A NEW MARINE *LABYRINTHULA* WITH UNUSUAL LOCOMOTION[1]

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QUICK, J. A., JR. 1974. A new marine *Labyrinthula* with unusual locomotion. *Trans. Amer. Micros. Soc.*, 93: 52–61. A new marine labyrinthula was isolated from the seagrass *Halophila englemannii* using serum-agar culture techniques. This phycomycete fungus, *Labyrinthula saliens* n. sp., is characterized by: (1) a distinctive, teardrop-shaped spindle cell having a morphologically differentiated anterior; (2) a peculiar spindle-cell locomotion consisting of intermittent rapid but short advances; and (3) a recurrent chytroid epiendobiotic sporangial stage.

The phylogenetic status of the organisms known as labyrinthulas remains uncertain. As reviewed by Pokorny (1967), they have been assigned to varied groups including protozoa, algae, and fungi; but, more recently, placement has been among the phycomycetous fungi, a decision with which I concur.

Mackin (personal communication) made extensive studies of labyrinthulas and many similar organisms as an adjunct to his work on the labyrinthuloid oyster pathogen, *Labyrinthomyxa marina* (Mackin, Owen & Collier) Mackin & Ray (= *Dermocystidium marinum*), and has listed the genera he believes belong to the fungal Labyrinthulales (Mackin & Ray, 1966). Amon & Perkins (1968), in their studies of *Labyrinthula* sp., noted that: (1) its zoospores were similar to those of most biflagellate phycomycetes, and (2) its vegetative stages and division figures were similar to the thraustochytrid *Schizochytrium aggregatum* Goldstein & Belsky.

Numerous phycomycetous fungi were isolated during my studies (Quick, 1971; Quick & Mackin, 1971) of *Labyrinthomyxa marina*. The genera *Labyrinthula*, *Thraustochytrium*, and *Schizochytrium* were common on oyster reefs, especially on algae and seagrasses. Most isolates of these genera differed from described species in varying degrees, and one of the more divergent labyrinthulas is described herein as *Labyrinthula saliens* n. sp.

MATERIALS AND METHODS

Culture on Nutrient Media

Labyrinthula saliens n. sp. was isolated on nutrient medium from a marine grass *Halophila englemannii* Aschers. Plants were collected by skin diving and promptly transported alive to the laboratory where small sections about 1 cm long were excised from various parts of the thalli. Each explant was superficially cleaned by vigorous shaking in four changes of sterile sea water and then placed on the surface of the agar medium. This nutrient culture medium was an adaptation of Watson & Ordal's (1956) blood serum agar and contained 10% v/v bovine serum (Difco stock 0260-61), 0.9% w/v purified granular agar (Difco stock 0140-01), 500 U.S.P. units/ml potassium penicillin G (Squibb list 6735), and 500

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μg/ml streptomycin sulfate (Squibb list 8377) and was made up in filter sterilized (0.22 μm) natural sea water diluted to 30‰ salinity with distilled water. For preparation, the agar/sea water solution was boiled, autoclaved, and equilibrated to a 50 C water bath. Antibiotics and serum were then added with swirling and petri plates (100 × 15 mm) poured immediately. Thin platings (9 ml) of this low viscosity medium were used to facilitate observation through the culture dish bottom using an inverted microscope (WILD M40 with long working distance bright field/phase contrast condenser).

Various organisms began to move off the grass inocula onto the agar surface after about two days at 25 C. Selected organisms were removed to fresh medium by hand-held micropipettes or with a mechanical micromanipulator (Leitz Wetzlar Co.) as required. All cultures were later cloned using the micromanipulator to insure fidelity. It was necessary to subculture labyrinthulas and thraustochytrids onto fresh media every two weeks to maintain viability. Cells were picked up and transferred in hand-held, thinly drawn Pasteur pipettes with mouth tubes attached, or small agar blocks containing the desired cells were used as inocula. All aseptic operations were executed in the flow of sterile air from a laminar flow hood (Agnew-Higgins model 48X with alterations) to prevent contamination. Cultures were grown in glass petri dishes incubated in a periodically disinfected (automatically timed germicidal UV lights) humidity chamber (85–95% RH) at 25–27 C.

