bodies of various sizes (Fig. 206). During development, the spore wall becomes minutely roughened (Fig. 207), and subsequently bullate (Fig. 202). The ornamentations are occasionally (Fig. 203) elongated and cylindrical.

The resting spore wall ornamentations suggest those of *Diplophlyctis verrucosa* Kobayasi & Ookubo (Ookubo, 1954). In the Iceland specimens, however, these are much more regular in shape and density than

is evidently the case in *D. verrucosa*, and, of course, the sporangia and resting spores are generally smaller in my plants as well. *Diplophlyctis verrucosa* is parasitic in *Chara*; in contrast, the fungus from Iceland is saprophytic.

Until more abundant material of this species on cellophane is collected and examined, its identity is best left undecided. Certainly from the sparsely developed collections at hand, little can be deduced of the organism's variability.

Rhizidiaceae

Representatives of four genera — *Rhizidium*, *Rhizophlyctis*, *Rhizoclosmatium*, and *Solutoparies* — have been collected (Howard, 1968).

POLYPHAGUS

Polyphagus laevis Bartsch (Figs. 272, 273)

The collection of this species (Herb. No. 2888) on encysted *Euglena* from a small pool in a pasture ditch near Thorlákshöfn (14 August 1970) constitutes the sole Icelandic record. Planonts were not observed, and in the rather sparse material there were few prosperangia (Fig. 273). The occasional resting spore (or zygosporangium) was truncate (Fig. 272) as is characteristic of the species.

RHIZIDIUM

Howard (1968) collected *Rhizidium varians* Karling on cellophane, and noted that his specimens had one to several rhizoidal axes. He expressed some perplexity in identifying his specimens with *Rhizidium*, but followed Karling's disposition of the species. I earlier (Johnson, 1973a) gave an account of some plants assigned to this genus, but was unable to culture the fungi and identify them satisfactorily. One additional species (following) is not identifiable with any of the known taxa in the genus.

Rhizidium sp. (Figs. 274–279)

Collected originally on roach wing bait on two occasions (Herb. Nos. 2167, 3381), specimens of this fungus were propagated in uni-

fungal culture on sterile roach wing (in potassium tellurite water) and transferred to pretreated sterile snakeskin. The morphology of the plants is altered substantially on the latter substratum, as the description indicates.

Sporangium thin-walled, hyaline; producing a single broad but shallow, apical or subapical exit papilla that at dissolution leaves a sessile or only slightly raised exit pore; on roach wing spherical or subspherical, 13–(17–26)—29 μ in diameter, subtended by a single, stout, sparingly branched rhizoid, 2–5 μ in diameter at its juncture with the sporangium; on snakeskin, spherical, subspherical or asymmetrically or broadly obpyriform, 16–(23–29)—37 μ in diameter, provided with one or more stout, richly-branched rhizoidal axes up to 10 μ in diameter at their junctures with the sporangium wall. Planonts posteriorly uniflagellate; endogenously formed; spherical; containing a single refractive globule; escaping through a large, circular pore, and clustering at the orifice in a rapidly dissolving matrix. Resting spores not observed.

Two characteristics mark this fungus. First, its sporangia are among the smallest of the species of *Rhizidium*. Secondly, the fungus develops a rhizoidal system of one or of many axes (Figs. 277, 278) depending upon the substratum. Multiple axes arise basally when the thallus grows at the edge of snakeskin bait (Fig. 277), but in some plants on this same substratum thalli consist of a single axis (Fig. 276) much as occur on roach wing. Thalli forming on the surface of snakeskin usually have multiple rhizoids arising from scattered points (Fig. 278) on the circumference of the sporangium.

The plants with several rhizoidal axes are of course assignable to *Rhizophlyctis* while those with a single axis are retainable only in *Rhizidium* in the strictest sense. In this one species, therefore, the distinction between the two genera fails. A somewhat parallel situation obtains in Karling's (1949b) *R. varians*. As more rhizidiaceous fungi are discovered, it becomes increasingly evident that these two gen-

era probably cannot be separated, and much may be gained in a practical way by combining them.

RHIZOCLOSMATIUM

Rhizoclosmatium globosum Petersen (Figs. 186–190)

The Iceland specimens seem to differ from the usual concept of the species only in the size and shape of the apophysis. While the apophysis may be fusiform (Fig. 186) as described for the species, it is quite large and often bulged (Fig. 187) or somewhat cylindrical (Figs. 188, 190). Occasionally, the apophysis is short but rather broad (Fig. 189). Howard (1968) reported that the specimens he examined had small, spherical to obovate apophyses.

The species is found at Mývatn during the season of midge infestation, but in surprisingly few of the cast-off exuviae.

RHIZOPHLYCTIS

Rhizophlyctoid fungi are usually relatively easy to recognize as such, save for those organisms that fall into the gray area between *Rhizidium* and *Rhizophlyctis*. Species limits in *Rhizophlyctis* are far from settled, and some taxa consequently are notoriously ill-defined.

Höhnk (1960) reported *Rhizophlyctis rosea* (as *Karlingia*) from Iceland, as did Howard later (1968). Howard (1968) also identified *R. petersenii* among his collections. In the following account, five species are considered, although others in Iceland may come to light as specimens are cultured, more precise limits are drawn, and collections are reexamined and reappraised.

Rhizophlyctis chitinophila (Karling) Sparrow (Figs. 259, 260)

One collection of *Rhizophlyctis* has been identified with this species (Herb. No. 2890). The large sporangia formed at the edge of the substratum are elongate and slightly angular (Fig. 259). On the substrate surface, they are generally spherical, and form prominent, cylindrical to long conical exit papillae (Fig.

260). The sporangia are hyaline, the only feature that distinguishes them from *Rhizophlyctis rosea*.

A conspicuous, hyaline, gelatinous plug is at the apex of each discharge papilla (Fig. 260). I have not seen spore discharge from any of the specimens collected; whether the sporangia are endooperculate or inoperculate is not known. The species was described as endooperculate and originally assigned to *Karlingia*.

In the absence of specimens characterized in culture I am not confident of the identification of this species.

Rhizophlyctis petersenii Sparrow (Fig. 219)

A *Rhizophlyctis* provisionally assigned to this species was recovered in a number of samples (from various sites) on roach wing, cellophane, and lens paper baits. Because I could not propagate any of these fungi, observations were limited to specimens appearing in gross culture.

Sparrow (1937) emphasized the large size of the pigmented (orange-brown) sporangia each with a single discharge tube. Among many collections of rhizophlyctoid fungi I have found very large pigmented (orange) sporangia accompanied by very stout rhizoids. Those specimens with multiporous sporangia I have identified as *Rhizophlyctis rosea*; the uniporous one were allied with Sparrow's species. This arbitrary manner of separating the two species is unsatisfactory, and proper identification must await the results of culture studies. There are representatives of *R. rosea* that have a single discharge papilla on the sporangium, but this papilla is smaller than that described for *R. petersenii*. Whether this size difference is constant enough to be a basis for separating the species from *R. rosea* remains to be determined.

Rhizophlyctis rosea (de Bary & Woronin) Fischer (Figs. 208–218; 220–231)

This is one of the most common chytrids in Iceland, its ubiquity matched only by its variation in most if not all of its key characters.

The discovery by Johanson (1944) of endoopercula in plants of *Rhizophlyctis rosea* led her to segregate out these representatives into a new genus, *Karlingia*. Some subsequent investigators failed to find endoopercula (Figs. 209–211, 226, 231) in *rosea*-like rhizophlyctoid fungi, and chose to retain the species in *Rhizophlyctis*. Even as astute an observer as Willoughby has identified the species first (1958) with *Karlingia* (with endoopercula) and later (1961, 1962) with *Rhizophlyctis*. Chambers and Willoughby (1964) studied the fine structure of an endooperculate fungus and retained for it the name *Rhizophlyctis rosea*. Sparrow (1960), regarding endooperulation as an inconsistent feature of the fungus, assigned the species to *Rhizophlyctis* while Karling (1947) retained it in *Karlingia*.

Whether the species should be assigned to *Rhizophlyctis* or *Karlingia* turns on the importance assigned to endooperulation. I have found endoopercula in some sporangia in all collections from which I have made cultures, but it is futile to search for endoopercula in discharged sporangia. They are, in fact, not always visible at the moment that active discharge begins. The gelatinous matrix that plugs the orifice of each exit papilla (Figs. 210, 211, 226, 231) is plainly visible just prior to planont emergence. I am defraying final judgment on generic assignment until a critical accounting is at hand of the relation of *Rhizophlyctis* to *Rhizidium*. The final disposition of endooperculate forms may well be influenced by the treatment given these two genera.

To *Rhizophlyctis rosea* I have assigned only those rhizophlyctoid specimens (on cellophane, lens paper, grass leaves, snakeskin, and roach wing baits) with pigmented sporangia. This admits to the species a wide range of variations in sporangial shape. Although the usual expression in the Iceland plants is that of spherical sporangia (Fig. 208), elongate ones (and a host of intermediate shapes) also exist (Figs. 215, 216). The species also is considerably diversified in number and size of exit

papillae: single papilla (Fig. 217), multiple, short conical ones (Fig. 214), or long, papillate or cylindrical evaginations (Figs. 213, 218).

Although the rhizoids of *Rhizophlyctis rosea* are always profusely branched (they may be fused and "sheet-like" as Chambers and Willoughby, 1964, note) their spatial relationship to the sporangium is to some degree dictated by the location of this structure on the substratum. When the sporangia develop at the edge of bits of cellophane, for example, the rhizoids orient along a single "axis" (Figs. 217, 218). Usually, however, the rhizoids are conspicuously radiating. Very commonly there are emergent rhizoids growing from the sporangium into the water and away from the substratum much as Chambers and Willoughby illustrate.

While variations such as the foregoing are detectable in specimens in gross culture, they are most readily seen on plants grown in pure or unifungal culture. The species can be cultured on YPSS agar (technique developed by Willoughby, 1958) made up in soil extract water. From plants growing on the surface of this medium, it is easy to transfer cultures onto sterilized baits (such as cellophane). The surface of YPSS medium supporting growth is flooded with about 10 ml of sterile tap water, and sterile bait floated on the surface. Within 12–18 hours, vigorous cultures have sporulated, the bait is infested with germinating planonts, and can be removed to other dishes containing only sterile, soil extract water. Mature thalli will develop in 10–14 days.

Pigmentation is somewhat variable among the specimens in gross and unifungal culture. The vast majority of the Iceland plants are a golden orange or "xanthine" orange, and only rarely are "salmon pink" or "rose red" sporangia produced. Many of the sporangia retain the pigmentation after planonts have emerged, indicating that color for some individuals is a property of the sporangium wall (as Willoughby, 1958, concluded). There were sporangia that were hyaline after spore release; pigmentation in these cases was associated with the emerging planonts. This, of

course, correlates well with the "rose colored" tints often ascribed to the planonts themselves (Sparrow, 1960). Since pigmentation is a critical diagnostic feature for *Rhizophlyctis rosea*, no gross culture collections consisting entirely of hyaline, discharged sporangia were identified with this species.

Rhizophlyctis rosea was collected on grass-leaf bait, and on this substratum the sporangia were predominantly spherical. Sporangia in two collections on grass leaves (Herb. Nos. 4626, 8555), however, were rarely spherical or subspherical, yet bore other characters — pigmentation, multiple exit papillae, mucilaginous plugs in the exit orifices — of *R. rosea*. These predominantly irregular or cylindrical sporangia (Figs. 220–225) were initially allied with Haskins' (1946) *Entophlyctis aurea*.

In gross culture, on grass leaves, the thalli produced elongate (Figs. 220, 221), angular (Fig. 222), tubular (Fig. 223) or lobed (Figs. 224, 225) sporangia. Generally, the rhizoids tended to be oriented parallel (Figs. 222, 224) to the leaf cells. Small sporangia were a bright golden yellow, or very pale yellow, but the larger ones were a bright golden-orange, a color not at all different from that in sporangia of *Rhizophlyctis rosea*. Moreover, pigmentation persisted after planont discharge, suggesting that color is a property of the sporangium wall. One to 18 short, broadly conical exit papillae were produced. The base of each papilla was closed by an endooperculum (Fig. 226), and the orifice was plugged by a hyaline, mucilaginous substance. As in *R. rosea*, endoopercula were never found in or associated with discharged sporangia. Posteriorly uniflagellate planonts, 3.5–4.5 μ in diameter, emerged at first through a single orifice, and clustered there as if in a matrix. When these clustered planonts assumed motility, spores still within the sporangium escaped through other exit orifices. Because of the irregularity of sporangia, it was difficult to assign fully adequate measurements: in diameter (at the broadest point), the sporangia ranged from 18 to 63 μ and in length from 32 to 187 μ .

Sporangia judged to be at incipient sporu-

lation were dissected from the substratum in one collection (Herb. No. 8555) and confined in small amounts of soil extract-potassium tellurite water (see Isolation and Culture) with sterile cellophane and lens paper. Unifungal cultures were developed in this fashion.

On cellophane and lens paper, the sporangia were predominantly spherical (Figs. 227, 229) and occasionally subspherical (Fig. 230) or elongate and fusiform (Fig. 228). None of the sporangia corresponded to the strongly irregular, tubular, or lobed ones seen on grass leaf bait. (Figs. 223, 225). Sporangia from thalli developed on cellophane and lens paper were generally multipapillate (as were those on grass leaves) but the papillae were noticeably elongated (Figs. 227, 229). Sporangium pigmentation and endopericulation (Fig. 231) were the same as those of plants in gross culture on grass leaves.

Thalli developed in culture (Figs. 227–230) from planonts of sporangia like those of *Entophlyctis aurea* (Figs. 220–225) are indistinguishable from thalli of *Rhizophlyctis rosea*. This unrefined experimental evidence substantiates Karling's (1947) claim that *Entophlyctis aurea* is *R. (Karlingia) rosea*, and Sparrow's (1960) and Barr's (1971) supposition that Haskins' species is at best a *Rhizophlyctis*. I am inclined to equate *E. aurea* with *R. rosea* although further more precise experimental evidence is needed before that is formally proposed.

Konno's illustrations (1972) of *Rhizophlyctis oceanis* warrant brief comment. The sporangia depicted by him on plate 6, figure J are extraordinarily similar to those formed by *Catenomyces persicinus* (Hanson, 1945a; Johnson, 1973b). Figure L of the same *Rhizophlyctis* is singularly like some sporangia commonly formed by *R. rosea*.

Empty sporangia in two collections of *Rhizophlyctis rosea* (Herb. No. 6411, 6522) on lens paper had a peculiar internal aspect. The large, cylindrical to angular sporangia contained 2–20 small, angular thalli (Figs. 1–3) with multiple exit tubes. These endogenous sporangia were pigmented ("xanthine" orange

to deep orange) as were the large thalli in which they occurred. At discharge, uniflagellate planonts emerged through one or more of the exit tubes (Fig. 3). Each discharge orifice was initially closed by a hyaline, gelatinous plug.

The endogenous sporangia (Figs. 1–3) were first thought to be similar to those of Persiel's (1960) *Pleotrachelus* sp. K, and were initially identified as this unnamed species. Their structure and pigmentation, however, point strongly to their being merely internally developed thalli of the *Rhizophlyctis rosea* itself. *Rhizophlyctis rosea* from the collections was propagated in unifungal culture on lens paper and in pure culture on agar (Willoughby, 1958), but the resulting plants failed to show any evidence of endogenous sporangia, and none could be "infected" by planonts from the internal sporangia in gross culture.

