

Notes on the Morphology and Taxonomy of *Micromyces* (Synchytriaceae, Chytridiomycota), with special attention to *M. longispinosus*, *M. grandis*, *M. furcatus* and *M. ovalis*

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ABSTRACT

Traditionally, family Synchytriaceae has been placed in order Chytridiales, phylum Chytridiomycota. Within the family, though, the taxonomic situation has been less clear. This family has been considered to contain only a single genus (*Synchytrium*), or as many as four genera: *Synchytrium*, *Micromyces*, *Micromycopsis* and *Endodesmidium* (cf. Sparrow, 1943, 1960; Karling, 1977)--either approach perhaps tenable. However, since the ‘separate genera’ appear distinct, and until contravened by molecular evidence, we recognize them here. Karling (1964), while adopting the single-genus approach (recognizing only *Synchytrium*, with a number of subgenera), nonetheless provided a helpful compilation of information. However, taxonomic attention is still needed in the family. We review taxa of the aquatic genus *Micromyces* (endoparasites of conjugate algae, i.e., Zygnemataceae). Sparrow’s (1960) key to species of *Micromyces* has stood well until the present. But, since Sparrow (1960) did not recognize *Micromycopsis* (including its species in *Micromyces*), and since we herein recognize *Micromycopsis*, adjustments to the *Micromyces* key were necessary. Also, certain potential species of *Micromyces* that were not included in Sparrow’s taxonomic key (i.e., *M. grandis* Miller, 1955 and *M. “furcata”* Rieth, 1962) required evaluation. We determine *M. grandis* to be a large variant of *M. longispinosus* Couch (1937). *Micromyces “furcata”* Rieth (1962), subsequently accounted for mainly in listings of Chytridiomycete names, is morphologically distinct, and is added to species in our key. The epithet “furcata” (Rieth, 1962) should be “furcatus,” viz. *M. furcatus* (*Index Fungorum*). *Micromyces ovalis* (Rieth, 1950) is nomenclaturally invalid (lacking the Latin diagnosis required at the time); an English diagnosis (see present rules of nomenclature) is here provided. In addition to various points of nomenclatural clarification, we hope that our observations of living material of *M. longispinosus* will add to morphological understanding of this species. Future molecular studies should inform as to relationships among *Micromyces* species, and how many genera of Synchytriaceae should be recognized. Published on-line www.phytologia.org *Phytologia* 100(1): 51-61 (Mar 16, 2018). ISSN 030319430.

KEY WORDS: host-parasite relationships, intracellular, *Mougeotia*, prosorus, resting spore, sorus, *Spirogyra*, sporangia, zoospores.

Synchytriaceous organisms are intracellular parasites of types of flowering plants, ferns, mosses, and green algae (Sparrow, 1960; Karling, 1977); one saprobic species has been reported (Longcore et al., 2016). Life cycles of taxa of Synchytriaceae are variably documented--usually by descriptive statements and line drawings--less often by photographs (helpful exceptions include Miller, 1955; Rieth, 1962; Longcore et al., 2016; and photographic illustrations, herein, of our collections of *Micromyces longispinosus*). Compared with most Chytridiomycetes, members of family Synchytriaceae have a complex life cycle (Karling, 1977), often involving formation of--not just of sporangia, but--a preceding prosorus, and a sorus (which, for a time at least, contains the sporangia). In many Synchytriaceae, a resting spore (or resting sporangium) may also form; the resting spore may function either as a prosorus or a sorus (or these latter structures can develop within, or from, the resting spore). Resting spores are, in fact, common in the family and often resemble prosori or sori; in many cases, for example, resting spores can be difficult to distinguish from prosori. In spite of unavoidable questions of structure identity, and of opposing taxonomic viewpoints, we herein recognize the four, historically recognized genera of the family: *Synchytrium*, *Micromyces*, *Micromycopsis* and *Endodesmidium*--the latter three of these genera having been, at times, submerged variously in one or more generic/subgeneric groupings, synonymies; cf.

Karling (1964, 1977), Sparrow (1960) and Dick (2001). Our dichotomous key serves to present these putative genera, emphasizing distinctions that are presently considered to be most dependable.

KEY TO THE GENERA OF SYNCHYTRIACEAE RECOGNIZED HERE

1. Occurring in conjugate algae (Zygnemataceae or Desmidiaceae); prosorus endobiotic, with a distinct discharge tube; sorus typically epibiotic (at apex of discharge tube), with a definite, somewhat thickened wall which may be smooth or spiny; zoospores typically released extra-matrically....*Micromycopsis*
1. Occurring in conjugate algae, embryophytes, or rarely free-living; prosorus (if any) and sorus developmentally endobiotic; sorus sessile on or formed within the prosorus (if present); sorus with or without a distinct surrounding membrane or wall (if present, typically not thickened); zoospores released intra- or extra-matrically.
 2. Parasitic in a number of flowering plants and certain mosses and ferns (there is also one reported saprobic species); young thallus not amoeboid; prosorus present or often lacking; sorus simple, frequently formed directly from (within) the thallus, relatively large (usually more than 35 μm in diameter); common soral wall or membrane present for a time at maturity.....*Synchytrium*
 2. Parasitic in green algae (Conjugatae); young thallus often amoeboid; prosorus present; sorus simple or compound, relative small (usually less than 35 μm in diameter), developed externally from the prosorus and remaining sessile upon it (the two structures thus continuing for a while to be 'joined'); sorus with or without a common surrounding membrane or wall at maturity.
 3. Found in members of the Zygnemataceae (e.g., *Spirogyra*, *Zygnema*, *Mougeotia*); prosorus wall frequently composed of distinct segments, often ornamented ('spiny'); sorus simple or compound, lacking a common wall or membrane at maturity (the thin wall sometimes segmenting); sporangia not amoeboid or flagellated; zoospores usually well more than 5 per sporangium...*Micromyces*
 3. Found in members of the Desmidiaceae (e.g., *Netrium*, *Cylindrocystis*); prosorus wall uniform, smooth; sorus simple, wall or membrane persisting, developing two, opposite papillae; sporangia amoeboid or allegedly even flagellated; zoospores 5 or fewer per sporangium....*Endodesmidium*