Observations of Cultures

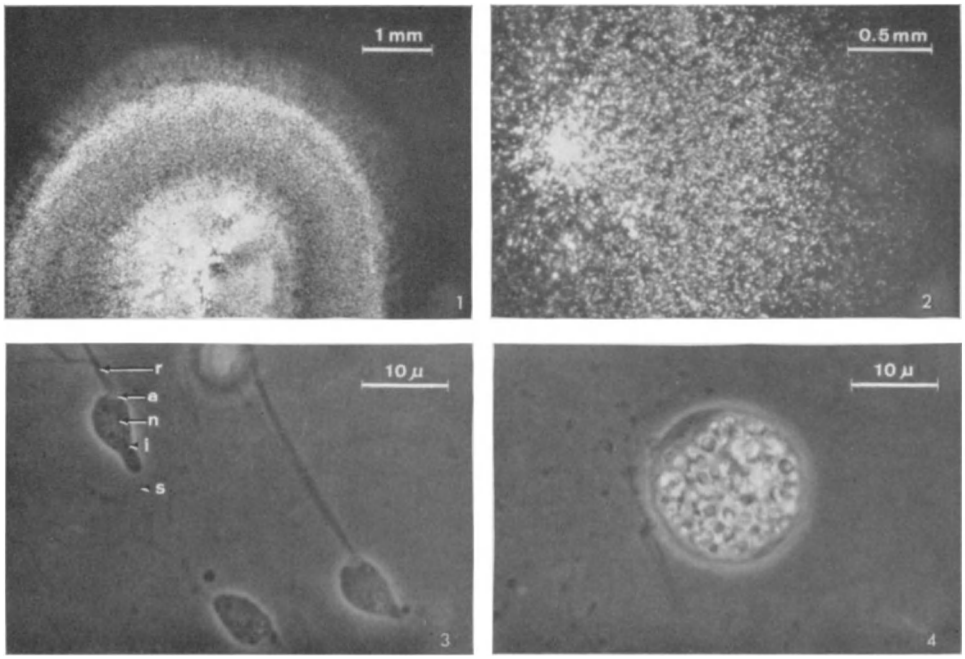
Colonies were transferred intact to microscope slides for detailed observation and photomicrography. To accomplish this, blocks of agar about 25 × 40 mm or smaller, containing selected colonies or portions of cultures, were aseptically removed to sterile slides, using two narrow-bladed spatulas. One spatula was used to lift and transfer the agar block while the other was used to guide the agar. Several drops of 30‰ sea water were then added to the agar block and a sterile coverglass floated into place to complete the preparation. Such slide cultures could be maintained alive for over two weeks by storing in plastic culture dishes containing small blocks of cellulose or polyurethane sponge soaked with water.

Permanent preparations could be made from slide cultures at any desired stage using a method similar to Watson's (1957). The complete preparation was submerged in Zenker's fixative with acetic acid (Guyer & Bean, 1953) for 18–24 hr and then removed and immersed in tap water. The coverglass with agar block adhering was quickly flipped perpendicularly away from the slide with the tip of a stiff needle. The agar block would then readily fall away from the submerged coverglass. The fixed, intact colony of *Labyrinthula* (or a thraustochytrid) would remain on the slide and/or coverglass and could be washed, treated in iodine to remove fixative artifacts, dehydrated, and stained as desired. Harris' hematoxylin with eosin (Guyer & Bean, 1953) was most commonly used, but other stains such as Heidenhain's iron-hematoxylin, Weigert's hematoxylin, and Giemsa stain also worked well.

Results

Diagnosis

Labyrinthula saliens n. sp. Sporangia are epiendobiotic, carpozoic, spherical to rounded, 12–30 μm in diameter, consisting of one to numerous, adherent, closely appressed compartments often lending a nodulose or rough surface form. Sporangia often form large palmelloid pseudosori 20–200 μm in diameter and



FIGS. 1–4. *Labyrinthula saliens* n. sp. Fig. 1. General view of a colony. The typical annular appearance results from periodic inclusion of nonmotile reproductive stages during colony growth. This colony is composed primarily of spindle cells, but a group of pseudosori is present near the center (lower middle). Living, dark field. Fig. 2. View of a large sporangial colony and the concentric spindle cell colony growing outward from it. Pseudosori and single sporangia appear on the surface in the central area (left middle) as larger white flecks. Living, dark field. Fig. 3. Moving spindle cells with both rhizoids (r) and slimeways (s). Typical spherical hyaline nuclei (n), lipoid inclusion bodies (i), teardrop shape, and shallow apical attachment pits (a) are shown. Living, phase contrast. Fig. 4. Enlarging, nonchambered aplanospore with numerous typical large lipid-like globules. Enlargement generally continues, forming prosporangia and eventually sporangia. Living, phase contrast.