Rhizophlyctis (?) willoughbyii Konno (Figs. 232–237)

Hyaline, rhizophlyctoid, nonspherical sporangia with a single exit papilla, appearing on cellophane and roach wing in three collections (Herb. Nos. 2203, 3513), were identified as this species. I propagated the fungus on cellophane in unifungal culture (30 ml sterile soil extract containing 0.01% potassium tellurite), and while its characteristics seemed reasonably constant under the conditions employed, I am not convinced that the species will be retained among the valid ones. Identification of the Iceland plants with Konno's is therefore subject to revision.

The inoperculate sporangia are generally broadly ovoid (Fig. 234) or obturbinate, but somewhat angular and elongate ones also occur (Figs. 232, 233). Only rarely are subspherical or spherical ones produced, and these seem to be limited to thalli on cellophane. Ovoid sporangia are 55–78 μ in diameter, and 83–115 μ long. Elongate sporangia reach 162 μ , and have a maximum diameter of 80 μ . A single apical or subapical discharge papilla is formed; this may be 25 μ broad at the base,

but is usually smaller (8–14 μ). When the papilla (Fig. 235) dissolves, the planonts escape and cluster in a spherical mass at the orifice before assuming motility. The rhizoidal system is “typically” rhizophlyctoid: multiaxial and richly branched. No resting spores were evident in any gross or unifungal culture.

Save for the fact that the sporangia are rarely spherical in specimens I have identified as *Rhizophlyctis willoughbyii*, the plants very strongly resemble Willoughby's (1965: p. 106, text. fig. 4a–e) *Rhizophlyctis* sp. 3.

Rhizophlyctis sp. (Figs. 169–177)

Sporangium spherical, subspherical or slightly angular; smooth-walled, hyaline; provided with a broadly conical and shallow, hyaline exit papilla, filled with an amorphous, gelatinous substance; developing from an encysted planont; 14–(22–30)–37 μ in diameter; inoperculate. Rhizoidal system consisting of 1–4 stout axes up to 150 μ long, and numerous slender, short ones springing from scattered points on the sporangium surface; main axes slender or stout and trunk-like; tapering, and moderately branched. Planonts posteriorly uniflagellate; ovoid; possessing a conspicuous, posterior or eccentric globule; 3–4.5 μ long by 2.5–3 μ in diameter; flagellum 15–19 μ long; escaping into an expanding matrix through a pore 4–8 μ in diameter dissolved in the apex of the exit papilla; remaining motionless for a time in the matrix, then assuming motility at its dissolution. Resting spores not observed.

On snakeskin: mud under roots of *Potamogeton* (?) *gramineus*, edge of Ellidavatn, 25 October 1972 (Herb. No. 10888), and water and organic debris, fish-rearing pond at Kollafjörður, 6 November 1972 (Herb. No. 11069).

This fungus was propagated in unifungal culture on pretreated snakeskin in soil extract-potassium tellurite water. The foregoing characterization was derived from plants grown in this fashion.

The sporangium is the product of planont enlargement (Figs. 172, 173), and early in thall-

us development the chief rhizoidal axes appear (Fig. 173). As growth continues, the exit papilla appears (before the planonts are cleaved; Fig. 169), and the expanding sporangium rudiment becomes invested with several short, stout or slender, rhizoids (Fig. 169, 175). Subsequently, planonts are cleaved endogenously.

Because of the variation expressed in the rhizoidal system, it is difficult to decide whether a single axis predominates (Figs. 171, 177) or more than one major axis is developed (Figs. 170, 175, 176). The production of a single axis on the thallus would of course require that the plants be assigned to *Rhizidium*, but the fungus does form multiple axes as well.

The short, rhizoidal outgrowths (Figs. 169, 170) constitute the only definitive character of recognition. Proliferation of a sporangial rudiment will occur (infrequently) and the resulting product is a sporangium free of secondary peripheral rhizoids (Fig. 176).

None of the known species of *Rhizophlyctis* accommodates this one from Iceland. Moreover, it cannot be equated confidently with any of the several unnamed representatives that have been described (such as *Rhizophlyctis* sp. 1 and sp. 2 of Willoughby, 1961). An unnamed *Rhizophlyctis* (on human skin bait) reported by Howard (1968) resembles this one on snakeskin to some degree: size, and formation of one discharge papilla, notably. In Howard's specimens, however, the sporangia have long, spine-like processes springing from the wall near the exit orifice. These are not even superficially like the rhizoids ornamenting the sporangia of my plants.

Since identifications in *Rhizophlyctis* (and indeed the boundaries of the genus) are notoriously uncertain, I choose not to add another species. It is possible that several species lurk in the complex of rhizophlyctoid fungi with hyaline sporangia, but sorting them out must await an extensive culture program.

SOLUTOPARIES

Solutoparies pythii Whiffen was recovered in Iceland by Howard (1968) but has not again appeared in any collections of *Pythium* species.

On two occasions I collected on lens paper bait in soil under *Equisetum* and *Rhacomitrium* at Vaglaskógur (Herb. Nos. 8306, 8332) ornamented resting spores indistinguishable in shape from those found by Dogma (1969) and assigned by him provisionally to *Solutoparies*. The shape of various ornamentations on the specimens I have recovered are identical to those figured by Dogma (1969: pl. 4, fig. 55). The spores themselves are pale yellowish, and 8–12 μ in diameter (inclusive of the ornamentations). Specimens found by Dogma (on lens paper) were golden-brown, and reached 16 μ in diameter. As I found no sporangia associated with the resting spores, and the fate of these ornamented cells is unknown, I cannot confirm Dogma's observations nor dispose of the organism into a proper taxonomic niche.

Cladochytriaceae

One (and perhaps a second) genus of this family is represented in the Icelandic aquatic mycoflora. Howard (1968) reported two species of *Cladochytrium*, and I have tentatively assigned a polycentric form on snake-skin to *Polychytrium* (Johnson, 1973b).

CLADOCHYTRIUM

One *Cladochytrium* aside from those reported by Howard (1968) has been found in Iceland. This is an unnamed species collected on human hair bait (Johnson, 1973c). Some remarks on endooperculum in *Cladochytrium* and *Nowakowskiella* are to be found elsewhere (Johnson, 1973b).

Cladochytrium hyalinum Berdan (Figs. 166–168)

By no means common in Iceland, this obviously polycentric species can occasionally be collected on wettable cellophane or on boiled grass leaves. Very often the sporangia devel-

oped on thalli on the edge of cellophane (bait) are obpyriform and elongate (Fig. 167), but are otherwise small and spherical to slightly angular or lobed (Fig. 166). None of the sporangia among my plants (with the possible exception of some positioned at the edge of pieces of bait) is apophysate, and none exhibits any tendency towards proliferation (Berdan, 1941). The specimens lacked endoopercula although it must be admitted that very few sporangia were seen to discharge spores (Fig. 168).

The fungus identified and illustrated by Konno (1972) as *Cladochytrium* sp. 1 might be more properly assigned to *Nowakowskiella* if its inoperculate condition should prove to be inconstant. Although Kobayasi, *et al.* (1971) recognized the similarity of some Greenland plants they collected to *Catenomyces persicinus* Hanson, they named their specimens *Cladochytrium granulatum* (Karling) Sparrow. At least one of the illustrations provided by Kobayasi, *et al.* (1971: fig. 5G) is of sporangia indistinguishable from those of Hanson's species. Short of propagating and characterizing pure or unifungal cultures of these polycentric forms such problems in identification are sure to persist. In my experience, endoopercula in the polycentric species are as likely to be absent as present, even in sporangia of the same thallus, hence endooper- culation is not always a dependable taxonomic characteristic.

Chytridiaceae

CHYTRIDIUM

Chytridium polysiphoniae Cohn parasitized by *Rozella marina* Sparrow was reported earlier (Johnson, 1966), as was *C. schenkii* (Dangeard) Scherffel (Johnson, 1972). Howard (1968) found uninfected plants of Cohn's species and gave descriptive notes on four additional species in the genus. A bountiful supply of chytrids with obviously discharged sporangia have appeared on filaments in various collections of freshwater algae in Iceland, but such fragmentary plants defy identification.

A paper by Karling, published in 1971,

bears prominently on taxonomy of the genus *Chytridium*. He emends and restricts the genus to include approximately 25 species. Those species of *Chytridium* with an endobiotic or intramatrical apophysis or prosperangium and resting spores are assigned to a new genus, *Diplochytridium*.

Chytridium olla Braun (Figs. 154, 155)

This is perhaps the most common of the alga-inhabiting chytrids known to occur in Iceland. At the seasonal time of decline of *Oedogonium* plants large developments of this *Chytridium* may appear.

Most of the collections at hand consist of specimens with a bulbous, nonrhizoidal endobiotic system (Fig. 154). Such apophysis-like intramatrical swellings have been noted for this species (see Sparrow, 1960), but a tubular system is apparently more commonly produced. If the endobiotic system is interpreted as an apophysis, the species would fall into Karling's *Diplochytridium*. Karling himself (1971) was unsure of the limits to be applied to an apophysate structure. He in any case chose not to use the 1 μ (diameter) limit as the dividing point between a rhizoid and an apophysis as Barr (1969) had done.

CHYTRIOMYCES

Five members of this genus (2 unnamed) were reported from Iceland earlier (Johnson, 1971). One additional species has been recovered.

Chytriomycetes (?) *poculatus* Willoughby & Townley (Figs. 137–143, 145)

This is a provisional identification of a fungus (with conspicuously lobed sporangia) found in one pollen-baited soil sample from a sheep pen (Herb. No. 10091).

The hyaline, operculate (Fig. 142, 143) sporangia, sessile on the substratum, were upright (Figs. 138, 139, 141) and 15–27 μ high by 9–17 μ in diameter, or decumbent (Figs. 140, 142) and 13–16 μ broad by 18–22 μ high. They were prominently lobed (hence often irregular), and one (rarely 2) of the lobes rup-

tured in a circumscissile fashion to form an operculum (Figs. 142, 143). The full extent of the endobiotic system was in all instances obscured, but that portion nearest the base of the sporangium was tubular or peg-like (Figs. 137, 138, 141, 142). Ovoid, posteriorly uniflagellate planonts, 3–4 μ long by 2.5–3.5 μ in diameter, emerged and swam sluggishly from the orifice at the dehiscence of the thin, shallow operculum (Fig. 143). There were no resting spores.

The description and illustrations of *Chytriomycetes poculatus* by Willoughby and Townley (1961) convey very clearly the distinctive feature of this chytrid, namely the thin, hyaline, overlapping cupules ornamenting the sporangia. Later (1965) Willoughby reported from Australia a collection (on snakeskin) of *C. poculatus* in which the majority of sporangia lacked cupules. Sparrow (1968) allied unornamented but lobed and upright, operculate sporangia on pollen to this species; Booth (1971a) and Booth and Barrett (1971b) likewise identified cupule-free plants of *C. poculatus*. The majority of specimens in my collection are more noticeably lobed or irregular than either Willoughby (1965) or Willoughby and Townley (1961) illustrate. With respect to general shape, the Iceland plants are more nearly comparable to those found by Sparrow (1968).

Admitting the lobed, nonornamented specimens to *Chytriomycetes poculatus* distorts the limits established by the authors of the species. However, since sporangia without cupules have been identified by Willoughby as belonging to the species which he and Townley described, there is some ground for uniting the Iceland specimens also with *C. poculatus*.

KARLINGIOMYCES

Rhizophlyctis species with exoopercula were removed from *Karlingia* Johanson by Sparrow (1960), as were those described in 1949(a) by Karling. These plants are now

disposed in *Karlingiomyces*. Although he expressed doubt about the identification of some rhizophlyctoid plants (on cellophane bait) as *Karlingiomyces marilandicus*, Howard (1968) was probably correct in applying this name to his specimens. The unnamed species (Howard, 1968) on human skin (bait) still remains a dubious member of the genus.

Karlingiomyces marilandicus (Karling) Sparrow (Figs. 178–181)

Characteristics of specimens in the two collections of this species agree refreshingly well with the circumscription given by Karling (1949a) and the pattern of planont discharge (Fig. 181) is as he described it. In the majority of sporangia, the operculum was positioned just below the apex of the discharge tube (Fig. 180).

Karlingiomyces sp. 1 (Figs. 182–185)

Sporangium spherical or subspherical; smooth-walled, hyaline; nonapophysate: provided with a shallow or prominently raised, broadly conical discharge papilla; operculum thin, shallow, usually positioned below the apex of the exit papilla; 47–83 μ in diameter. Rhizoids stout, extensive, sparingly branched; arising from several points on the sporangium wall; not constricted. Planonts posteriorly uniflagellate, endogenously formed; containing a large, eccentric, refractive body; spherical; emerging slowly, at the dehiscence of the operculum, into a gelatinous matrix, clustering motionless at the exit orifice, with dissolution of the matrix, assuming motility; 4–5 μ in diameter. Resting spores not observed.

On snakeskin in mud and water from a drainage ditch, near Skálholt, 16 November 1972 (Herb. No. 11224).

The fungus grew sparsely in gross culture, and in unifungal culture on pretreated snakeskin developed only immature sporangia. The *Rhizophlyctis*-like operculate sporangia place the organism in *Karlingiomyces*. Additional specimens, particularly of thalli with resting spores, are needed before the fungus from

Skálholt can be properly characterized and assigned a name.

Karlingiomyces sp. 2 (Figs. 191–196)

Sporangium broadly obpyriform to lobed and irregular; smooth-walled, hyaline; nonapophysate; provided with one conspicuous, long-conical or long-cylindrical exit tube 8–24 μ in diameter at the base, and up to 54 μ long; operculum thin, shallow; 38–(52–77)–94 μ long by 20–(38–54)–71 μ in diameter at the widest point (including lobes). Rhizoids stout, richly branched, not constricted, but main axes often of unequal diameters at various points along their length; occasionally coiled or twisted; usually arising from several points on the sporangium wall, but occasionally only 2–3 main axes are produced. Planonts posteriorly uniflagellate, endogenously formed; spherical; containing a large, conspicuous, eccentric refractive body; only a portion of those produced escape into an enlarging matrix formed on dehiscence of the operculum; many planonts remaining in the sporangium and escaping sporadically and slowly through the orifice; 7–8.5 μ in diameter; flagellum 35–40 μ long. Resting spores not observed.

On cellophane, in pasture soil, farm west of Selfoss, 9 September 1966 (Herb. No. 749), and in pasture soil, farm south of Hveragerdi, 22 October 1972 (Herb. No. 10858).

Specimens appeared in both collections along with *Diphlophlyctis* sp. The foregoing description is compiled from plants propagated in unifungal culture on pretreated snakeskin in sterile soil extract water.

The large, prominent lobes on most sporangia (Figs. 191–194) constitute the distinctive feature of this *Karlingiomyces*, but sporangia without lobes (Fig. 196) also occur. None of the main rhizoidal branches is constricted, though there is a marked irregularity (Fig. 191) to many of them.

It is tempting to place this fungus in *Karlingiomyces dubius* (Karling) Sparrow inasmuch as large, oval and oblong sporangia occur in that species (Karling, 1949a). The plants

from Iceland lack both the multiple exit tubes and the constricted rhizoids characteristic of *K. dubius*. So far as I am aware, *K. dubius* does not produce lobed sporangia. These differences seem of sufficient prominence to prevent identifying my plants with *K. dubius*.