SELECTED ASPECTS OF GENERIC HISTORY OF FAMILY SYNCHYTRIACEAE

There is no need here to comprehensively review the history of this large family of Chytridiomycetes; yet, some aspects of this history are pertinent to discussion. Sparrow (1943) recognized three genera of Synchytriaceae: *Synchytrium*, *Micromyces*, and *Micromycopsis*. Sparrow (1960) still recognized three genera, but only two were the same as in 1943: Sparrow (1960) recognized *Synchytrium* and *Micromyces*, but considered *Micromycopsis* to be encompassed within a broadly defined *Micromyces* (a viewpoint adopted by Dick, 2001); Sparrow (1960), though, additionally recognized *Endodesmidium* (Canter, 1949)--according to Canter, a relatively simple, putatively primitive genus (but see Karling, 1954, 1977, for another viewpoint on primitive vs. advanced genera/species within the Synchytriaceae). Couch (1931), while emphasizing resemblance in morphology and life cycle between *Micromyces* and *Synchytrium*, nonetheless retained these genera. Karling (1953, p. 278), however, merged *Micromyces* and *Synchytrium*, based on "fundamental structural and developmental similarities," transferring species of *Micromyces* to *Synchytrium*. Karling (1964) subsequently enumerated six or seven (cf. p. 118 vs. pp. 114-115) subgenera within *Synchytrium* (some subgenera traceable to earlier authors, e.g., Fitzpatrick, 1930); subgenus *Microsynchytrium* housed, among other species, species previously classified in *Micromyces*. In Karling (1964), all genera and species of Synchytriaceae were subsumed under *Synchytrium*. Enigmatically, Karling (1977)--retaining the subgenera of *Synchytrium*, as *de facto* an

additional presentation within his overall coverage--resurfaced recognition (perhaps for pragmatic reasons) of the four, classic genera of Synchytriaceae (*Synchytrium*, *Micromyces*, *Micromycopsis* and *Endodesmidium*). The question of genera vs. subgenera, within the Synchytriaceae, has remained unsettled. But, because it has *not* been shown through molecular analysis that aquatic genera such as *Micromyces* and *Endodesmidium* should be merged with the terrestrial *Synchytrium*, there is still no definitive argument against recognizing the four 'traditional' genera of Synchytriaceae--including *Micromycopsis*--which seem morphologically and adaptively distinct (see generic key, above). It bears mention that several other alleged genera of Synchytriaceae have been named; however, these are generally considered synonyms of *Synchytrium* (see Karling 1977, p. 50). *Johnkarlingia* Singh & Pavgi--a parasite of roots of cauliflower and cabbage--is listed as a genus of Synchytriaceae in *Index Fungorum* (IF), but Karling (1977) included this ('intermediate') genus under coverage of Olpidiaceae.

MORPHOLOGY AND LIFE CYCLE OF *MICROMYCES LONGISPINOSUS* (Figs. 1-6, 11-22)

Micromyces longispinosus, described by Couch (1937)--based on earlier observations of what Couch (1931) initially thought was a collection of *M. zygonii*--occurs in vegetative cells of *Spirogyra* and *Mougeotia* (see Sparrow, 1960), often in the vicinity of the nucleus. The young thallus develops into a generally spherical, hyaline to yellowish or brownish, uninucleate prosorus (10-33.6 μm in diameter, not counting the spines) which typically exhibits 12-24, straight or curved, transparent, slender, gradually tapered spines which can be at least 22 μm in length (averaging ca. 12 μm , and usually exceeding 9 μm). The often irregularly reticulate prosoral wall or membrane can eventually become partitioned into several or a number of segments (each bearing one or more spines), as can the thinner-walled sorus. The sorus develops from the prosorus, is spherical, smooth-walled or somewhat spiny, and sessile upon the prosorus; nuclear divisions typically take place in the sorus (pursuant to migration of the prosoral nucleus into the sorus). The soral membrane disappears at maturity (or its segments become incorporated in sporangial walls/membranes)--revealing 8 to 24 (possibly more), thin-walled sporangia, which are not flagellated or amoeboid. The rounded to somewhat elongate (sub-conical), sometimes angular sporangia--typically 8 and 10 μm in size--can each release (through a pore in the narrowed apex) numerous, minute (ca 1 μm each), posteriorly uniflagellate zoospores--often inside the algal host-cell which, in response to parasitism, may or may not exhibit hypertrophy (when present, similar to that caused by *M. zygonii*; see Sparrow, 1960, pp. 195, 197). The sub-spheroid to ovoid zoospores typically manifest the lipoid globule (or two globules, oppositely placed) characteristic of chytrid zoospores; zoospores *may* fuse, in pairs, apparently functioning as gametes (further confirmation desirable, cf. Karling, 1977, p. 50). Resting spores brownish, resembling prosori but averaging smaller (16-21 μm) and developing a more thickened wall, functioning as prosori (Fig. 21) or directly as sori (Fig. 19). Photographs from collections WB293 (Northport Trestle, temporary ponds) and WB294 (Marrs Spring), environs of Tuscaloosa, AL.