produce prominent, tapered, straight or curved, subdicotomously branched, often entangled rhizoids 50–150 μm long without vesicular apophyses. Spindle cells burst forth singly through minute wall fissures in individual sporangial compartments and move outward, initially along the sporangial rhizoids. Spindle cells are generally fusiform or clavate but change shape continuously and substantially. The 4–9 μm spindle cells project a fibrous field of thin, smooth rhizoids ahead from a shallow anterior pit and leave an irregularly thickened slime trail along their path. The peculiar movement consists of intermittent, short (1–6 μm) but rapid advances, usually about 1/min. Spindle cells usually enlarge slightly and become small, rounded, single chambered, holozoic sporangia which in turn release 4–20 or more spindle cells. Fission may occur, resulting in elaboration into the chambered sporangial form. True plasmodia or planonts were not observed. This marine organism grows on *Halophila englemannii* Aschers.

Sporangia epiendobiotica, carpozoica, sphaerica ad rotundata, 12–30 μm diam., ex uno ad numerosa compartmenta adhaerentia arcte appressa quae tenturam superficiem nodulosam asperosamque saepe praebent constantia. Sporangia pseudosoros magnos, 20–200 μm diam., palmelloideosque saepe formant, necnon rhizoidea (50–150 μm) manifesta attenuata recta curvatave, subdichotome ramosa saepe implicataque, sine apophysibus vesicularibus efficiunt. Fusi-cellulae e fissuris membranae minutis in compartmentis sporangialibus singulis singulatim

erumpunt, et primum secundum rhizoidea sporangialia extrorsus movent. Fusi-cellulae plerumque fusiformes clavataeve, continue lateque, autem, formam mutant. Fusi-cellulae 4–9 μm aream fibrosam rhizoideorum tenuium leviumque prae efficiunt, necnon vestigium muci irregulariter incrassatumque secundum viam reliquunt. Motus ipse e progresibus intermissis brevibus (1–6 μm) celeribus, autem, ratione solita uno in omni parte sexagesima horae, constans. Fusi-cellulae plerumque paululum accrescunt, et sporangia parva holozoica, unum loculum habentia fiunt, haec sporangia vicissim quattuor ad viginti fusi-cellulas liberant. Fissio binaria necnon efficitur, et sporangia in formam sporangialem loculos habentem (supra) saepe evolvunt. Plasmodia vera aut unicellulae flagellatae non observata. Hic organismum marinus *Halophilam englemanii* Aschers colet.

Type-Specimen Data

Holotype: Slide number P10-ML-3H89 (1-16-69) Marine Research Laboratory Herbarium, Florida Department of Natural Resources, 100 Eighth Avenue SE, St. Petersburg, Florida 33701.

Type Substrate: *Halophila englemannii* Aschers.

Type Locality: 30° 04′ 34″ N, 84° 10′ 57″ W (Station 14, Quick & Mackin, 1971), SW of St. Marks Lighthouse, Wakulla Co., Florida.

Isolation from Seagrass

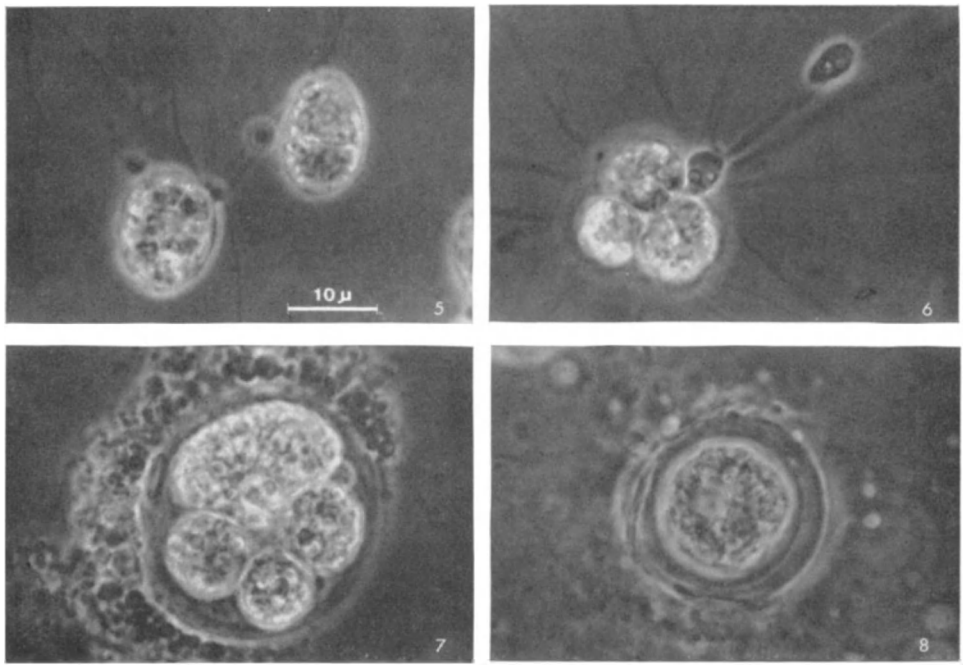
Labyrinthula saliens was isolated in culture from explants of *Halophila englemannii* taken in two samplings near St. Marks Lighthouse in Apalachee Bay, Florida in June 1968 and September 1969 at depths of about one meter (MLW). A total of 12 plants were collected and cultured, but only one from each sampling harbored the fungus. *L. saliens* was common, however, on all exposed parts of these two infected thalli except the youngest leaves. The *Labyrinthula* did not appear to displace any of the other phycomycetous fungi normally isolated from this host.