All named species of *Karlingiomyces* have resting spores. In the absence of these in the Iceland material, the fungus can only be partially characterized, and therefore is best left unnamed.

(?)*Karlingiomyces* sp. (Figs. 197–201)

Sporangium pyramidal, angular, oblong, or spherical and lobed; smooth-walled, hyaline; nonapophysate; provided with one or two conical, prominent exit tubes; elongate ones 27–46 μ long by 16–28 μ in diameter; pyramidal, conical, or lobed ones 20–44 μ in diameter. Rhizoids slender, richly branched, constricted at intervals, and terminating in fine, thread-like extensions; arising from two to several points on the sporangium wall. Planonts and resting spores not observed.

The foregoing describes a fungus that occurred but once — and sparingly — on cellophane bait (Herb. No. 10966), and defied attempts at isolation and propagation.

The constricted rhizoids recall *Catenochytridium* (Berdan, 1939), but fungi in that genus are apophysate; this one from Iceland is not. Although the degree of constriction in the rhizoids of the Iceland plants seems much greater than occurs in any species of *Karlingiomyces*, the general aspect of sporangia recalls this genus. Planont discharge shall have to be seen before a proper location for this fungus can be found.

Megachytriaceae

Representatives of this family — in the genus *Nowakowskiella* — are treated elsewhere (Johnson, 1973b).

BLASTOCLADIALES

Catenariaceae

Species of *Catenomyces* are reported in a separate account (Johnson, 1973b).

CATENARIA

Catenaria anguillulae Sorokin (Figs. 163–165)

This species was found once, growing abundantly in the appendages of mites in soil and water cultures (Herb. No. 129). In this substratum, septa in the sterile intersporangial segments are rare. In the smaller appendages of the infested mites in particular, the sporangia in some parts of the polycentric thalli lack sterile, interconnecting filaments, hence appear olopidioid (Fig. 165). The long, single exit tubes (Fig. 163) and blastocladiaecous planonts (Figs. 164) readily serve as identifying characters for this species.

Booth (1971a) reported that rhizoids developed from the sporangia as well as from the sterile isthmuses in his cultured specimens. Rhizoids are very rare in the Iceland specimens, and were never seen to spring from the sporangium wall. This is seemingly a nutritionally controlled response in this species.

Blastocladiaecae

BLASTOCLADIA

Blastocladia pringsheimii Reinsch (Fig. 238–249)

Extreme variation in the habit of the basal cell characterizes plants assigned to this species (see Sparrow, 1960: p. 685). The plants from Iceland — collected on apples and fruits of *Sorbus* near Vaglaskógur, in the deep streams at Thingvellir, and in ponds at Heidmörk — were no exception to this alleged variability. Thalli produced only the narrowly cylindrical, fusiform, ellipsoidal, or siliquiform sporangia (Figs. 238, 239, 241), resting spores (Fig. 243) alone (Fig. 242), or both sporangia and resting spores (Fig. 240). Setae were usually present among the sporangia and resting spores.

In an occasional isolated pustule, or (more frequently) mixed with thalli bearing the long, cylindrical sporangia, were plants with short, ovoid, broadly fusiform or ellipsoidal sporangia (Figs. 244–246). The basal thallus of these plants was indistinguishable in size and shape from those of *Blastocladia pringsheimii*. The sporangia were 20–(30–38)–57 μ long by

9–(11–14)–18 μ in diameter, and thus were substantially smaller than comparable structures described for *B. pringsheimii*. None of these small sporangia bore an apical plug such as has been recorded for this species, but not all representatives assigned to Reinsch's species produce such accessory structures.

The immature sporangia of the "form" are smooth-walled and bear internally, spherical, scattered, faintly refractive bodies (Fig. 247). Only a few planonts are cleaved in these small sporangia (Fig. 248). They escape as large, ovoid, posteriorly uniflagellate cells, each with a conspicuous nuclear cap (Fig. 249). No evanescent matrix or vesicle (such as sometimes occurs in *Blastocladia pringsheimii*) accompanies spore release.

It is evident that a number of thallus variations in *Blastocladia pringsheimii* have been segregated out as distinct species. Since none has been single-spore cultured, their status remains uncertain. Nothing is to be gained by naming yet another segregate from among the many variants to be found in pustules.

BLASTOCLADIELLA

Blastocladia sp. (Figs. 250–256)

On snakeskin (bait) in a wet soil sample from the edge of a small tributary stream near Geysir (8 September 1972) I collected what was first identified as a rhizophlyctoid fungus (Herb. No. 6823). Single sporangia were dissected from the bait; planonts from these established sparsely populated unifungal cultures on pretreated snakeskin (the fungus would not grow on YPSS agar made up in tap water or in soil extract-potassium tellurite water). A description of the plants follows.

Sporangium globose, subglobose, or erect-ovoid; hyaline, thin-walled; provided with a single conical or short-cylindrical, apical or subapical discharge papilla; globose ones 31–48 μ in diameter, subglobose or ovoid ones 38–74 μ in diameter by 28–66 μ high. Rhizoidal system consisting of 3–several stout, moderately branched main axes arising in a group from one area on the sporangium; variable in diameter and extent. Planonts posteriorly

uniflagellate, endogenously formed, ovoid to ellipsoidal; escaping, on apical dissolution of the exit apparatus, into a quickly evanescent matrix, then becoming sluggishly motile; possessing a conspicuous, hemispherical or lunate nuclear cap and one or two eccentric, refractive bodies; 5–7 μ long by 3.5–4 μ in diameter; flagellum 22–25 μ long. Resting spores spherical; wall light golden brown, reticulate; usually lying loosely in a hyaline, subspherical cell with an irregularly thickened wall, and provided with a stout, branched, basal rhizoidal system of 2 or more axes; occasionally filling the container; 41–60 μ in diameter; germination not observed.

Two instances of spore release were observed among the very sparse sporangial thalli. In both instances, a matrix accompanied emergence of the first few planonts (Fig. 253), but they quickly escaped as if the matrix rapidly dissolved or was not truly confining. All of the sporangial thalli had "clustered" rhizoidal axes, that is, ones arising from one area on the sporangial wall (Figs. 250–252). The resting spore thalli (Figs. 254–256) were similarly equipped with rhizoids.

Morphogenesis of the sporangium was not observed, but a few resting spore thalli in various developmental stages were seen. The rudimentary resting spore is hyaline and spherical (Fig. 256). As it enlarges, the wall becomes lightly pigmented, and small, angular markings (Fig. 255) appear very faintly on its surface. Maturation beyond this point was not observed, hence how the spherical, reticulate spore is cleaved from its container is not known. In instances where the resting spore fills the container, the adjacent walls are tightly appressed, and are indistinguishable as separate entities. As with the sporangial thalli, the sparseness of resting spore thalli prevented a more detailed analysis of structure and development.

The general aspect of some sporangia (Fig. 250, for example) recalls *Blastocladia britannica* (Horenstein and Cantino, 1961), a species first discovered in the English Lake District by Willoughby (1959) and char-

acterized by him. Furthermore, there is a striking similarity between the resting spore containers in the British and the Iceland plants; in both, the thallus wall is irregularly thickened. Only the reticulate nature of the wall in resting spores of my specimens separates them from those of *B. brittanica* (in this species they are minutely pitted). A more complete structural analysis of a greater number of specimens than those at hand is needed before any firm identification can be made.

HYPHOCHYTRIALES

Hyphochytriaceae

HYPHOCHYTRIUM

Hyphochytrium catenoides Karling (Fig. 156–162)

Höhnk (1960) and Howard (1968) report this species from Iceland. Howard retrieved plants from soil samples only on snake-skin bait as did Booth and Barrett (1971). Barr (1970b), and Booth (1971a,b), however, collected the fungus in pollen grains used as bait. It is in *Hyphochytrium catenoides* that Howard (1968) found an undescribed species of *Sorosphaera*. This very curious biflagellate parasite, though named, was not formally authenticated in publication.

Although *Hyphochytrium catenoides* is far

from common in soils of Iceland, two forms have appeared. Both have been isolated and cultured on ¼ strength YPSS agar containing potassium tellurite. In one form, the sporangia are generally spherical (Fig. 156), while in the other they are angular and elongate (Fig. 159). Both forms have multiple exit tubes. Planonts are cleaved and discharged in like fashion in the two forms. At discharge, the undifferentiated sporangial protoplast emerges (Fig. 160), through an orifice dissolved in the apex of the exit tube. The planonts form exogenously (Figs. 157, 161), and then separate as oval or elongate, oftentimes somewhat flattened, anteriorly uniflagellate cells, containing a number of small, refractive granules (Figs. 158, 162).

In a well-conceived culture study, Barr (1970b) propagated four isolates of *Hyphochytrium catenoides* on various media. Variations were induced, but none, he concluded, was of any taxonomic significance. My cultures seem also to clarify a troublesome point regarding Siang's (1949) report of this species as an airborne aquatic "phycomycete." Siang's fungus grew yeast-like in culture, as opposed to the distinctly mycelial growth which my plants effected. Barr (1970b) has suggested that the fungus Siang had reported as *H. catenoides* was, in fact, not this species.

ACKNOWLEDGEMENTS

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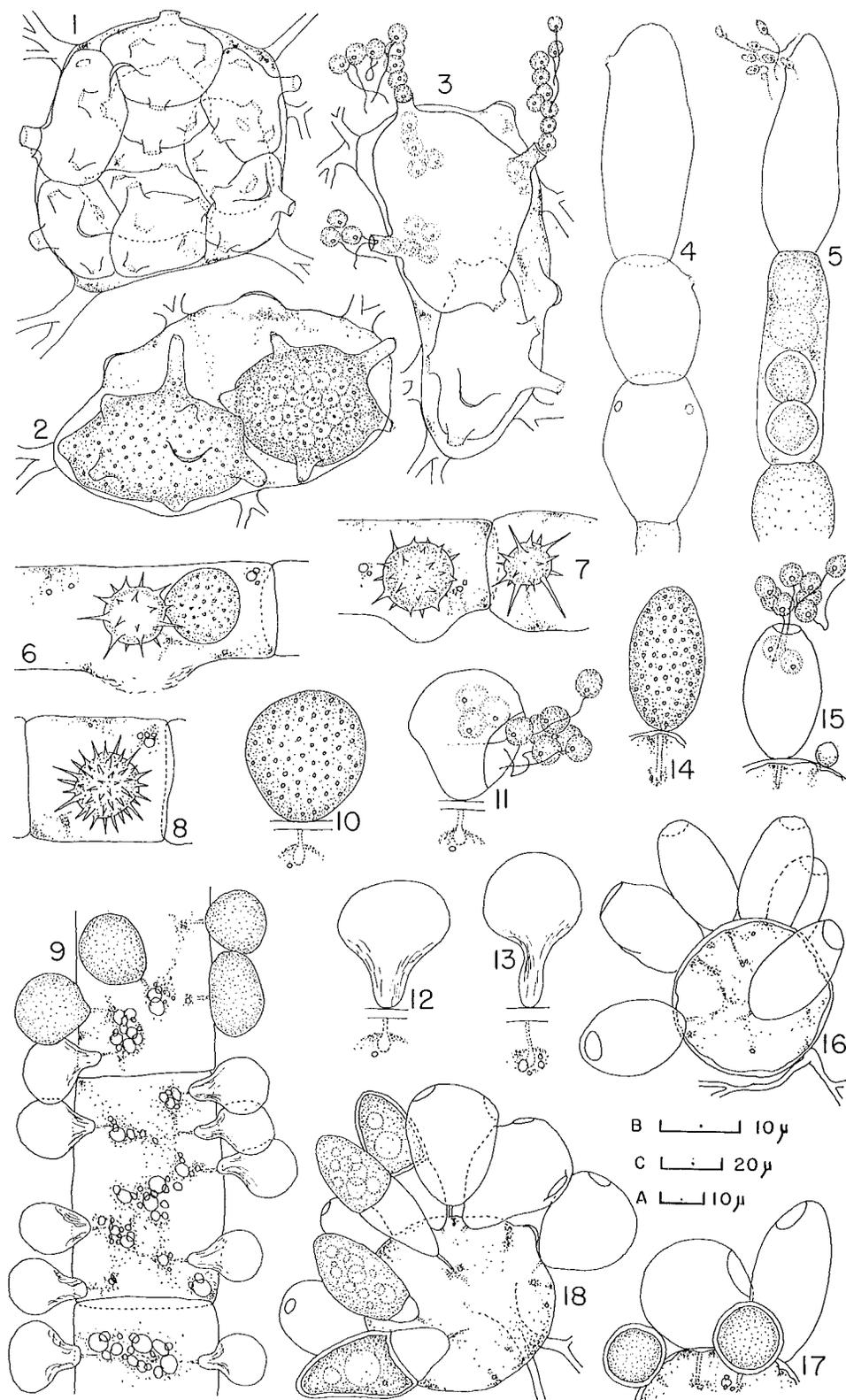
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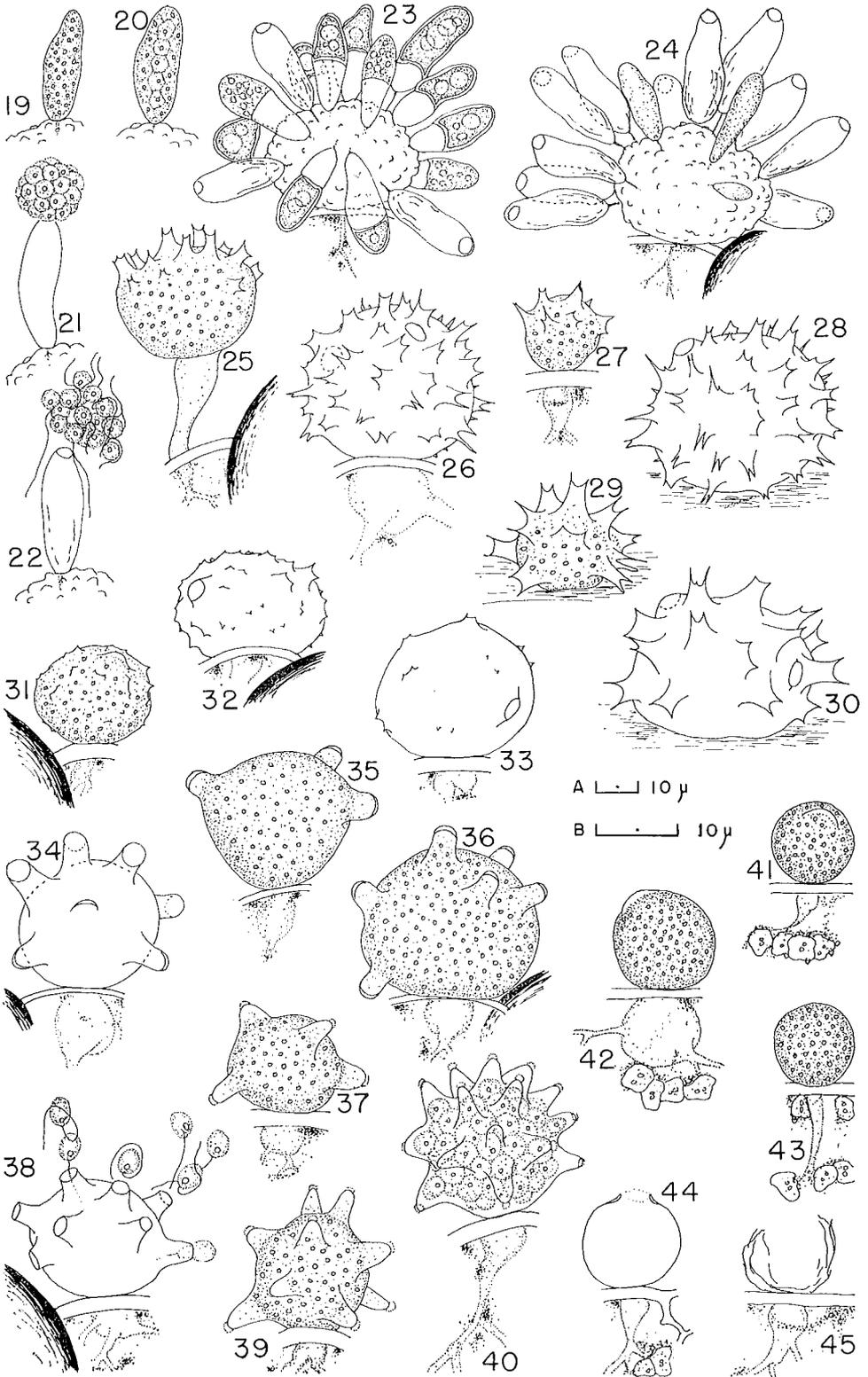
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PLATES AND
EXPLANATIONS OF PLATES