MICROMYCES GRANDIS (Figs. 7A,B), COMPARED WITH *M. LONGISPINOSUS*

Miller (1955) described *M. grandis* as a new species of *Micromyces*. *Micromyces grandis* was noted by Sparrow (1960) but--perhaps due to a publication date close in time to the preparation of his monumental manuscript--not included in his *Micromyces* species key. *Micromyces grandis*, occurring in a large *Spirogyra* (not named to species), is very similar to *M. longispinosus*, except for (Miller, 1955, p. 254) its "large size in all phases of its life cycle," and [causing the] "unique hypertrophy of the host cell resulting in peculiar geniculations [enlarged bends]." Miller precisely described and illustrated this 'new species,' including its thallus (which becomes the prosorus) and an association between the developing prosorus and the nucleus of the *Spirogyra* host--a phenomenon also observed in *M. longispinosus* (see our Figs. 1-4, and 14)--invoking interesting questions as to the details of host-parasite relationships. In any event, the problem, taxonomically, is the striking similarity of *M. grandis* to *M. longispinosus*, in almost all characters, including potential causation of hypertrophy of the host cell (see our Fig. 12 of *M. longispinosus*). Palpable differences lie in size comparisons, *M. grandis* averaging larger than *M.*

longispinosus. But even as regards size, there is some character overlap. The prosorus of *M. grandis* ranges, according to Miller, from 30.4 to 51.2 μm ; however, the prosorus of *M. longispinosus* may exceed 31 μm . Lengths of prosoral spines of *M. grandis* are, as indicated by Miller, longer than (some perhaps twice the length of) those of *M. longispinosus*; but, in this case, one is merely comparing long spines with, morphologically very similar, longer spines. Resting spores overlap in diameter, and zoospores of *M. grandis* average only about 1 μm larger than *M. longispinosus*. Zoosporangial measurements are larger in *M. grandis*, yet verge on intergradation with *M. longispinosus*. Though *M. grandis* is on the whole larger, it is otherwise essentially identical to *M. longispinosus*, and does not seem to warrant species distinction; *M. grandis* should probably be considered a large example of *M. longispinosus*. Size differences of *M. grandis* (compared to *M. longispinosus*) may have as much to do with its occurrence in a large *Spirogyra* host as with its own ‘unique’ characteristics. We note in passing that Karling (1964, p. 124) transferred *M. grandis* to *Synchytrium* as *S. grandis* (*S. “grande,”* cf. Dick 2001, p. 427), a combination pertaining only if *Micromyces* is considered part of *Synchytrium* (not presently defensible).

THE STATUS OF *MICROMYCES FURCATUS* (Figs. 8 and 9)

Compared with other species of *Micromyces*, *M. “furcata”* (Rieth, 1962) has been largely overlooked; the timing of publication (1962) in part accounts for this. This species was described after Sparrow’s (1960) revised treatise of “Aquatic Phycomycetes.” It is also not in Karling’s (1964) account of the Synchytriaceae (perhaps ‘in press’ when *M. ‘furcata’* became known). Karling’s (1977) coverage of Chytridiomycetes contains a brief reference to this taxon—in a figure legend (his fig. 31, plate 16); Karling noted in this legend: “Resting prosorus of *S. furcata* (Rieth) comb. nov., with reticulate outer wall bearing dichotomously branched spines (Rieth, 1962).” Karling (1977) was thus attempting transfer of *Micromyces “furcata”* to genus *Synchytrium*. But even if one accepts this taxon in *Synchytrium* [We believe it should be retained, presently, in *Micromyces*], Karling possibly did not provide enough nomenclatural information to validate a new combination (Article 33, *International Code*). Longcore’s (1996) enumeration of Chytridiomycete names (since 1960) included *M. “furcata”* Rieth (1962) under *Micromyces*. *Index Fungorum* (IF) lists this taxon under *Micromyces* (not *Synchytrium*), adjusting the epithet spelling (correctly) to *M. “furcatus.”* Hence, after Rieth (1962), other than Karling’s (1977) ‘transfer,’ *M. furcatus* appears in two itemizations of chytrid names (Longcore, 1996; and IF, present), without further information. It was not listed by Dick (2001, pp. 429-431) among taxa of Synchytriaceae.

Rieth (1962) set forth his original description of *Micromyces “furcata”* in a relatively obscure supplement to the publication *Die Kulturpflanze*--unintentionally contributing to this taxon being, initially, poorly known. Nonetheless, Rieth’s descriptive presentation and illustrations are clear. Even though released zoospores were not observed, there is no question of the identity of the organism as *Micromyces*, or its distinction as a species. Rieth, writing in German, provided a Latin description--validating the species name (*M. furcata*). He also provided an English description (p. 294-295), quoted below (with adjustments for current usage, e.g., μm for μ) since the reference proved hard to obtain:

“Prosorus spherical, 15.5-21 μm in diameter (23-28.5 μm including spines), outer wall regularly reticulate, bearing dichotomously branched, hyaline spines. Sorus emerging through a circular pore formed in the wall of the prosorus, at first spherical, 16.5-22 μm in diameter, internally dividing in 8-16 sporangia with rather thick uncolored external wall (correspondent with the wall of the sorus). Liberation of the zoospores not seen. Resting spores spherical (7.5-)16.5(-22) μm in diameter (without the spines), outer wall regularly reticulate, covered with hyaline, dichotomously branched spines (1-)3.5(-9) μm long.” [For photographs, see Rieth, 1962, Taf. II] “Parasitic in *Spirogyra longata*...Germany.”