Halophila englemannii is probably the true host, although positive identifications of *L. saliens* were made only on cultures and not directly on fresh host material. It is unlikely that epiphytes of *Halophila* serve as hosts since most were removed by the decontamination washing and several colonies of the fungus were obtained from epiphyte free areas. In addition, *Labyrinthula saliens* would probably have been easily observed had it been present in or on epiphytes. No host tissue reactions or other symptomatic evidence of parasitism or pathogenicity due to this fungus were discerned, and the absence of *Labyrinthula* on healthy young tissue indicated spread of the phycomycete to be slow and unaggressive.

L. saliens may be host specific, since no isolations were obtained from numerous other substrates (e.g., algae, angiosperms, and detritus) collected concomitantly with *Halophila*. Furthermore, this fungus was not identified from numerous cultures of marine algae, seagrasses, molluscs, and crustaceans collected throughout Florida. Most other labyrinthulas studied invade a wide variety of hosts (usually representing several taxonomic classes) and, when present, infect almost every available host organism. No evidence of phagocytic nutrition was observed even in the presence of diverse bacteria and other contaminants, thus suggesting a direct subsistence on the plant host. A requirement for sea water was demonstrated in culture.

Appearance of Cultures

Labyrinthula saliens normally undergoes an alteration of cultural forms between spindle-cell colonies and sporangial colonies. Macroscopically, spindle-cell colonies appear as hazy, spheroid, milky embedments in the agar which become discoid with growth due to the limited culture medium depth. Colonies are denser toward the center and often show concentric layers 0.5–1.5 mm thick toward the periphery (Fig. 1). The colonies grow slowly, generally less than 1



FIGS. 5–8. *Labyrinthula saliens* n. sp. Fig. 5. Aplanospores enlarging into sporangia. The cell on the right enlarged from a stalled spindle cell and completed the first division within the intact mother cell wall. Fig. 6. The moment of sporulation. Spindle cell adjacent to the sporangia burst forth from the uppermost sporangium less than 2 sec before it was photographed. The other spindle was released about 10 min earlier from the same fissure and is moving away on a sporangial rhizoid. These three sporangia resulted from division and separation of a single cell and are thus a minute, mature pseudosorus. Fig. 7. A heavily walled, compartmented, young sporangium. Fig. 8. A thick-walled cyst with a single large nucleus and lipoid globules. (All organisms shown living, phase contrast, same magnification.)