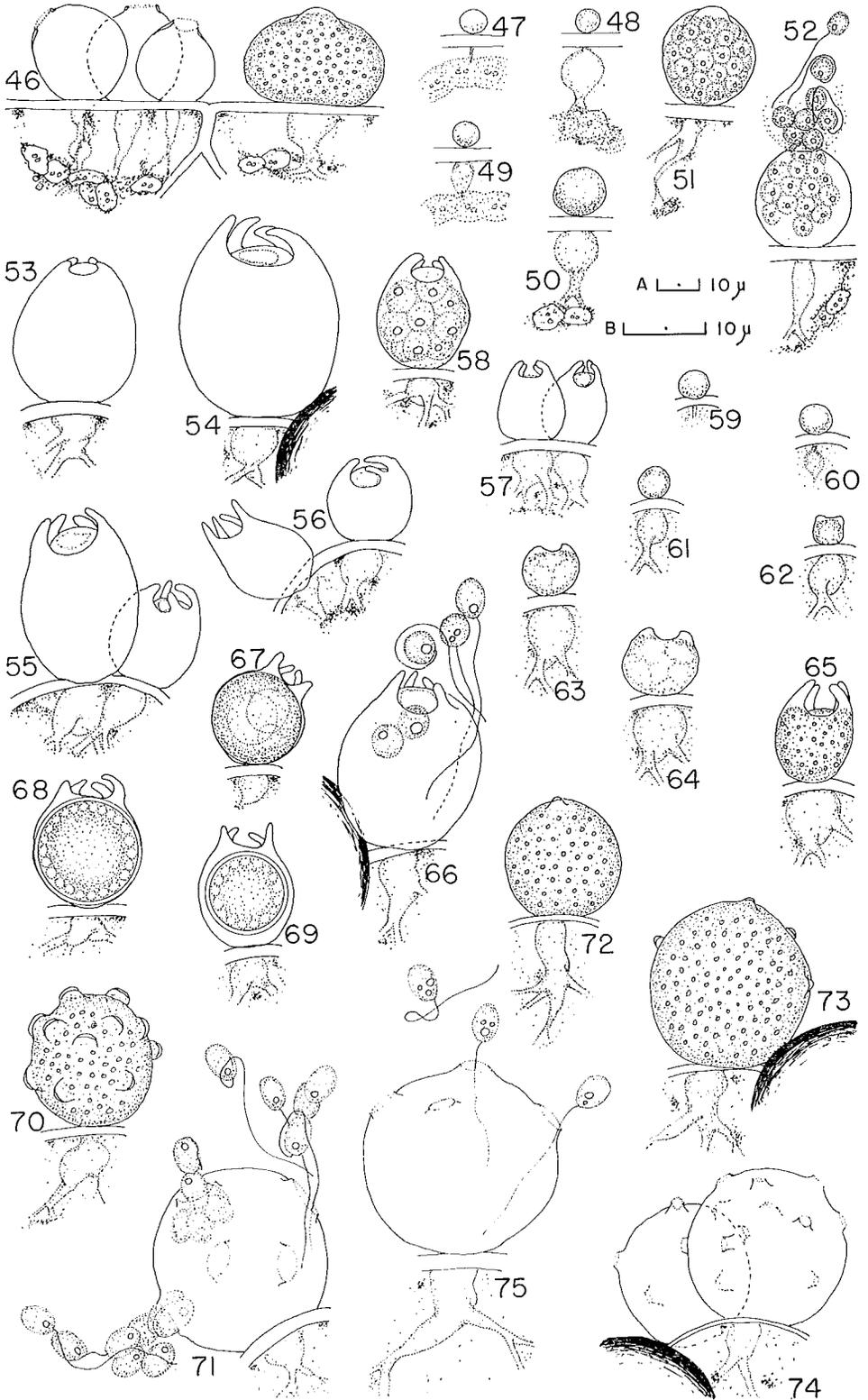
Figures 1–3. *Rhizophlyctis roea*. 1. Several discharged endogenous sporangia. 2. Immature endogenous sporangia, one with spore initials. 3. Two endogenous sporangia, upper one in the process of discharge. Figures 4, 5. *Rozella* sp. 4. Empty sporangia; segmentation of hypal tip, and enlargement. 5. Apical portion of infected hypha showing discharge of planonts, and immature resting spores. Figures 6–8. *Micromyces zygonii*. 6. Spiny prosorus and immature sorus. 7. Ornamented prosori; variations in length of spines. 8. Densely echinulate prosorus. Figures 9–13. *Phlyctidium tenue*. 9. Immature and discharged thalli on filament of host alga. 10. Immature sporangium. 11. Same sporangium discharging planonts through large, lateral orifice. 12. Same sporangium after discharge, showing basal collapsing. 13. Discharged sporangium. Figures 14–17. *Phlyctidium* sp. 1. 14. Immature sporangium. 15. Planont discharge. 16. Cluster of empty sporangia. 17. Two empty sporangia, and two (?) resting spores. Figure 18. *Septosperma rhizophidii*. Empty sporangia and two-celled resting spores on *Rhizophyidium* sp. Figures 4, 5, scale C; figs. 10–18, scale B; others, scale A.



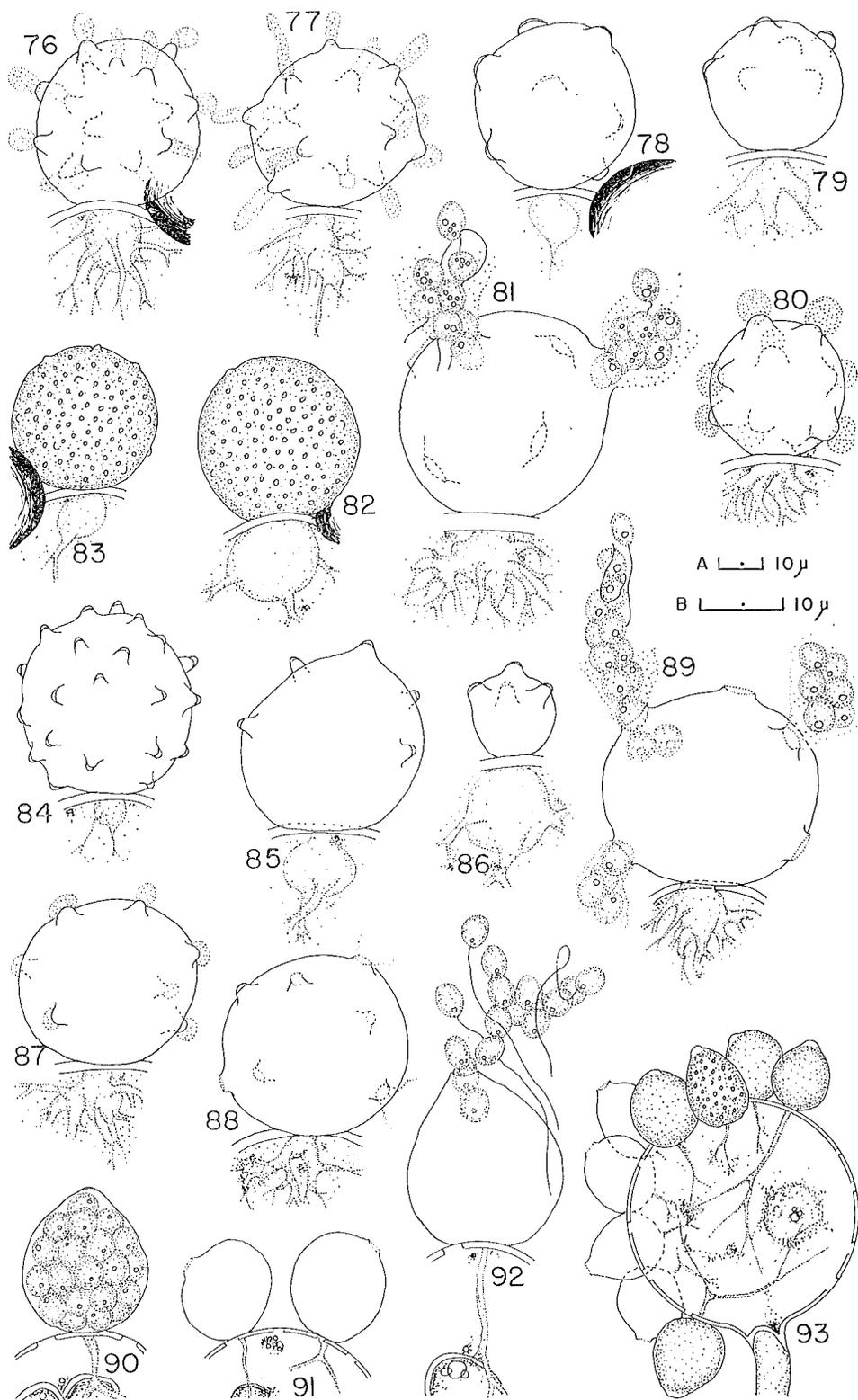
Figures 19–24. *Septosperma anomala*. 19–22. Stages in formation and discharge of planonts. 23. Two-celled resting spores, and discharged sporangia on *Rhizophyidium* sp. 24. Sporangia. Figures 25–33. *Phlyctochytrium aureliae*. 25. Immature, stalked sporangium. 26. Discharged sporangium on pollen. 27. Small, immature sporangium. 28–30. Variations in size and ornamentation in sporangia on cellophane. 31–33. A “form” of the species with inconspicuous, sparse ornamentations. Figures 34–36. *Phlyctochytrium papillatum*. 34. Discharged sporangium; prominent, cylindrical or broadly-papillate discharge tubes. 35, 36. Immature sporangia. Figures 37–40. *Phlyctochytrium reinboldtae*. 37. Young sporangium with tapering, mammiform exit papillae. 38. Planont discharge. 39. Immature sporangium. 40. Densely papillate sporangium with endogenous planont initials. Figures 41–45. *Phlyctochytrium lagenaria*. 41–43. Immature sporangia, and variations in endobiotic apophysis. 44. Discharged sporangium. 45. Collapsed and disintegrating sporangium. Figures 34–36, scale A; others, scale B.



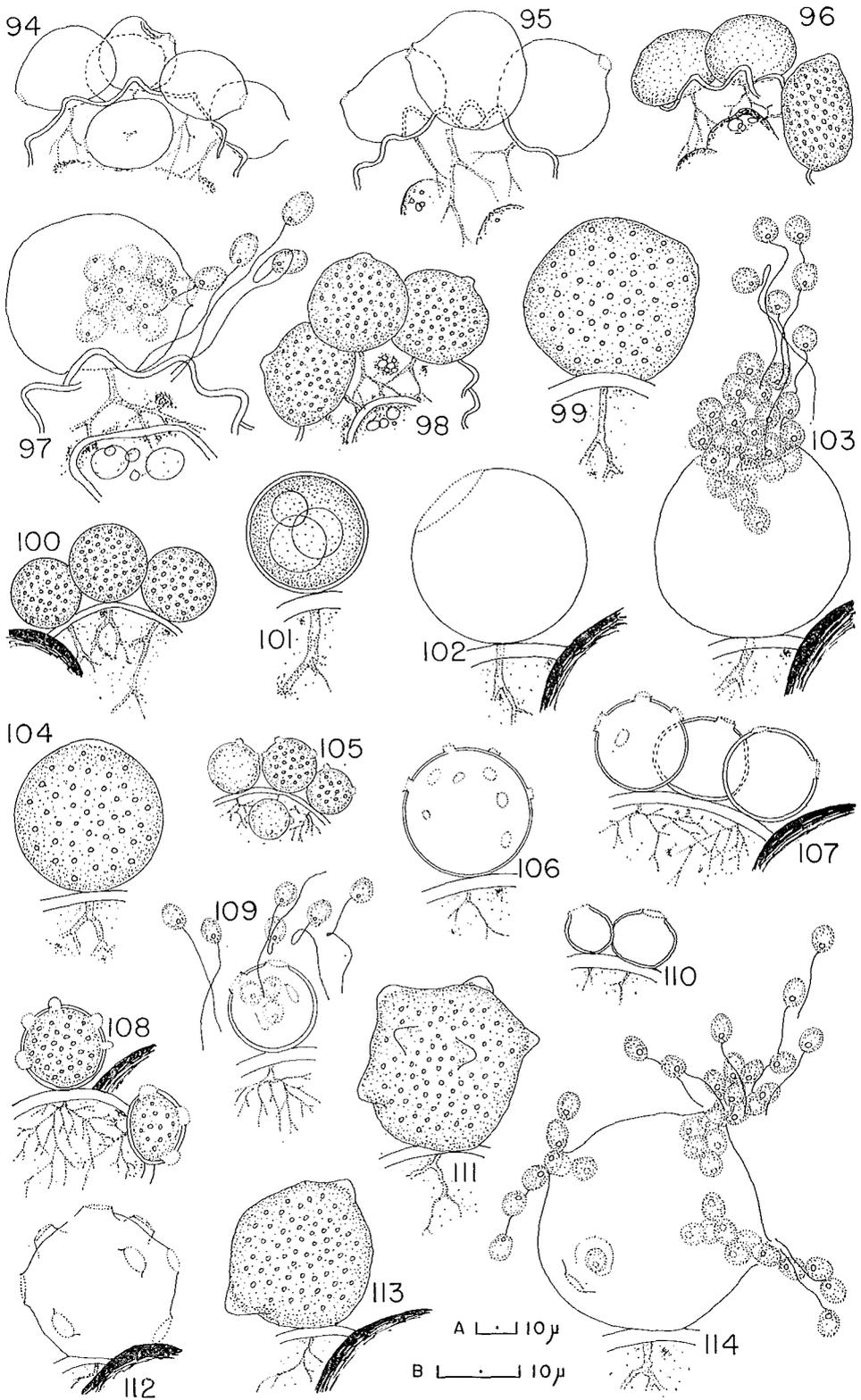
Figures 46–52. *Phlyctochytrium lagenaria*. 46. Three discharged sporangia, and a subglobose, immature one. 47–50. Successive stages in development of the apophysis (endobiotic) and sporangium (epibiotic). 51. Mature sporangium containing endogenously-formed planonts. 52. Planont discharge. Figures 53–69. *Phlyctochytrium planicorne*. 53–57. Discharged sporangia showing variations in size and shape, and in nature of the subapical ornamentations around the exit orifice. 58. Sporangium containing endogenously-formed planonts. 59–65. Successive developmental stages in the endobiotic apophysis and epibiotic sporangium. 66. Planont discharge. 67. Immature resting spore. 68. Mature resting spore filling the container. 69. Mature resting spore lying loosely in the sporangium-like container. Figures 70, 71. *Phlyctochytrium semiglobiferum*. 70. Immature sporangium with broad, dome-like exit papillae. 71. Planont discharge. Figures 72–75. *Phlyctochytrium africanum*. 72. Spherical, immature sporangium with a single, small, conical discharge papilla. 73. Immature sporangium with four exit papillae. 74. Discharged, multiporous sporangia. 75. Planont discharge; spores contain more than one refractive body. Figures 70, 72–74, scale A; others, scale B.