As Rieth (1962) noted, *M. “furcata”* [= *furcatus*] is distinguished (from other species of *Micromyces*) by *branched* spines (Figs. 8,9), on the surface of the prosorus and resting spore. These spines are mostly (distally) dichotomously branched, but may be trichotomously or otherwise branched,

rarely simple (as per Rieth's original figs. A-F, "Abb. 4"); the spines average shorter than those of *M. longispinosus* (see our account of *longispinosus*). Rieth considered that the regularly reticulate wall, of the prosorus and resting spore (Fig. 9) of *M. furcatus*, was distinctive; however, similar if somewhat more irregular reticulation or segmentation may occur in *M. longispinosus* (cf. Couch, 1937; Sparrow, 1960). Spines of *M. furcatus* (cf. Rieth, 1962) appear more regularly arranged (somewhat more helically seriate) than the scattered spines of *M. longispinosus*--see Couch, 1937--which can themselves though sometimes be in local radial or polygonal arrangements. The relatively thin, soral wall-segments of *M. furcatus* (as perhaps in some other species of *Micromyces*) may become incorporated in, or attached to, portions of the walls of sporangia (Fig. 8). In any event, we believe (especially based on the unique, distinctly branched spines of both the prosorus and the resting spore) there is sufficient evidence to recognize *M. furcatus* Rieth (1962) as a distinct species of *Micromyces*, and we include it here in our key to species.

TAXONOMY AND NOMENCLATURE OF *MICROMYCES OVALIS* (Fig. 10)

Rieth (1950, Österr. Bot. Z., 97: 516) described a new species of *Micromyces*, *M. ovalis* (included and accepted by Sparrow, 1960). This species is distinguished (see Fig. 10) by separated or spaced circles of spines (each spine shark-toothed-shaped) around the perimeter of an ellipsoid prosorus, and formation of four (usually four only), tetrahedrally placed sporangia within the sorus--the soral wall not always completely tearing open. Rieth's (1950) description and illustrations are definitive; he provided his description in German, but not, however, in Latin--leaving this name (*M. ovalis*) invalid by nomenclature pertaining at that time. As permitted by current rules of nomenclature, the name is *here validated* by *English translation* of Rieth's original (German) description [Rieth did not give an account in English]:

DESCRIPTION (translated from Rieth, 1950, p. 516): Prosorus ellipsoid, 12 to 18 μm long, 8 μm wide; outer wall with 4 to 6 rings or circles of shark's-tooth-shaped spines (these apparent circles sometimes preceded by a more spiral arrangement of the developing spines). Sorus spherical or nearly so [perhaps eventually becoming somewhat distended], developing four (tetrahedrally disposed) sporangia within; these sporangia, as a rule, not completely separating from one another, the inner walls of the sporangia tending to remain connected at a mutual point; the sometimes lightly granulated sorus-wall may tear open around the tangent [outer surface] of each sporangium. Swimmers [zoospores] numerous, essentially spherical, 1 μm in diameter (each with a single, backwardly directed flagellum), escaping the sporangium (into the host cell) by one or two pores in the sporangial wall, their further destiny unknown. Resting cells [resting spores] probably prosorus-like [re: appearance and probable function].

TIPIFICATION: As indicated by Dick (2001), the type locality of *Micromyces ovalis*, originally described by Rieth (1950), is near Tübingen, Germany ('woods-pond' at Spitzberg; found parasitizing *Mougeotia* sp.). Dick noted that type material was "not verified;" actually, it appears not to have been designated. Hence, we here designate Rieth's Fig. ("Abb.") 3; in Österr. Bot. Z., 97: 511 (1950)--showing prosorus, sorus, and developing sporangia--as Holotypus of *M. ovalis* (see our Fig. 10 for a similar depiction). ETYMOLOGY: The epithet, *ovalis*, refers to the ovoid [ellipsoid] form of the prosorus.

OTHER COLLECTION: See discussion by Sparrow and Barr (1955) as concerns a collection of *M. ovalis* (their var. *giganteus*; cf. Literature Cited, and our Species Key below), parasitic in *Zygnema*, from Smith's Bog, Cheboygan Co., Michigan, in 1954. Sparrow and Barr (1955) incorrectly reported Rieth's (1950) original collection of 'typical' *M. ovalis* as being from Austria, rather than Germany.

CITATION OF AUTHORSHIP: Based on presentation, above, of an English translation of Rieth's (1950) initial German description (and designation here of the Type)--thus validating Rieth's species name--a more complete citation of authorship, from this point, is: *Micromyces ovalis* Rieth ex W. H. Blackw., in Blackwell, Letcher & Powell (this publication).

GENE SEQUENCE, ZOOSPORE ULTRASTRUCTURE: No *Micromyces* species has yet been sequenced or examined ultrastructurally. MYCOBANK # for *M. ovalis* = 301031 (preexisting).

UPDATED KEY TO SPECIES OF GENUS *MICROMYCES* Dangeard (1889)

(Questionable species, cf. Sparrow, 1960, or those transferred to *Micromycopsis*, not included)

1. Prosorus wall smooth.....*M. laevis* Canter, 1949
1. Prosorus wall ornamented (typically 'spiny,' in one form or another).
 2. Spines of prosorus distinctly (often dichotomously) forked.....*M. furcatus* Rieth, 1962*
 2. Spines of prosorus simple.
 3. Prosoral spines (9-)12 to 22 μ m in length (sometimes exceeding 40 μ m in the '*grandis*' form), slender, straight or generally curved, gradually tapered..*M. longispinosus* Couch, 1937**
 3. Prosoral spines typically less than 8 μ m long (rarely as much as 12 μ m), narrowly to broadly conical, straight or somewhat curved (the tip gradually or abruptly attenuating).
 4. Spines of prosorus relatively few, scattered, short-conical or sometimes more elongate; zoospores spindle-shaped, averaging 6 μ m by 2 μ m, sometimes amoeboid...*M. petersenii* Scherffel, 1926
 4. Spines of prosorus more numerous, usually covering the surface, elongate-conical; or shorter and occurring in distinct, separated circles; zoospores spheroidal, 1-2 μ m in diameter, not amoeboid.
 5. Prosorus spherical, the spines narrowly conical, numerous, generally covering the prosoral surface.....*M. zygonii* Dangeard, 1889***
 5. Prosorus ellipsoidal, the spines coarser (shaped like shark's teeth), occurring in 4 to 6, distinct, spaced rings.....*M. ovalis*, see Rieth, 1950****

*Not included in previous keys.