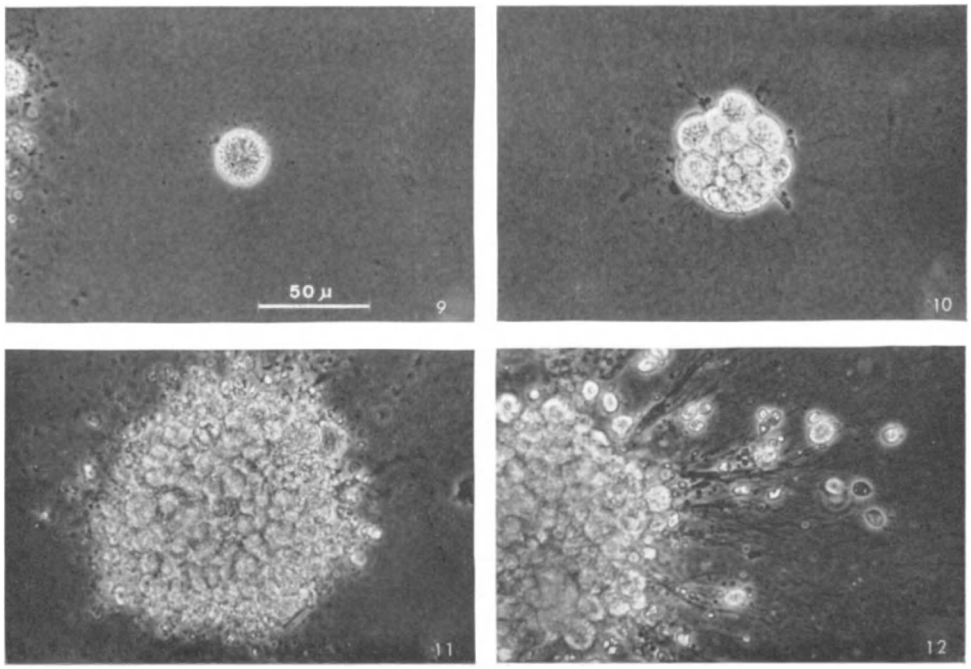
mm per day, until cessation of growth after 7–10 days. Maximum colony diameter is commonly near 1 cm. Cells apparently die after 14–16 days at 25–27 C, since subsequent subcultures are generally inviable.

Subcultures from living spindle-cell colonies generally form sporangial colonies appearing as groups (0.3–0.8 cm diameter) of minute white flecks (pseudosori) of varying sizes on the upper and lower surfaces of the agar. After about five days, a spindle-cell colony forms within the agar from the persisting sporangial colony (Fig. 2). Inocula from any part of the culture usually result in re-formation of a spindle-cell colony.

Morphology and Life History

The shape of *Labyrinthula saliens* spindle cells (Figs. 3, 15, 16) varies greatly from spheroid to lanceolate but is typically pandurate to clavate with a distinctly constricted, sometimes pointed, posterior and a rounded, inflated anterior. A shallow, but distinct, anteroventral depression is characteristic. Each hyaline, 4–10 μm long cell has a relatively large, 1.5–2 μm, diameter, clear, spherical nucleus surrounded by a clear, homogeneous cytoplasm included by a small number of opaque granules and lipid-like refractive globules.

Each motile spindle cell extends a rhizoid (similar to a slimeway but projected outward from a cell) forward from the anterior pit. These rhizoids usually have

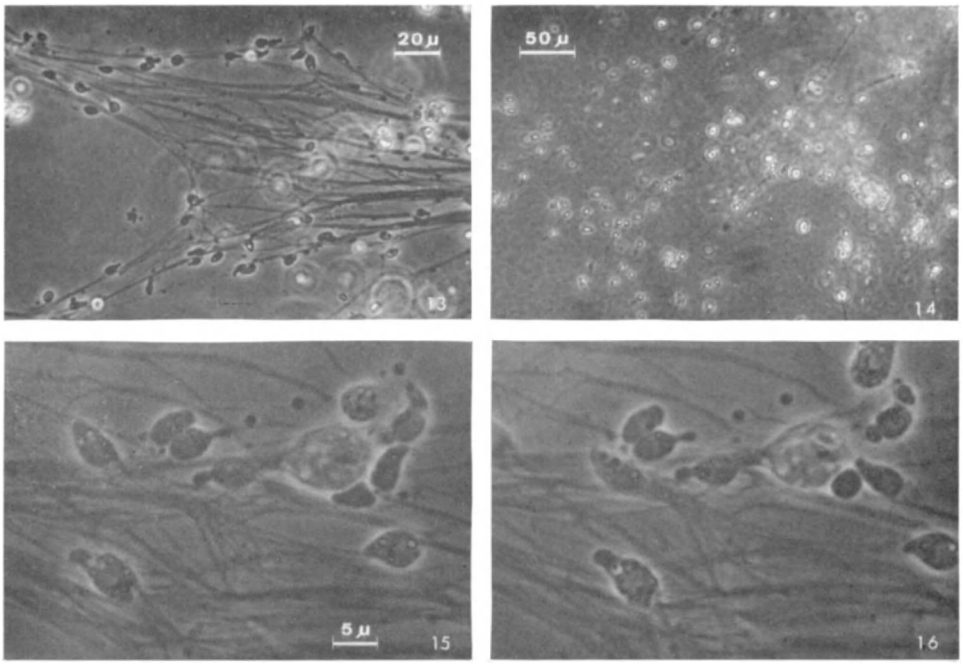


FIGS. 9–12. Sporangia and spindle cells of *Labyrinthula saliens* n. sp. Fig. 9. Large unicellular prosporangium near the maximum size reached before division and/or internal partitioning begins and produces a pseudosorus or sporangium. Fig. 10. Various division-products of such a prosporangium. Individual chambers are enlarging, forming more chambers, and beginning to separate in this early stage of pseudosorus formation. Portions of the original sporangial wall are still intact. Fig. 11. Large immature pseudosorus prior to initiation of rhizoids and sporulation. Fig. 12. Early sporulation of a large, mature pseudosorus with prominent rhizoids. Some of the young spindle cells can be seen beginning to divide again. (All organisms shown living, phase contrast, same magnification.)