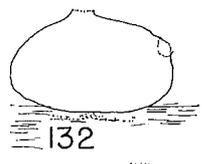
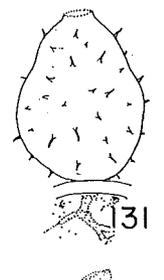
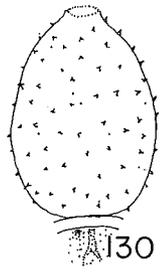
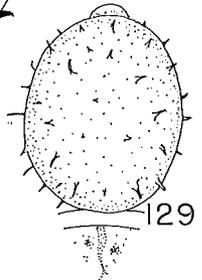
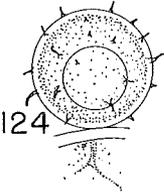
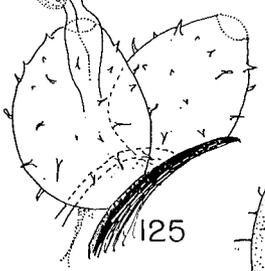
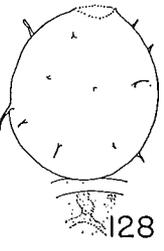
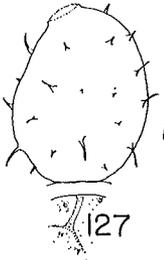
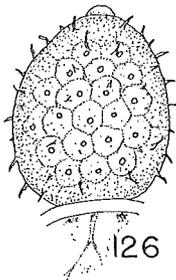
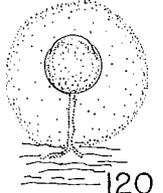
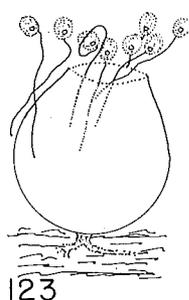
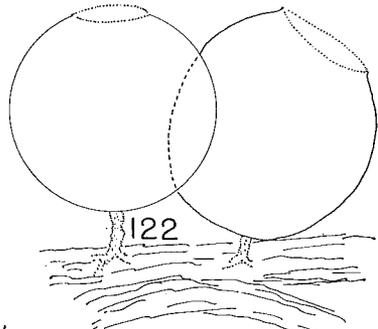
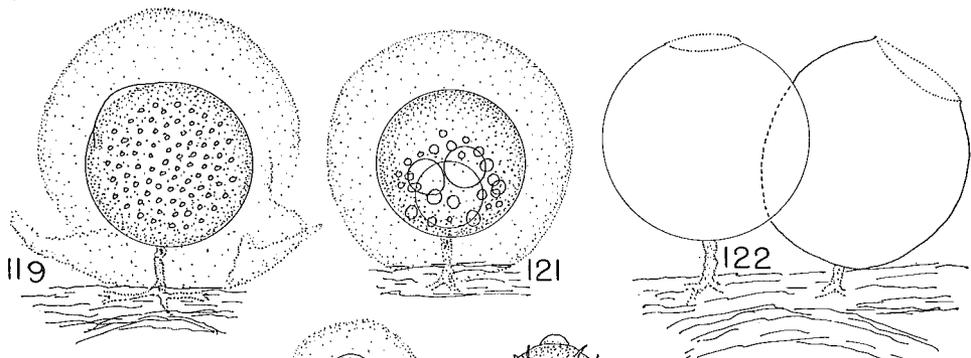
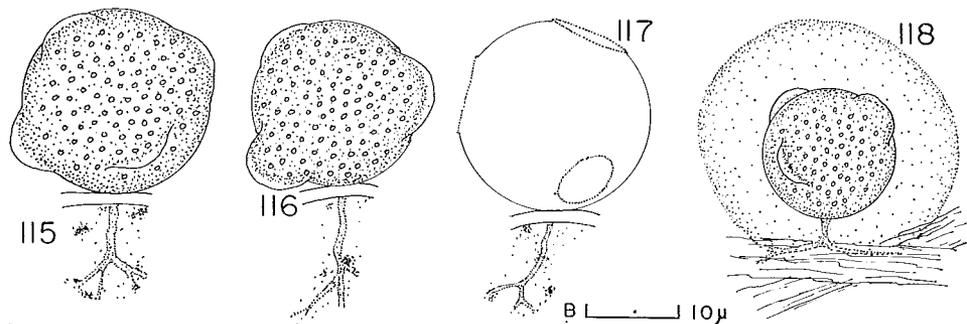
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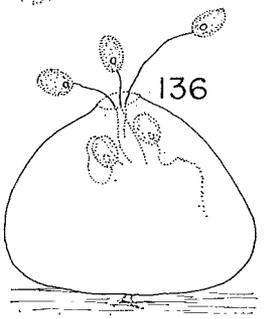
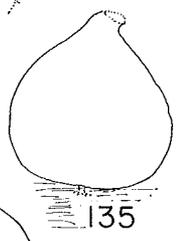
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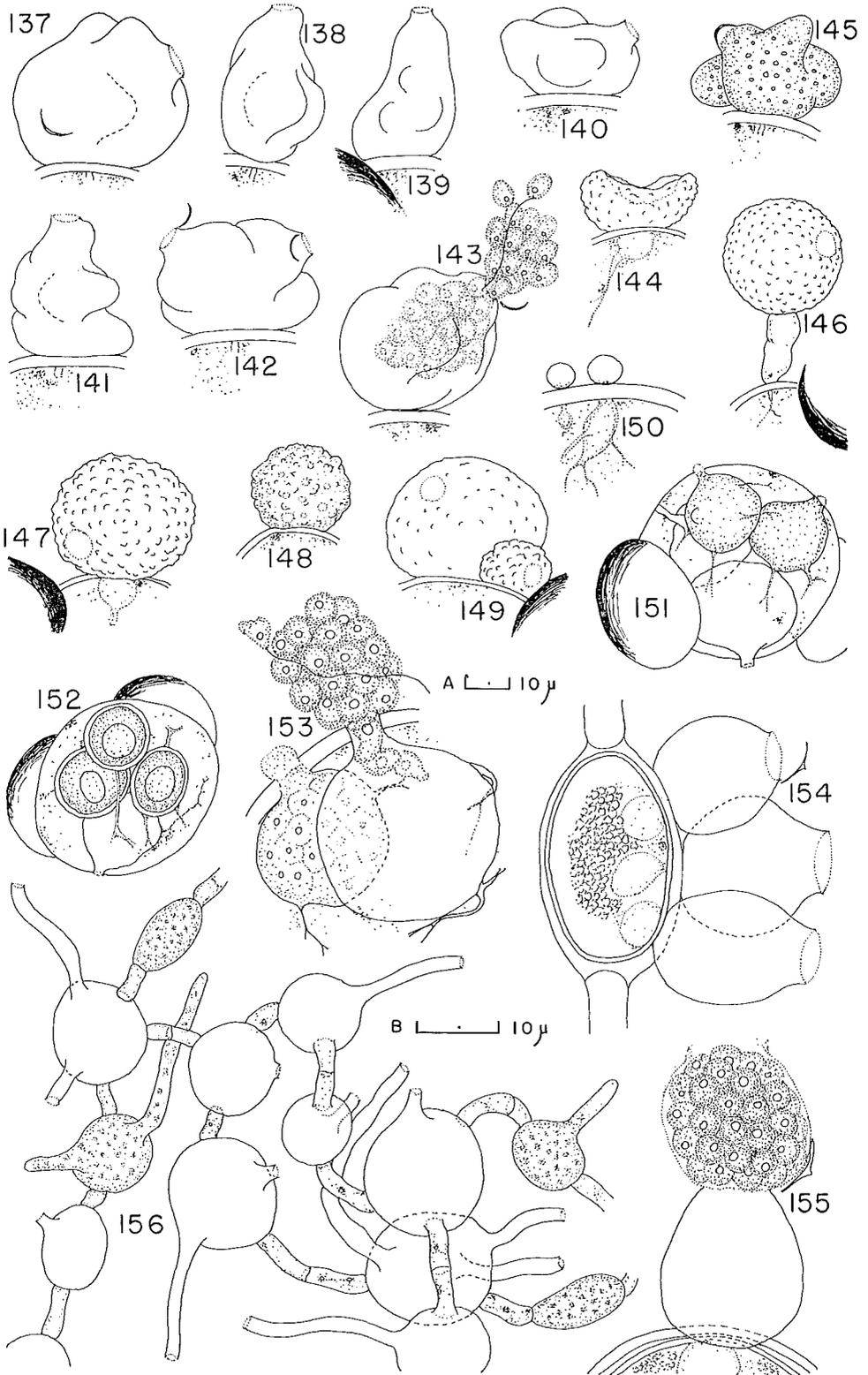


A \perp 10 μ
C \perp 20 μ



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Figures 137–143, 145. *Chytriomycetes* (?)*poculatus*. 137–142. Discharged sporangia showing variations in shape. 143. Planont discharge; sporangium is operculate. 145. Immature sporangium. Figures 144, 146–149 (?)*Phlyctochytrium* sp. 144. Discharged, collapsed, verrucose sporangium. 146. Empty, verrucose sporangium with an epibiotic, cylindrical apophysis. 147. Discharged sporangium. 148. Immature sporangium. 149. Two sporangia, showing variations in size and in prominence of wall ornamentations. Figures 150–153. *Entophlyctis confervae-glomeratae*. 150. Planont germination, and a stage in development of the endobiotic thallus. 151. Sporangia (two immature) in a pollen grain. 152. Eucarpic resting spores. 153. Two endobiotic, eucarpic sporangia, one with spore rudiments, and one discharging planonts. Figures 154, 155. *Chytridium olla*. 154. Three discharged sporangia on an oögonium of *Oedogonium*; bulbous apophyses. 155. Planont discharge from a small sporangium. Figure 156. *Hyphochytrium catenoides*. Portion of polycentric thallus of a form with globose sporangia. Figures 137–143, 145, 150, 153, 155, scale B; others, scale A.



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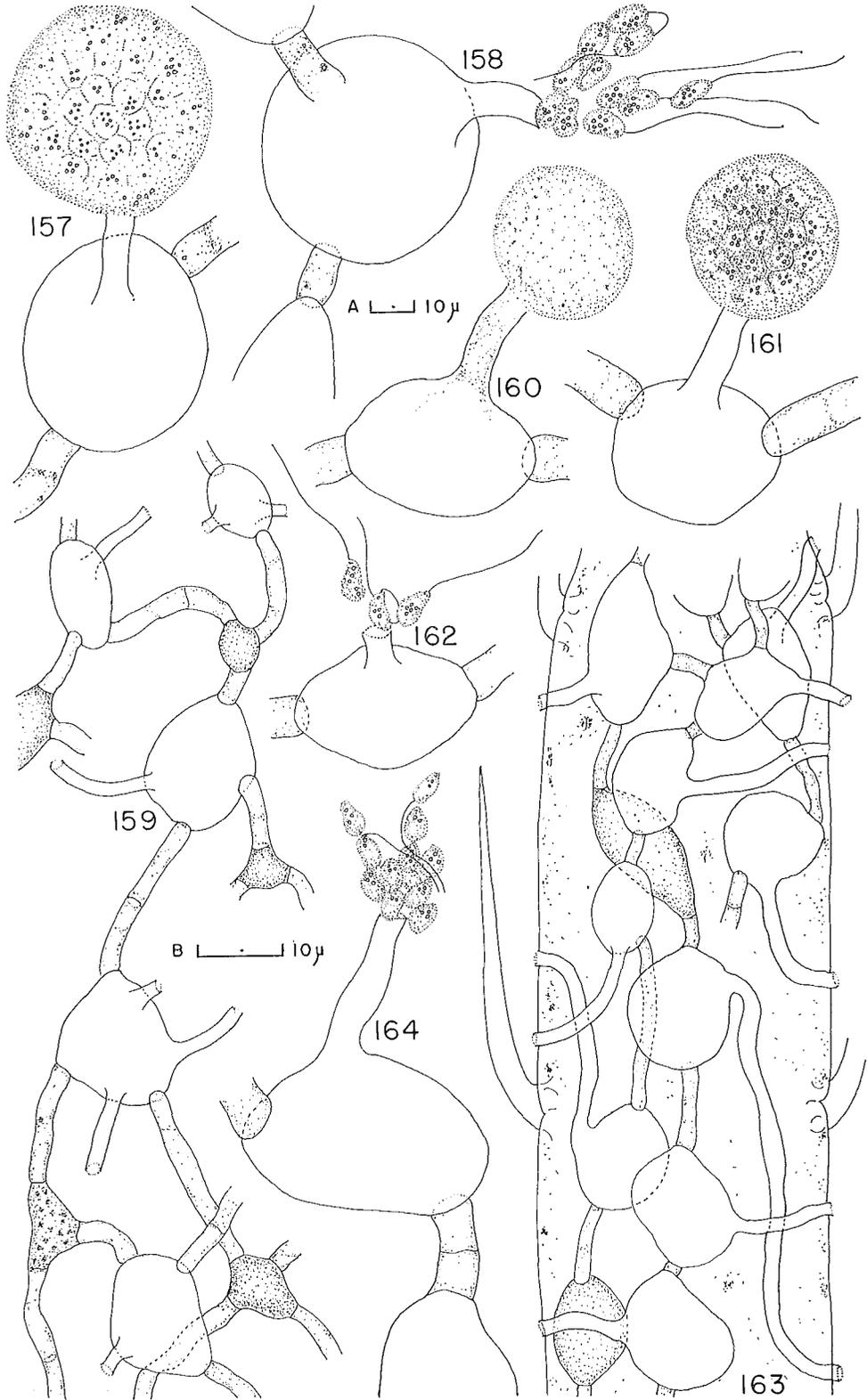
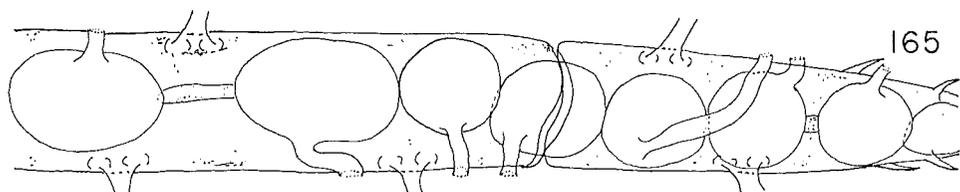
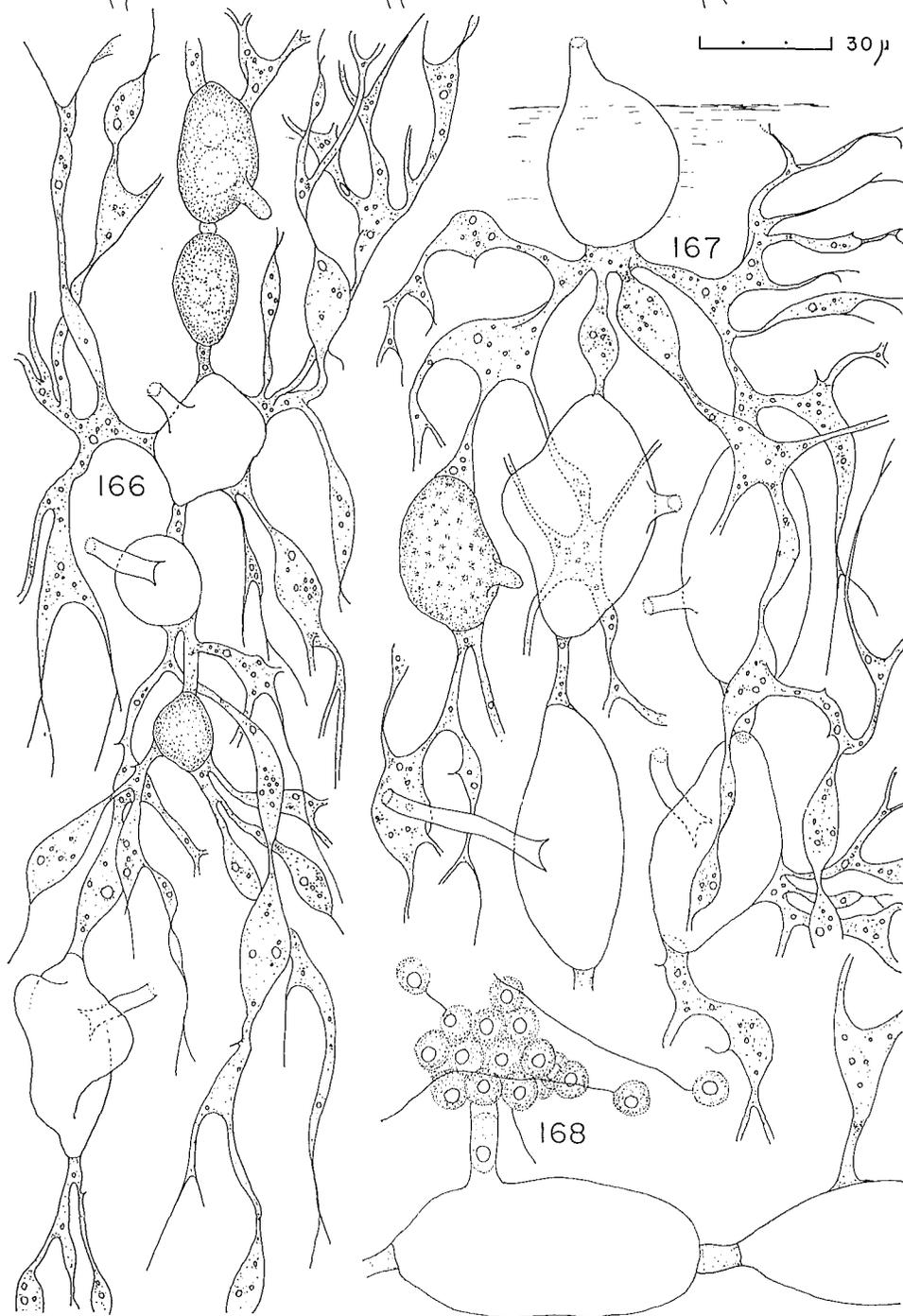