**Interpreted here to include *M. grandis* Miller (1955), apparently a larger variant.

****M. zygonii* is the Type of *Micromyces*. *Micromyces bulbosus* Kadłubowska (1999), considered a nomenclaturally invalid name by IF, is in any case likely assignable to *M. zygonii*. Sparrow (1960) mentioned *Micromyces mesocarpi* De Wildeman (1900) under discussion of *Micromyces zygonii*; however, in light of the "mince canal" (slender discharge tube?) to the exterior of the algal host (see Wildeman, p. 1), *M. mesocarpi* probably belongs in genus *Micromycopsis*.

****A variety, *M. ovalis* var. *giganteus*, was described by Sparrow and Barr (1955), which would nonetheless still key out at the same point (above) as 'typical' *M. ovalis*; Sparrow (1960) noted that Rieth (1956) considered the 'prosorus,' indicated (by Sparrow and Barr) for this 'new variety,' to most likely represent merely a resting spore stage [of typical *M. ovalis*].

MOLECULAR CONSIDERATIONS

Of the four genera we recognize (see generic key), the only taxa of Synchytriaceae that have apparently been sequenced (18S, i.e. SSU, rDNA)--see Smith et al., 2014; and GenBank--are species that would be placed (cf. various classification: Sparrow, 1943, 1960; Karling 1977; Dick, 2001) strictly in the

terrestrial genus *Synchytrium*--including the recently described, saprobic species, *S. microbalum* (Longcore et al., 2016). DNA sequence information is seemingly still unavailable for aquatic members of the Synchytriaceae, i.e., species traditionally placed in *Micromyces*, *Micromycopsis*, or *Endodesmidium*. We note that Karling (1964) considered species of *Micromyces* to be in subgenus *Microsynchytrium* of genus *Synchytrium*, and we note that Smith et al. (2014) included several species from *Microsynchytrium* in their analysis. However, the species of subg. *Microsynchytrium* included in Smith et al. (2014) were terrestrial--no aquatic species (as might be placed in *Micromyces*) were included. Until putative genera other than *Synchytrium* (*sensu stricto*) can be included in molecular studies of Synchytriaceae, the traditional taxonomy of the group (recognizing four genera, based on morphology; see our generic key) should be retained--i.e., there is presently insufficient evidence to argue against this viewpoint; this conclusion is drawn in spite of Karling's (1964) suggested, admittedly useful, sub-generic breakdowns of *Synchytrium* (in which he recognized no genus of Synchytriaceae other than *Synchytrium*). It is already apparent, though, from molecular analyses (Smith et al., 2014; Longcore et al., 2016) that some subgenera of *Synchytrium*, recognized by Karling (1964), are polyphyletic (including subgenus *Microsynchytrium*).