a smooth, often gently curved, thickened trunk (Fig. 3) extending 5–25 μm and diverging into several thinner, generally more rugose branches which may extend an additional 60 μm before tapering to invisibility. Branches commonly form a narrow angle to the trunk but may be quite irregular. Rhizoids seem to anastomose on contact but extensive "net plasmodia" seen in other labyrinthulas do not result, probably due to the embedded, rather than surface, spindle cell growth.

Actively motile spindle cells move about once each minute by a short (1–6 μm) but rapid (1–5 sec) advancement (Figs. 15, 16) along the rhizoid trunk. A distinct relengthening and thickening of the rhizoid usually occurs during the quiescent interval between advances or, occasionally, a second rhizoid is produced and one is abandoned during subsequent cell progression. Time-lapse photography shows that limited lateral movement occurs in some surface rhizoids. Spindle cells always move in the direction of the rhizoid, and no sidewise or backward movement has been observed other than a waving or pivoting of the cell body about the rhizoidal attachment point, the anterior pit.

A slimeway (remnant "rhizoid" after cell passage) is left behind by a moving spindle cell (Fig. 3). Like spindle-cell rhizoids, slimeways seem to originate at the anterior pit but pass posteriorly appressed to the cell surface, becoming visible only after they diverge onto the agar. Slimeways seem to be rhizoids



FIGS. 13–16. Spindle cells of *Labyrinthula saliens* n. sp. Fig. 13. Spindle cells moving outward (toward left) along rhizoids of the mother sporangium. Movement of spindle cells over sporangial rhizoids changes the arboreal appearance shown in Figure 12 to the more stretched, anastomosing configuration seen here. Fig. 14. Marginal area of a colony. Spindle cells, remote from preformed sporangial rhizoids, tend to be more fusiform and project rhizoids from the anterior ends as slimeways appear to stream from the posterior tips. These spindles and division stages show the typical, even, vertical distribution through the agar. Figs. 15, 16. Photomicrographs of the same field taken one min apart. Most spindle cells show movement toward the right along rhizoids of the mother sporangium (out of view to left). Changes in position and thickness of various rhizoids can also be detected. The large spindle cell at upper right is shown in quaternary division that terminated in release of daughter cells four min later. (All organisms shown living, phase contrast.)

altered by passage of motile spindle cells and appear as very thin, often discontinuous, sometimes branched, smooth or beaded strands. Slimeways are persistent and remain intact even if the spindle cells are removed, while the more permutable rhizoids take on a withered, moniliform, lifeless appearance somewhat reminiscent of a slimeway. Neither do slimeways show any movement or growth, and they slowly disappear in older colonies. The slimeways thus seem to be simply passive trails remaining after transit of spindle cells. Surface spindles seem to be attached by the apical pit to the rhizoid-slimeway juncture and commonly wave and pivot freely about this point. The slimeways of spindle cells embedded in the agar may be tube-like, however, because the rhizoid, cell, and slimeway are usually lined up (Fig. 14) as in the labyrinthulas with fusiform spindles.

Spindle cells exhibit decreasing movement after about 20 hr and slowly become rounded, thick-walled aplanospores (Fig. 4). The protoplast begins binary fission into two to over eight daughter cells which then escape singly by bursting through a single small fissure in the wall and move rapidly away (Fig. 6) as initially spheroid and then characteristically ovoid spindle cells. Each aplanospore ceases to produce new spindle cells after a variable time period, but it