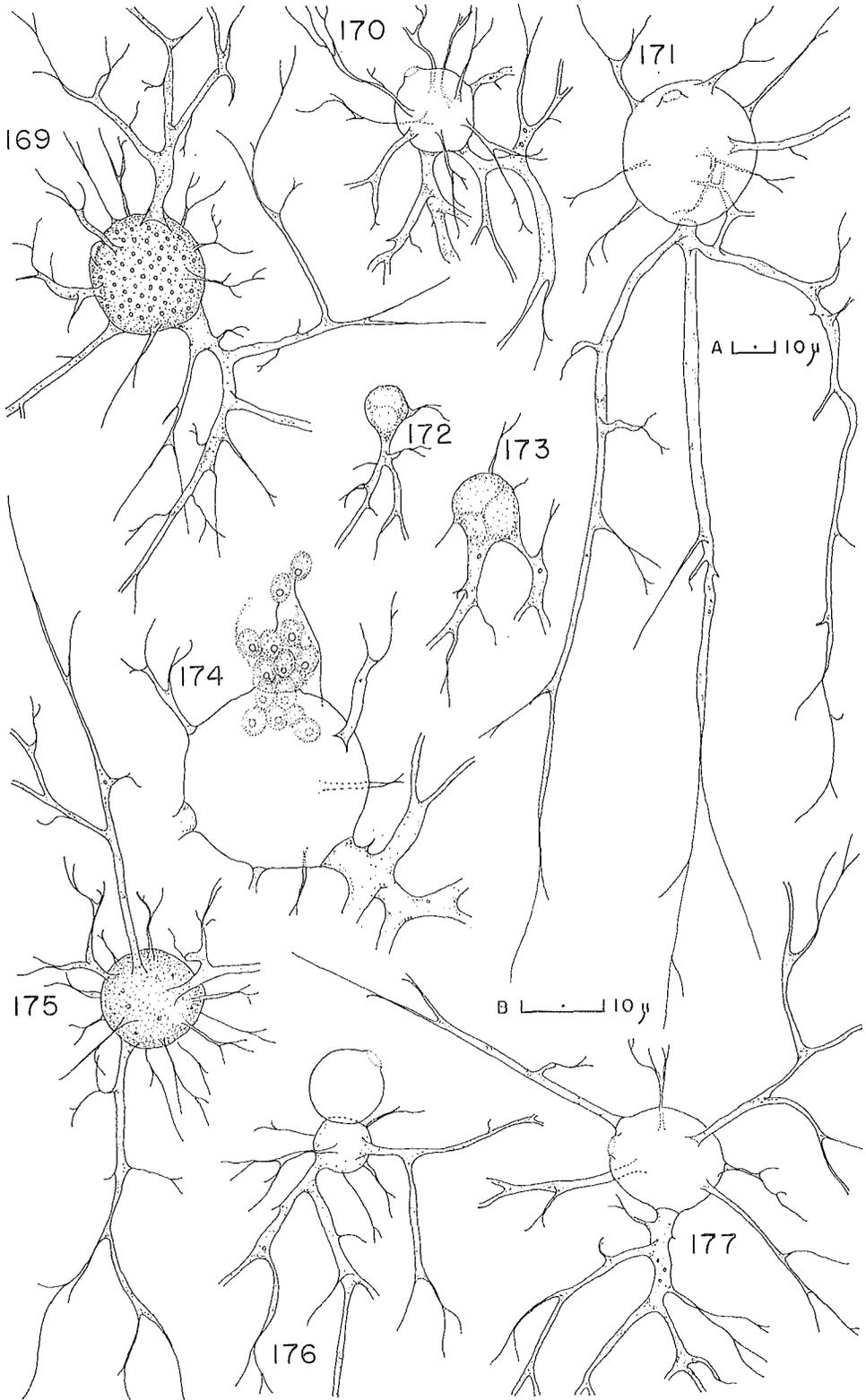
Figure 165. *Catenaria anguillulae*. Portion of a linear, polycentric thallus; some sporangia are not separated by a sterile element, hence appear ophioid. Figures 166–168. *Cladochytrium hyalinum*. 166. Portion of polycentric thallus with small sporangia and sporangial rudiments. 167. Portion of polycentric thallus developed at edge of substratum; sporangia are large and generally elongate. 168. Planont discharge from an intercalary sporangium. All figures same scale.



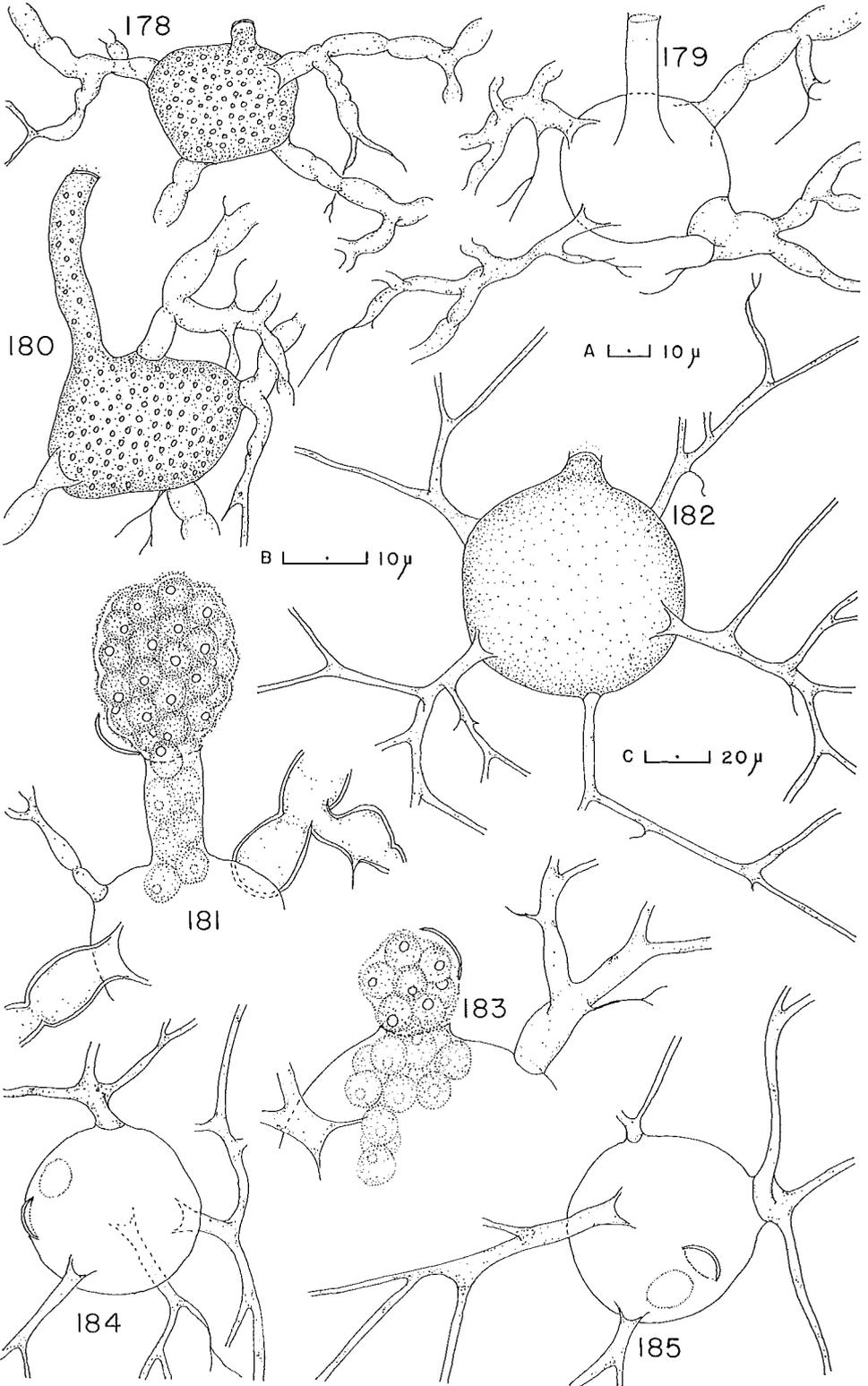
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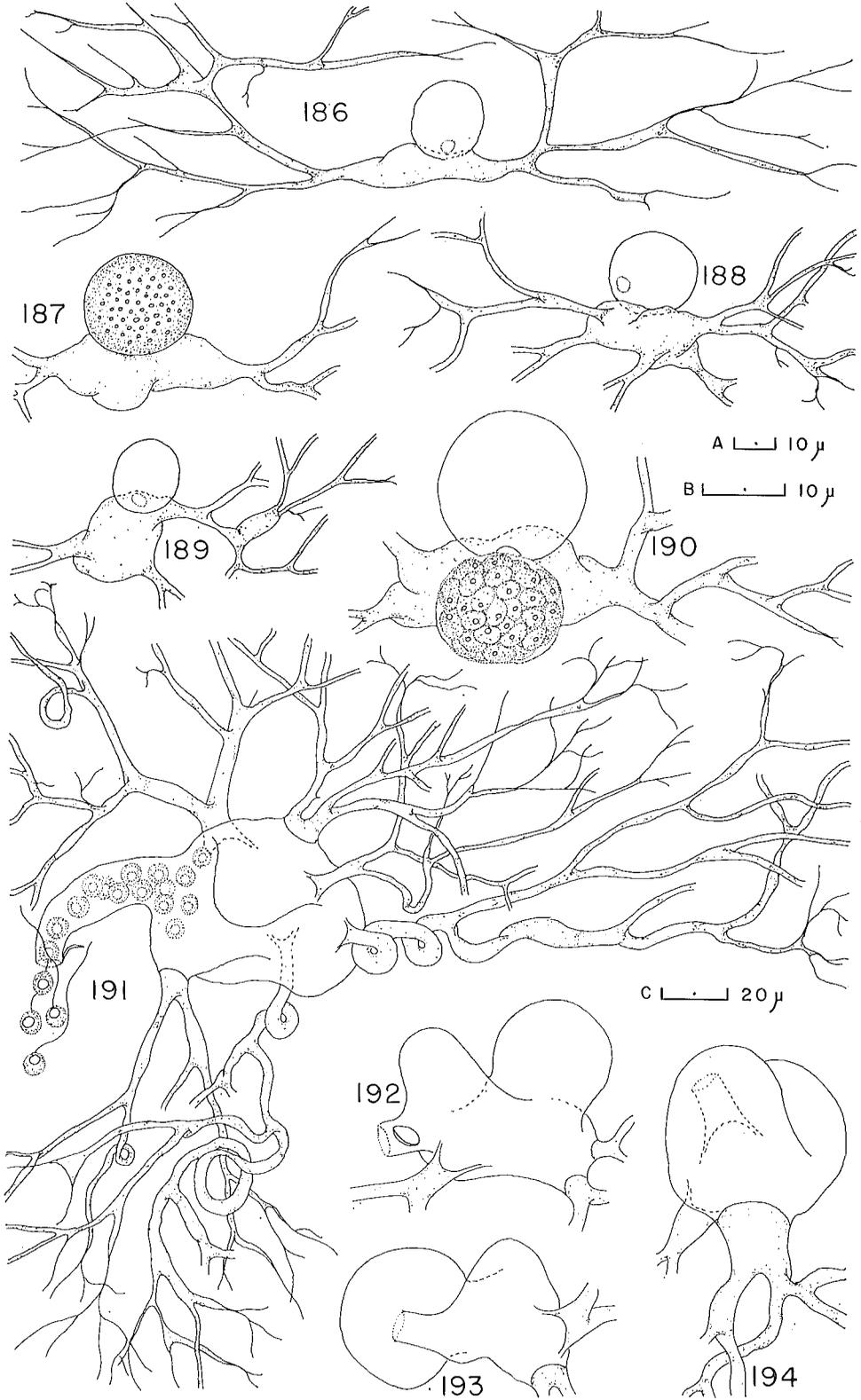
Figures 169–177. *Rhizophlyctis* sp. 169. Immature sporangium with two stout rhizoidal axes. 170. Discharged sporangium with two main rhizoidal axes. 171. Discharged sporangium with a single (but branched) chief rhizoidal axis. 172, 173. Two stages in thallus development. 174. Planont discharge. 175. Immature sporangium. 176. Apophysate sporangium. 177. A discharged sporangium bearing a single main rhizoidal axis. Figure 174, scale B; others, scale A.