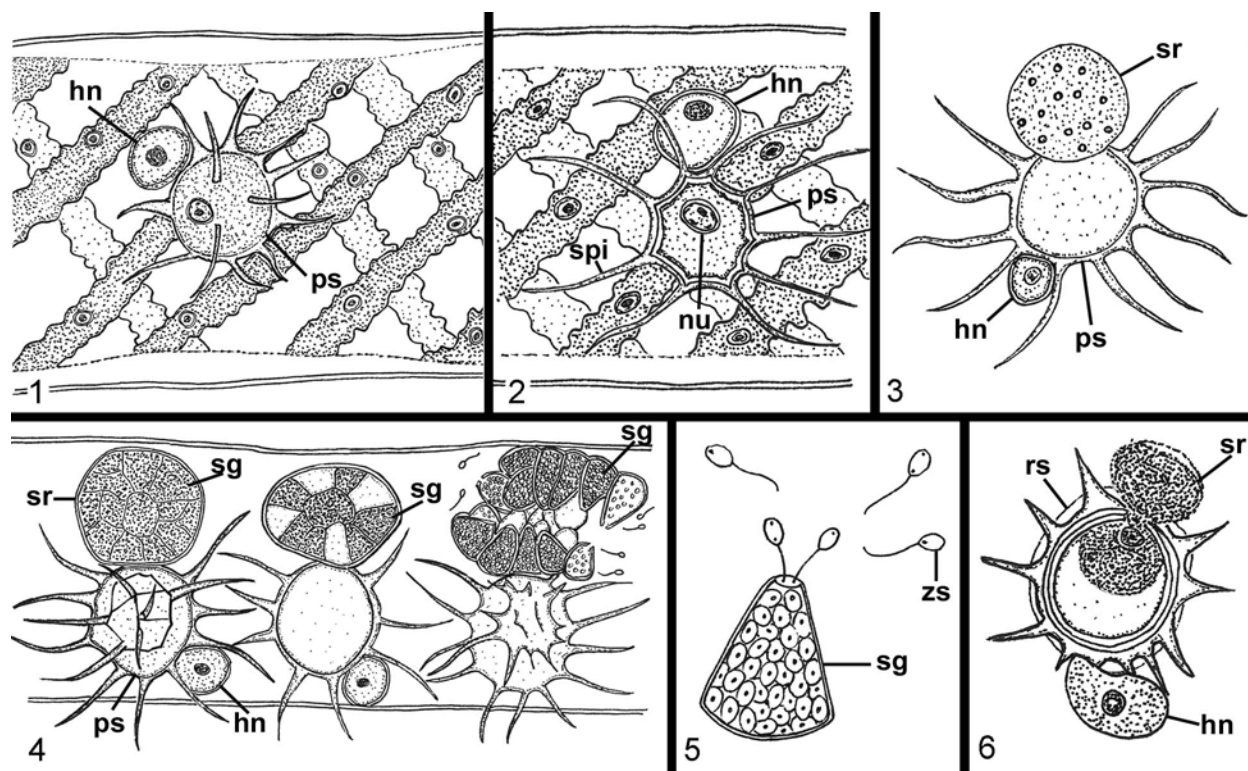
ACKNOWLEDGEMENTS

We thank reviewers of this manuscript: Dr. Sonali Roychoudhury, Patent Agent and Scientific Consultant, New York; and Dr. Robert W. Roberson, School of Life Sciences, Arizona State University.

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Figures 1-6. *Micromyces longispinosus*. **Fig. 1:** Developing prosorus (ps) in host cell (*Spirogyra*); note association of prosorus with host nucleus (hn). **Fig. 2:** Older prosorus (ps) continues to have a single nucleus (nu) and also remains in association with the host nucleus (hn); spines (spi) of the prosorus have become more elongate. **Fig. 3:** Germinated prosorus (ps); sorus (sr) developing from and sessile upon the prosorus, the sorus becoming multinucleate; host nucleus (hn) remaining in association with prosorus. **Fig. 4:** Prosorus (ps), sorus (sr) and host nucleus (hn) still associated; sorus (sr)--left to right--developing sporangia (sg) within, the sporangia slowly separating (right) as the soral membrane has broken down. **Fig. 5:** Sporangium (sg) releasing uniflagellate, ovoid zoospores (zs) from its apex. **Fig. 6:** Thickened-walled, spiny resting spore (rs) functioning as a prosorus and germinating to form a sorus (sr); host nucleus (hn) seen in association with the resting spore. Fig. 1 after Couch 1931, Sparrow 1943. Fig. 2 after Couch 1937, Karling 1964. Fig. 3 after Couch 1931, 1937; Karling 1964. Fig. 4 after Couch 1931, 1937. Fig. 5 after Couch 1937, Karling 1977. Fig. 6 after Couch 1931, 1937.