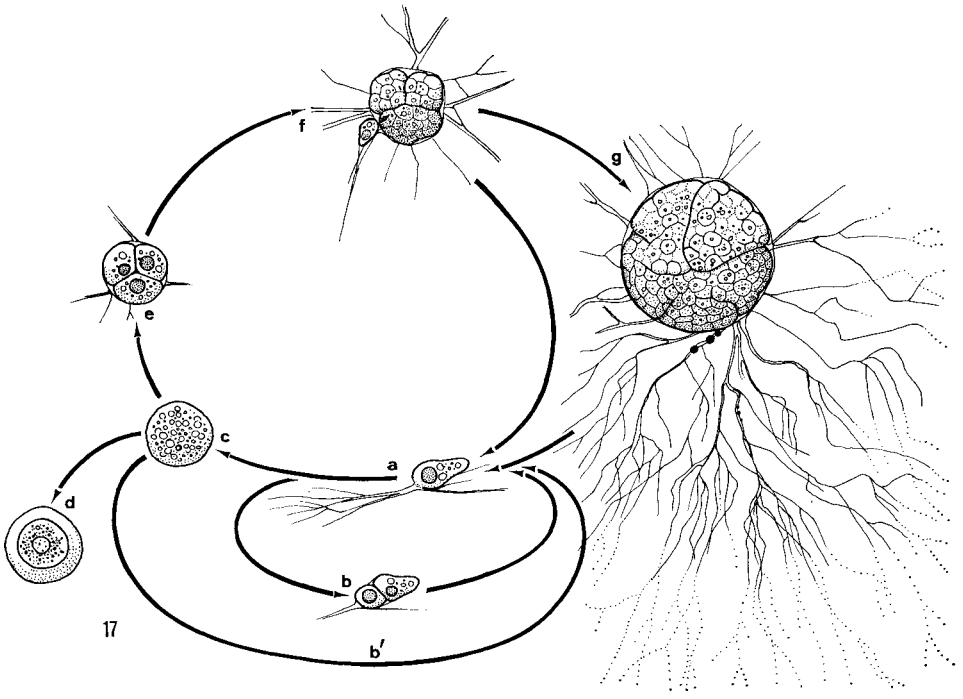


FIG. 17. Life cycle of *Labyrinthula saliens* n. sp. in culture. Motile spindle cell (a) may become temporarily stationary and reproduce holozoically (b) or become an aplanospore and begin enlargement (c) into a cyst (d) or prosporangium (e). Aplanospores also may represent the extreme of holozoic spindle cell reproduction (b'). Prosporangia enlarge and partition to produce carpozoic sporangia (f) which may continue enlargement, subdivision (g), and separation into pseudosori. (Drawn from life, approx. × 1,000.)

usually persists thereafter and still appears filled with protoplasm. The degree of rounding out and cell wall thickening varies greatly in individual aplanospores, but both tendencies generally become more pronounced with increasing culture age. In older cultures, formation of very thick walls plus variable enlargement may result in aplanospores that are morphologically indistinguishable from simple sporangia (Fig. 7). In young cultures, on the other hand, little if any change may occur in spindle cells prior to division, such that a simple binary fission of slightly rounded spindles results; and both daughter cells resume a motile existence (Fig. 5), the cell wall either remaining with the progeny or deliquescing.

Sporangial development begins with the rounding out and enlargement of aplanospores. When these prosporangia reach about 20 μm in diameter (Fig. 9), they begin unequal asynchronous divisions that result in a compartmented structure similar to sporangia of the thraustochytrid *Schizochytrium* Goldstein & Belsky, 1964. Groups of these compartments may cleave slowly from the growing parent structure and then proceed to develop independently until a large discoid mass or pseudosorus of young sporangia is formed (Figs. 10, 11). Individual sporangia in a pseudosorus may mature as early as 48 hr after initiation as indicated by the production of prominent rhizoids and well-developed internal partitioning into 10 to over 50 cells. Most sporangia reach maturity in about three days and pseudosori become surrounded by radial fields of rhizoids. Individual mature rhizoids usually have a single, somewhat irregularly thickened trunk or

stalk 10–30 μm long with irregular antrorse branching, especially away from the base, into numerous thin, straight to crumpled filaments. These may branch sparsely as they taper to invisibility 50–150 μm from the sporangium (Fig. 12).

Spindle cells burst singly through minute fissures in the sporangial walls during sporulation and move away along the sporangial rhizoids. Individual sporangia may have one to several expulsion sites located on various sporangial compartments at any time. The movement of spindle cells over the sporangial rhizoids (Figs. 15, 16) causes the texture to acquire a stretched and fused aspect (Fig. 13). Spindle cells continue to move uninterruptedly on their own rhizoids after passing the limit of the sporangial rhizoids, but the cells generally change direction to move radially toward the colony edge.