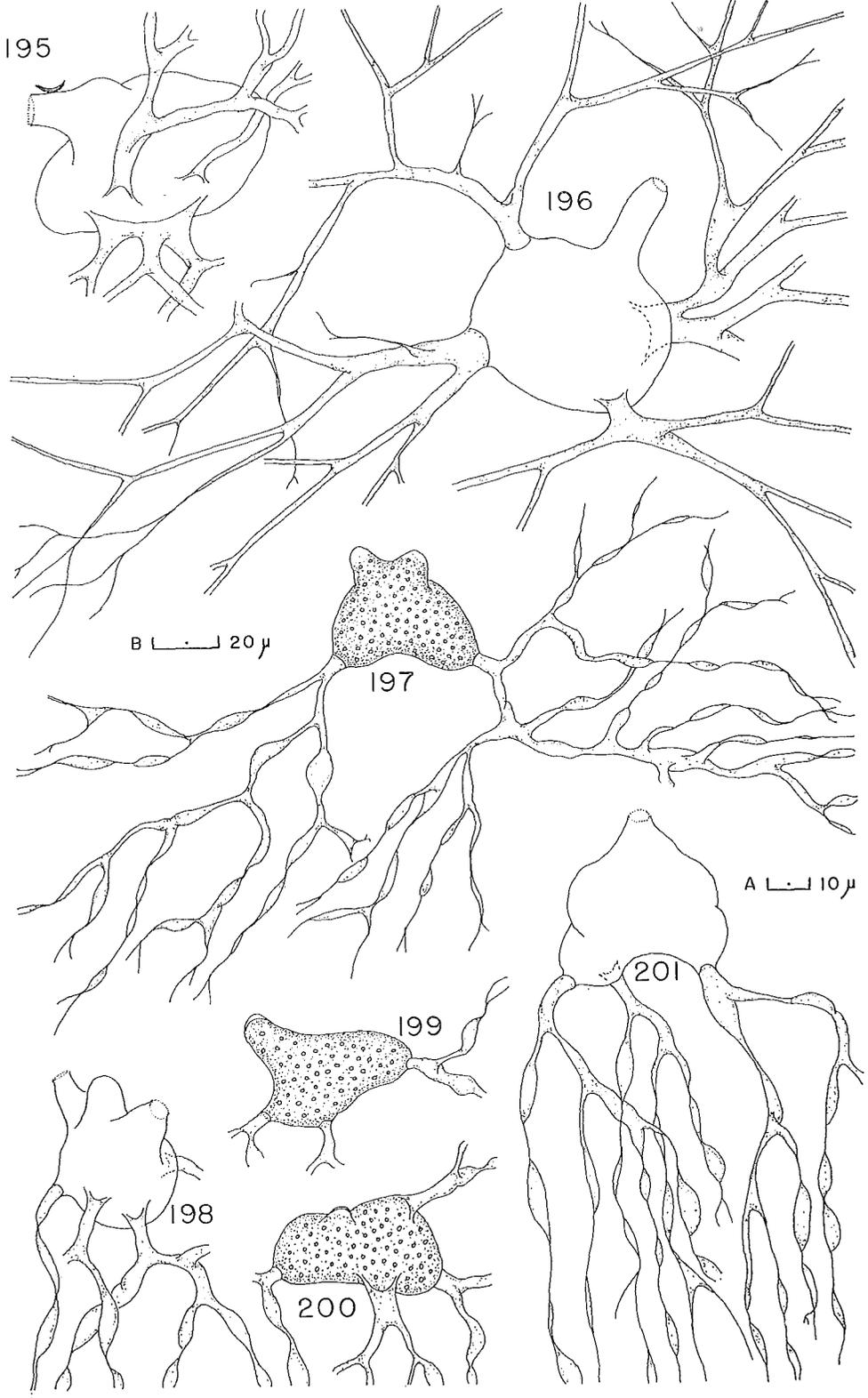
Figures 178–181. *Karlingiomyces marilandicus*.
178. Immature sporangium with a short-cylindrical discharge tube. 179. Discharged sporangium. 180. Immature sporangium with a long-cylindrical discharge tube. 181. Operculate discharge of planonts.
Figures 182–185. *Karlingiomyces* sp. 1. 182. Young, spherical sporangium with a sunken operculum. 183. Planont discharge. 184. 185. Discharged sporangia showing prominent exit pore and displaced operculum. Figures 178–180, scale A; figs. 181, 183, scale B; others, scale C.



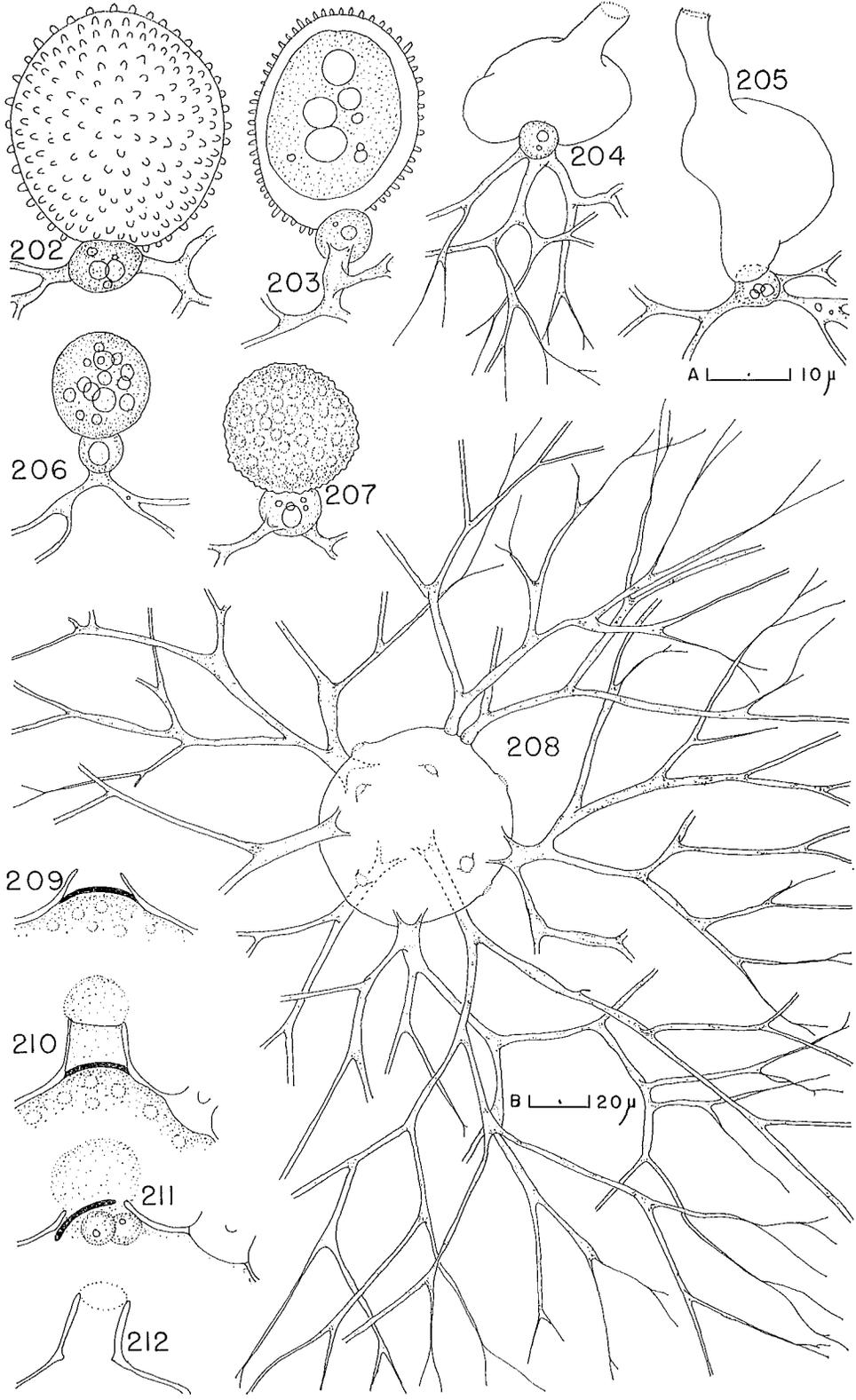
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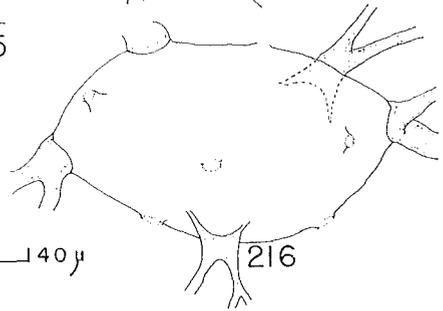
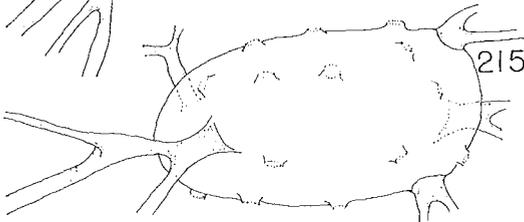
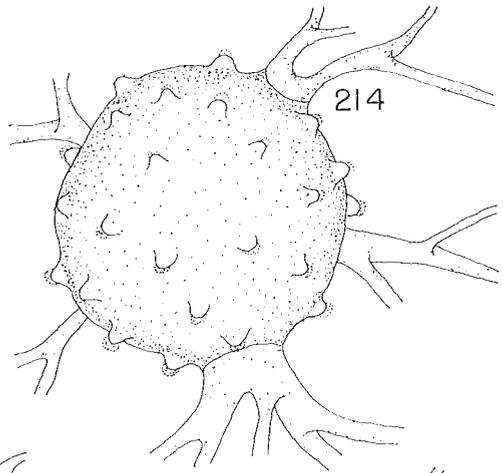
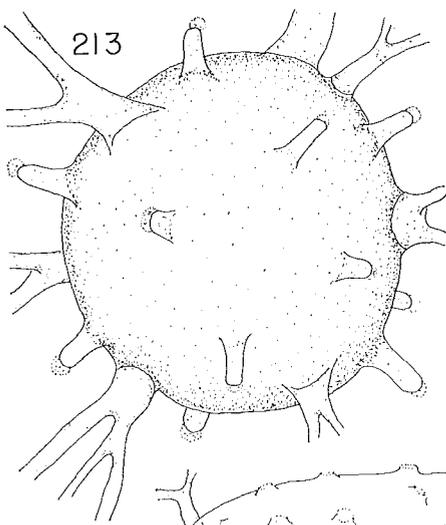
Figures 195, 196. *Karlingiomyces* sp. 2. 195. Discharged, irregular, operculate sporangium. 196. Discharged, subglobose sporangium. Figures 197–201. (?)*Karlingiomyces* sp. 197. Thallus with an immature sporangium and fusiform, catenulate swellings in the rhizoidal branches. 198. Discharged sporangium with two exit pores. 199, 200. Immature sporangia showing thickened apex of the exit apparatus. 201. Discharged sporangium. Figures 195, 196. scale B; others, scale A.



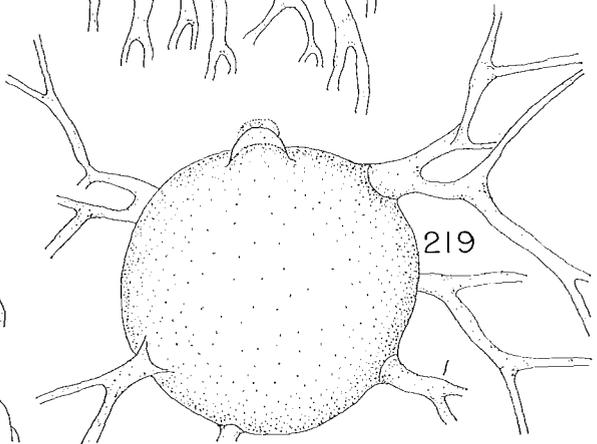
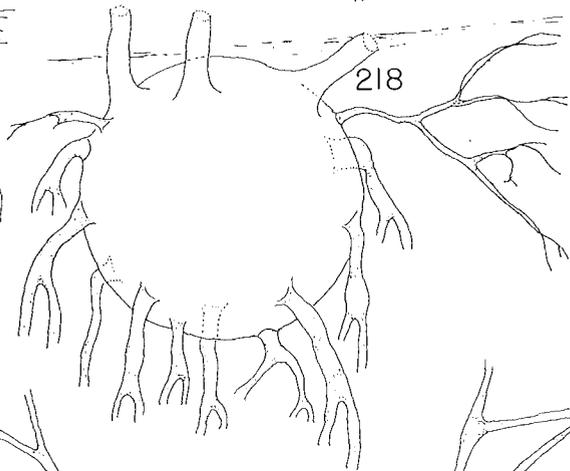
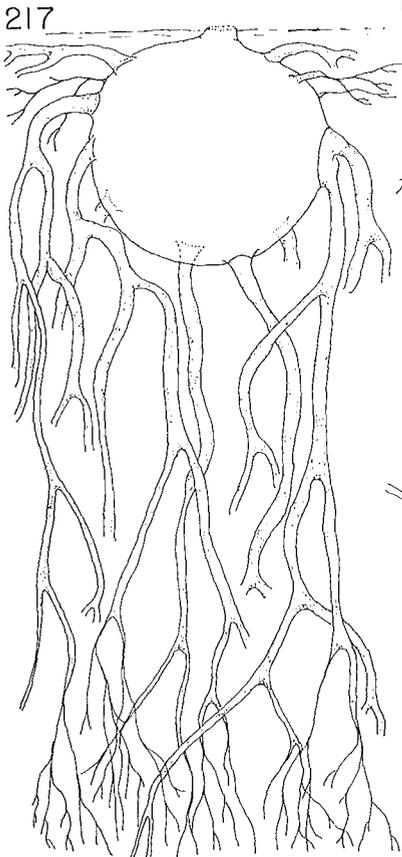
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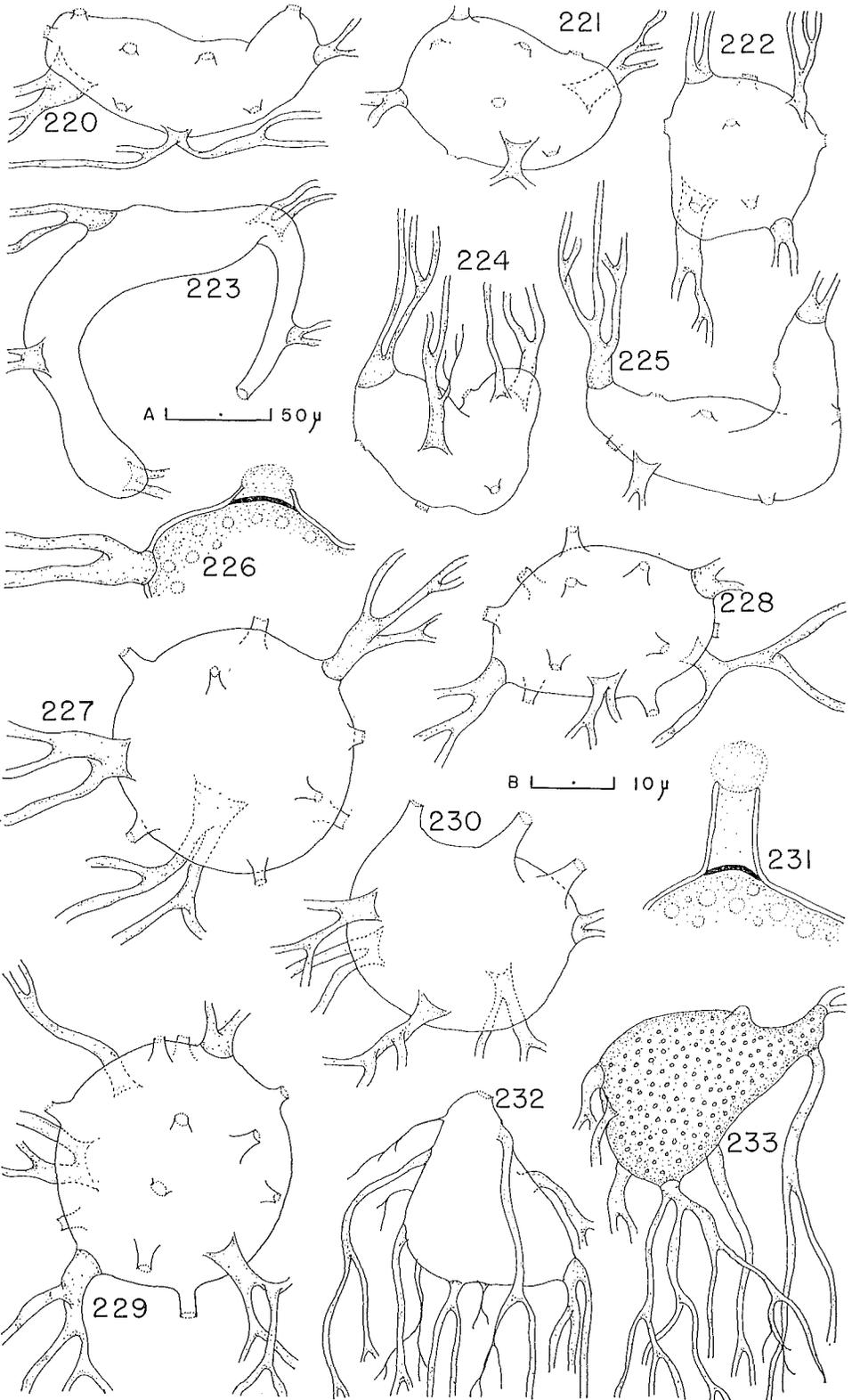
Figures 213—218. *Rhizophlyctis rosea*. 213. An immature, spherical sporangium with prominent, long, tapering discharge tubes, each containing a hyaline, gelatinous plug in the apex. 214. An immature sporangium with numerous, short, conical exit papillae. 215, 216. Discharged, elongate sporangia. 217. Spherical sporangium with a single, apical discharge papilla, and the subtending rhizoidal system (on cellophane). 218. Discharged sporangium, on cellophane, bearing three prominent, cylindrical discharge tubes. Figure 219. *Rhizophlyctis petersenii*. Immature sporangium with a single, large, terminal discharge papilla. All figures, same scale.