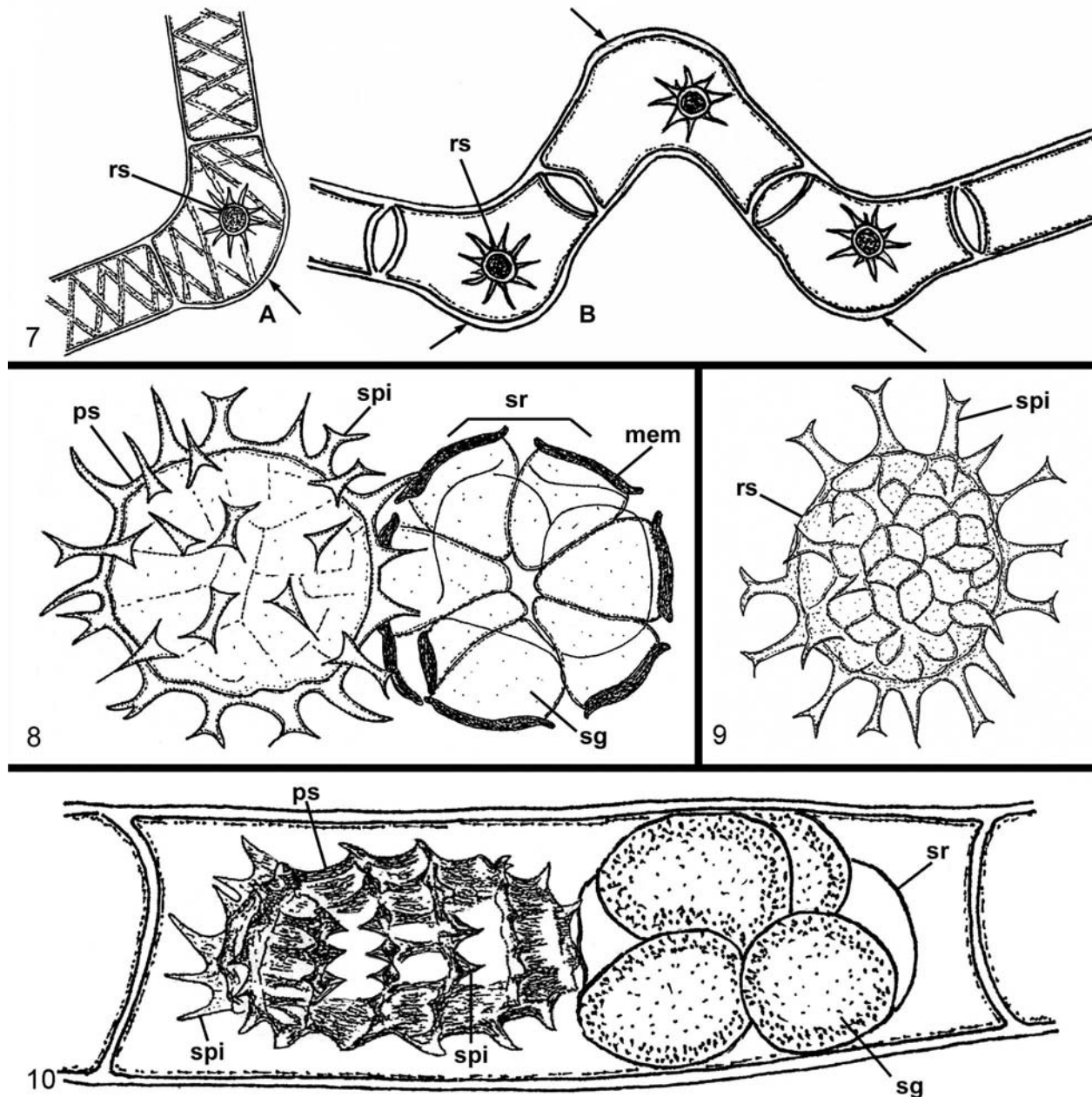
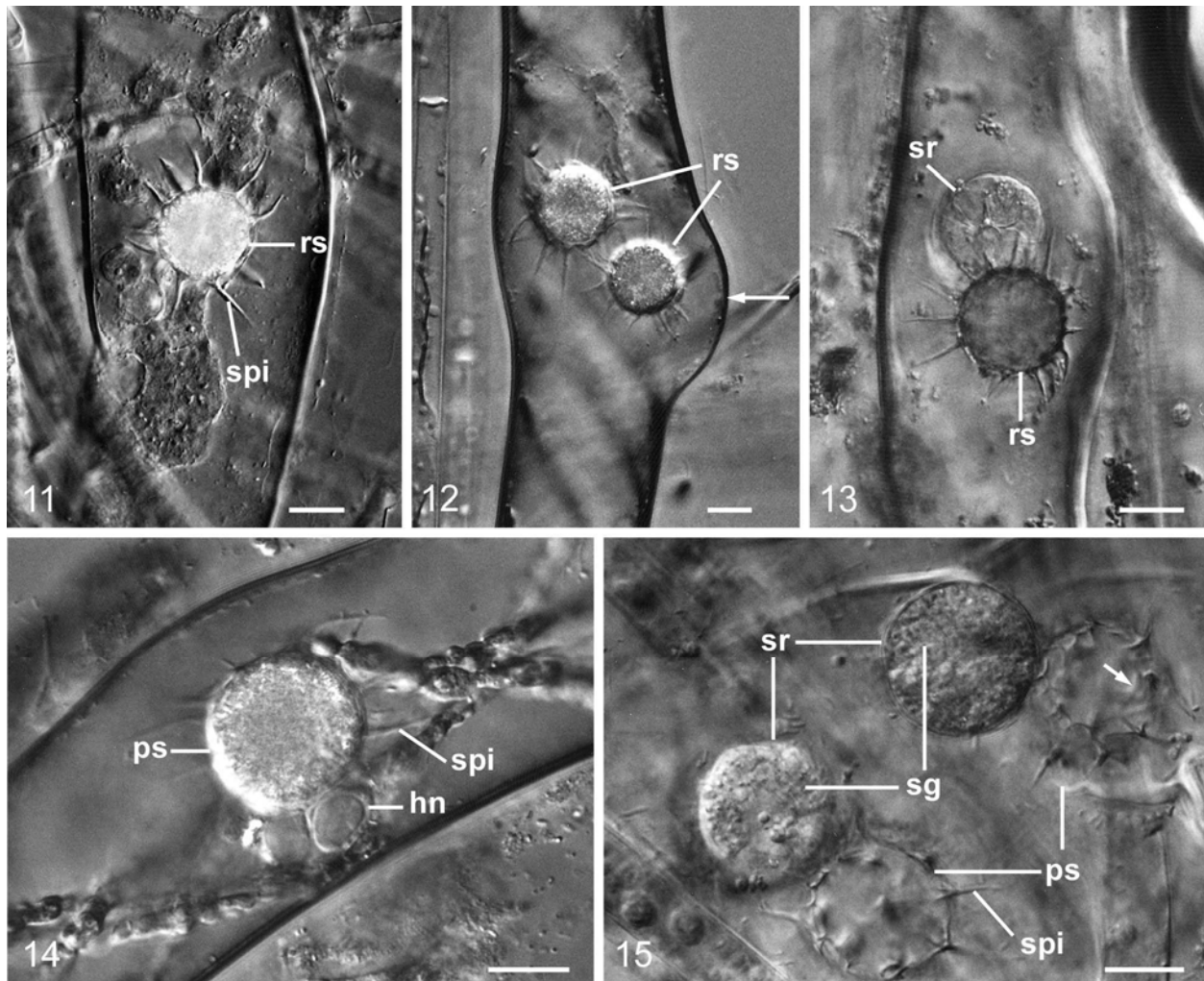
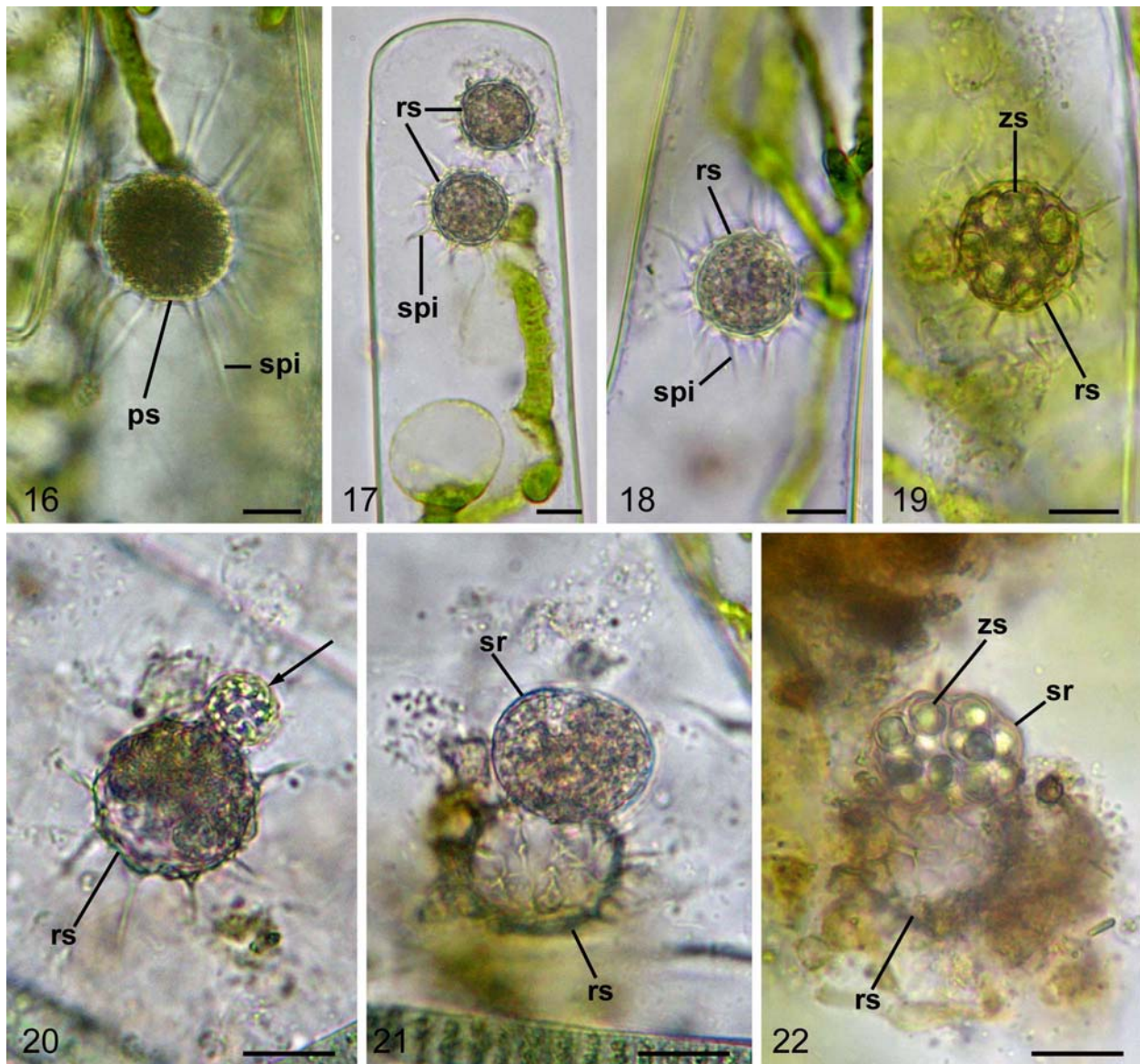