Cyst-like bodies are often formed, especially in the central area of older colonies when spindle cells round up as if for division but produce a thick, transparent cell wall (Fig. 8) with or without undergoing internal division. Such cysts do not seem to be resistant to adverse culture conditions, or to have increased longevity, and frequently die before spindle cells or sporangia in the same colony. No cyst germination was ever observed.

Discussion

Labyrinthula saliens differs from all other described labyrinthulas (summarized by Pokorny, 1967) by: (1) the shape of its spindle cell, (2) its locomotory style, and (3) the inclusion of sporangia as a usual reproductive stage. Unlike other forms, active spindle cells have a readily identifiable anterior end because of the anterior pit and longitudinally asymmetric cell shape. Also uniquely, rhizoids, and probably slimeways, originate from this pit rather than from general areas of the spindle cell surface. The predominantly rounded shape of *L. saliens* spindle cells immediately distinguishes it from all other species except *L. minuta* Watson & Raper, 1957. *L. saliens* also resembles *L. minuta* in the diminutive width of its slimeways.

The locomotion of *L. saliens* by alternating short, rapid advances with pauses is quite distinct from the slow, continuous gliding motion of the other described labyrinthulas and prompted the specific epithet meaning "leaping" (L.). Spindle cells of *L. saliens* always move forward, anterior end foremost, a distinction from *L. minuta* which reverses direction periodically (Watson & Raper, 1957). Spindle cells of *L. saliens* in culture move more readily through the agar than on the surface, a preference the reverse of other cultured species. Enlargement of the colony results from spindle cells moving outward individually without the distinct massing of cells around the periphery as in other species, several of which were cultured concurrently with *L. saliens* for direct comparison (*L. minuta*, *L. chattoni*, *L.* sp. RM, and *L.* sp. LC-RM).

The regular inclusion of a distinct, almost chytroid, sporangial stage seems to be unique in *L. saliens*' life history. *L. minuta* (Watson, 1957) and several other labyrinthulas regularly form multinucleate giant cells which often fragment, but reproduction does not seem to be their normal function. *L. minuta* also forms multinucleate plasmodia (Watson & Raper, 1957) which, by direct comparison, appear identical to very thin-walled prosporangia (Fig. 10), often seen in young pseudosori of *L. saliens*. In no case, however, do the sporangia-like stages of other labyrinthulas produce complete, prominent rhizoids or exhibit a complete sporangial reproductive cycle as does *L. saliens*.

L. saliens was placed in this genus principally because spindle cells moving on slimeways constitute its major life cycle stage. In addition, the spindle cells produce rhizoids as Watson (1957) reported for all the species he studied (he called them "initial net plasmodia"). These rhizoids disappear when they are

bypassed by the spindle cell, but the slimeway remaining afterward is persistent as in other described species. Spindle cell cytology is also similar, the cell wall being thin and flexible—allowing much plasticity of shape—and the cytoplasm being relatively clear and without excessive numbers of inclusions. Cell division occurs within the persisting parental cell wall in a manner similar to Vishniac's strains of *Labyrinthula* sp. (Watson, 1957), giant cells of *L. algeriensis* (Hollande & Enjumet, 1955), ellipsoidal sori of *L. roscoffensis* (Chadefaud, 1956), and cysts of *L. macrocystis* (Cienkowski, 1867). *L. saliens* forms plasmodia or young sporangia very similar to stages described for *L. minuta* (Watson, 1957). Furthermore, my strains RS^{D} and RS^{Z} of *L. minuta* produce complete functional sporangia almost identical to *L. saliens*; they even have diminutive chytroid rhizoids. Also, like most other labyrinthulas and numerous chytrids and thraustochytrids, *L. saliens* was found on a marine plant, was cultured on blood serum agar, and required marine salts.

The resemblance of the sporangia of *L. saliens* to those of the supposedly unrelated thraustochytrids is particularly noteworthy. Direct comparisons between *L. saliens* and several isolates of *Thraustochytrium* and *Schizochytrium* (*T. proliferum*, *T. pachydermum*, *T. globosum*, *T.* spp., *S. aggregatum*, *S.* sp.) under identical cultural conditions showed rhizoidal structure and behavior to be almost identical; and sporangia and pseudosori to have great similarity, especially in gross structure, protoplasmic inclusions and organelles, division and proliferation methods, and propagule release. The absence of planonts among the observed stages of *L. saliens* discourages the attachment of concrete taxonomic significance to these similarities, but posteriorly or laterally biflagellate planonts have been observed in at least two *Labyrinthula* (Amon & Perkins, 1968; Watson, 1957).

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