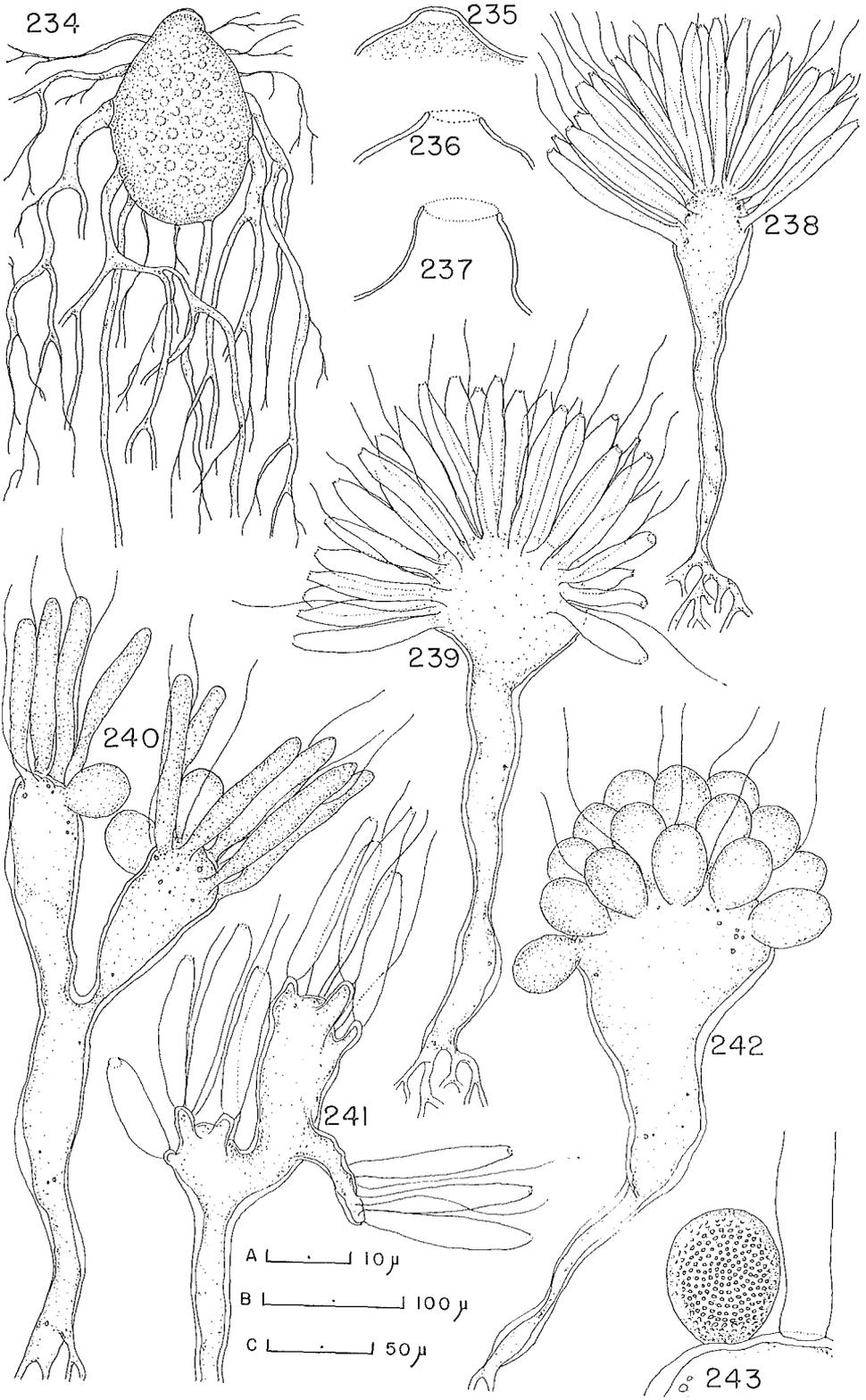
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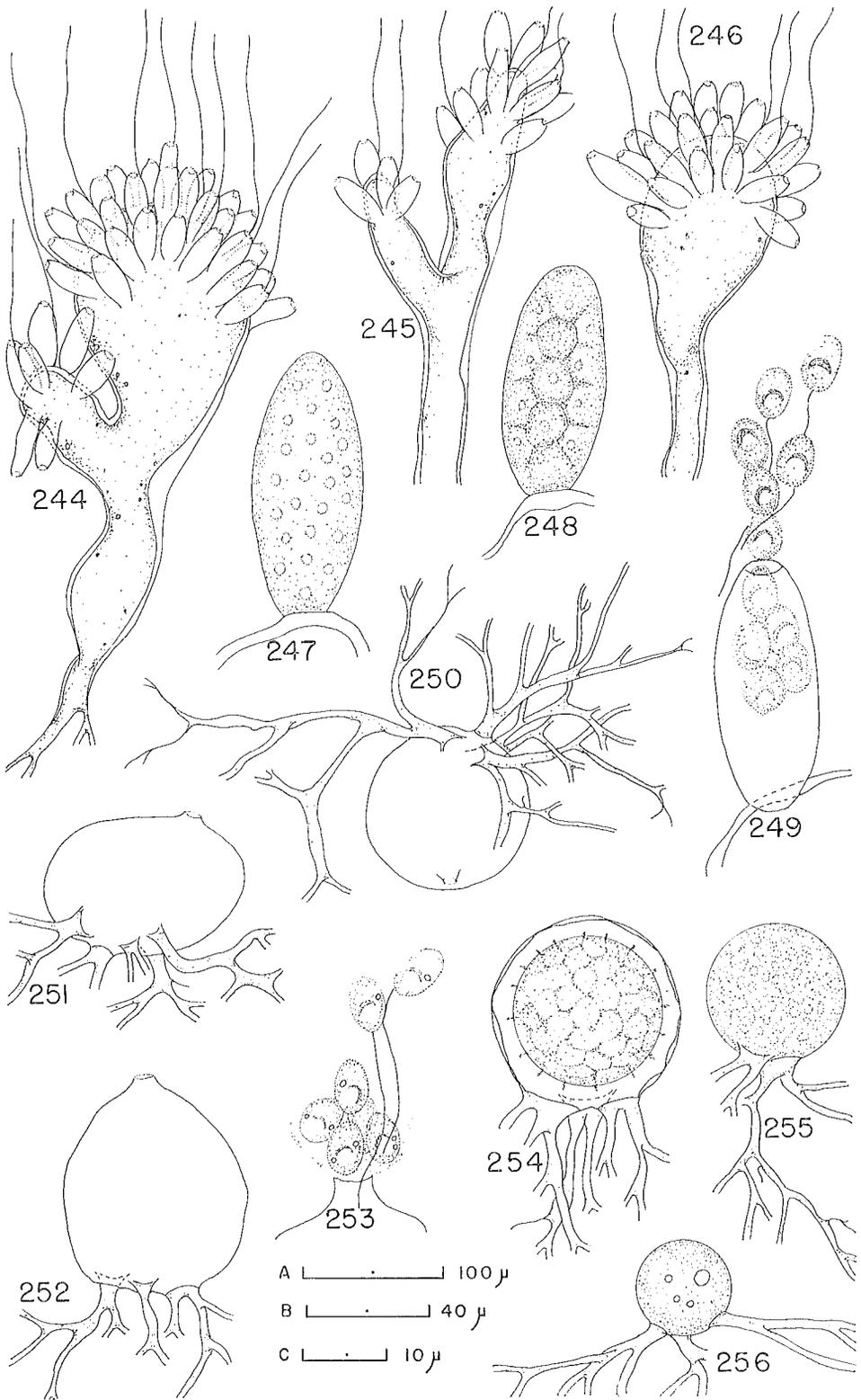
Figures 220–226. *Rhizophlyctis rosea* in grass leaf. 220–225. Variations in sporangial shape, and in position and number of exit papillae. 226. Endooperculum. Figures 227–231. *Rhizophlyctis rosea* on lens paper (transfers from thalli in grass leaf). 227. Globose sporangium with elongate exit papillae. 228. Elongate sporangium. 229. Globose sporangium. 230. Discharged sporangium with three elongate discharge tubes. 231. Endooperculum. Figures 232, 233. *Rhizophlyctis* (?) *willoughbyii* 232. Discharged, conical sporangium. 233. Elongate-pyramidal, immature sporangium, with a single, small exit papilla. Figures 226, 231, scale B; others, scale A.



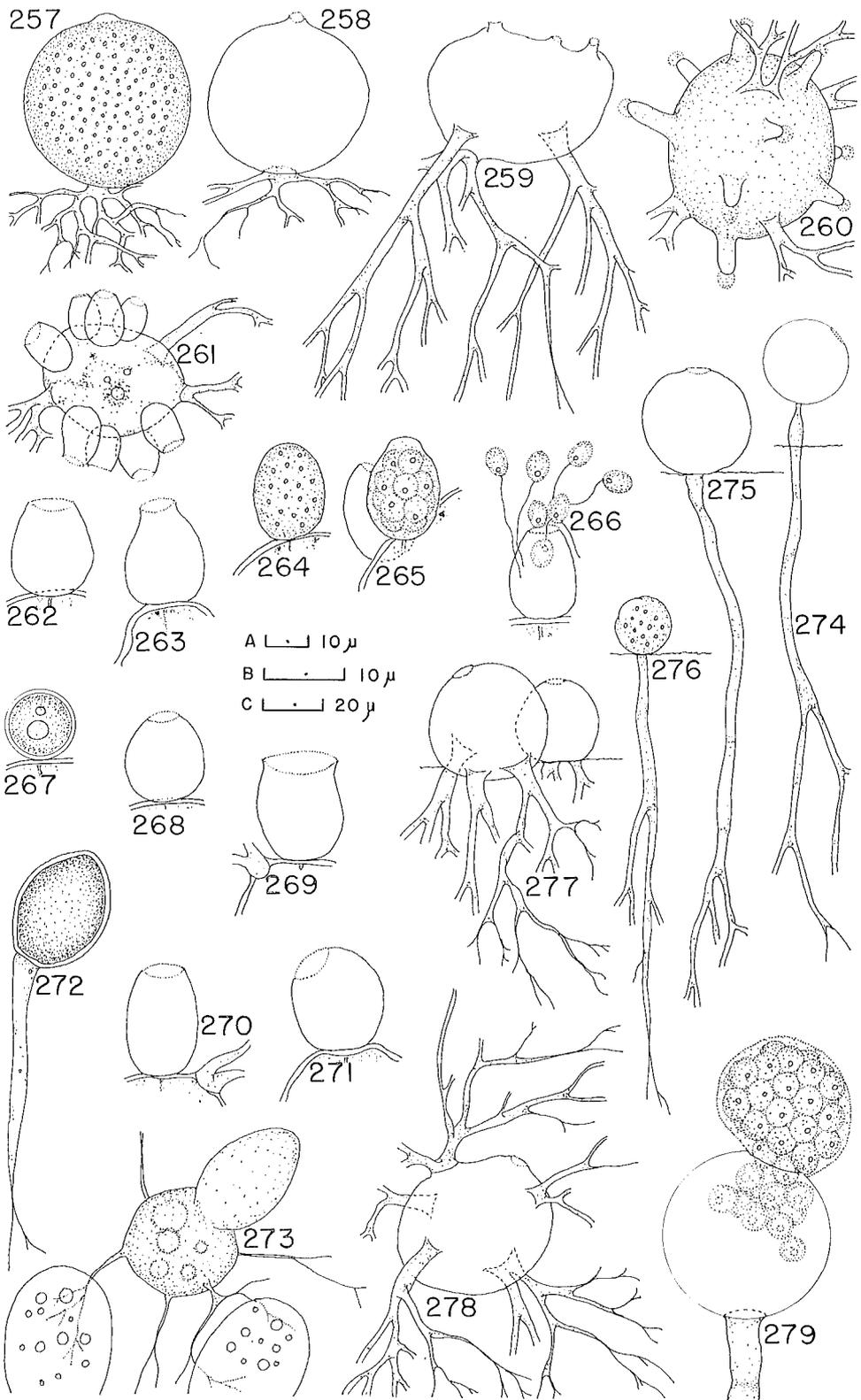
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