Figure 7 (A,B): *Micromyces grandis*--seemingly a large variant of *M. longispinosus*--in *Spirogyra* host. Resting spores (rs) of '*M. grandis*' in association with hypertrophy (bends, bulges--arrows) of host cells. **Figures 8-9:** *Micromyces furcatus*. **Fig. 8:** Prosorus (ps) with *forked* spines (spi); sorus (sr) containing sporangia (sg); segments of soral membrane (mem) contribute to 'outer walls' of sporangia. **Fig. 9:** Resting spore (rs) showing forked spines (spi) and reticulate wall surface. **Figure 10:** *Micromyces ovalis*: Ellipsoid prosorus (ps) with separated rings of tooth-like spines (spi); distended sorus (sr) with four sporangia (sg). Fig. 7 generally after Miller 1955 and descriptive information in Sparrow 1960. Figs. 8-9 after Rieth 1962, Karling 1977. Fig. 10 after Rieth 1950, Karling 1964.



Figures 11-15. Black & White (Nomarski) photomicrographs of *Micromyces longispinosus* in *Spirogyra* host. **Fig. 11:** Developing resting spore (rs); note distinct spines (spi). **Fig. 12:** Two young resting spores (rs); note bulge (hypertrophy) of host cell (arrow). **Fig. 13:** Resting spore (rs) functioning as a prosorus and producing an external sorus (sr) sessile upon it. **Fig. 14:** Relatively young prosorus (ps); note scattered spines (spi) and association of host nucleus (hn) with prosorus. **Fig. 15:** Two prosori (ps) which have each produced a sorus (sr); note spines (spi) and some evidence of reticulation (arrow) on prosoral wall; note early cleavage, into sporangia (sg), within the sori. Scale bar = 10 μ m.



Figures 16-22. Color photomicrographs, *Micromyces longispinosus* in *Spirogyra* host. **Fig. 16:** Prosorus (ps) with slender, elongate spines (spi). **Figs. 17-18:** Resting spores (rs); note spines (spi) somewhat shorter and 'stouter' than those of prosorus. **Fig. 19:** Resting spore (rs) functioning (internally) as a sorus (forming groups of zoospores, zs). **Fig. 20:** Resting spore (rs) early germination stage (arrow). **Fig. 21:** External sorus (sr) developed from resting spore (rs) functioning as a prosorus. **Fig. 22:** Zoospores (zs) cleaved within external sorus (sr) developed from resting spore (rs). Scale bar = 10 μm.