

SYNOPSIS OF *OBELIDIUM* (CHYTRIDIOMYCOTA)**Will H. Blackwell, Peter M. Letcher and Martha J. Powell**Department of Biological Sciences, University of Alabama,
Tuscaloosa, AL 35487, USA**ABSTRACT**

Three species of *Obelidium*—*O. mucronatum* Nowakowski (1876), *O. hamatum* Sparrow (1937), and *O. megarhizum* Willoughby (1961)—have been described and are reviewed. Our collection of *O. megarhizum* from a North Carolina river is a new geographic record. A possible taxon of *Obelidium*, represented by specimens initially assigned with a question mark (Sparrow, 1937) to *O. mucronatum*, is discussed but not recognized because of insufficient evidence. Generic distinction of *Obelidium* has become less clear over time; consideration is thus also given to related chitinophilic genera. *Siphonaria petersenii* Karling (1945) merits special attention because of similarities to *Obelidium*. Additional molecular data will be required to conclusively resolve the systematics of *Obelidium* and related genera. *Phytologia* 94(1): 103-117 (April 2, 2012).

KEY WORDS: Chitin, chytrid, epibiotic, inoperculate, insect exuviae, interbiotic, mucro, resting spore, rhizoids, sporangium, zoospores.

Obelidium taxa are interbiotic or epibiotic, chitinophilic, eucarpic, monocentric, inoperculate Chytridiomycetes; the ellipsoid-ovate-spheroid, spine-bearing sporangium develops a subapical to lateral zoospore discharge pore (Sparrow, 1960; Karling, 1977). *Obelidium* and similar genera, saprophytic on kinds of insect exuviae, are obtained in culture with chitin bait (e.g., clarified shrimp exoskeleton), and may sometimes be cultured on chitin agar (Karling, 1967). *Obelidium* was established on *O. mucronatum* Nowakowski (1876)—characterized by a solid, apical sporangial spine (mucro) and a cup- or stalk-like sporangial base. The taxonomy of *Obelidium* became more uncertain as additional taxa (*O. hamatum* and *O. megarhizum*) were described, and another possible taxon discussed (first assigned, questionably, to *O. mucronatum*). We hope this revision of *Obelidium*

will encourage further ultrastructural and molecular work on the genus.

POSSIBLE GENERIC RELATIONSHIPS

Sparrow (1960, p. 429) noted similarities of the following four exuviae-inhabiting genera: *Obelidium*, *Siphonaria*, *Rhizoclostratum*, and *Asterophlyctis*—listing allegedly unifying features: “method of development, general structural features, possession of a subsporangial apophysis, type of zoospore discharge, and habitat.” These features, however, are indefinite or problematical. Regarding method of development, even within one species (*Obelidium mucronatum*) more than one mode of development was noted (Sparrow, 1938); Karling (1945) postulated two types of life cycles for *Siphonaria*. A further example of developmental variation is that the sporangium of *Asterophlyctis sarcoptoides* may form either from the zoospore cyst or from a swelling of the germ tube (cf. Antikajian, 1949; Karling, 1967)—see Karling (1977) versus Dogma (1974) concerning the systematic disposition of *Asterophlyctis*. “General structural features” refer to an overall resemblance of these genera on insect exuviae. However, some forms—e.g., *Asterophlyctis sarcoptoides*, with its angular, lobed, or even “stellate” sporangia—are distinctive. Sporangia of *Asterophlyctis irregularis* Karling (1967) possess tapering, peg-like projections. *Obelidium* taxa and *Siphonaria petersenii* have “spiny” sporangia, whereas other taxa of these four genera generally lack spines. *Obelidium mucronatum* and *Siphonaria petersenii* are, in fact, morphologically similar, as we discuss. A subsporangial apophysis is often present in these genera, but there are exceptions. *Obelidium mucronatum*, considered apophysate, occasionally lacks an apophysis; *O. hamatum* and *Siphonaria petersenii* apparently lack an apophysis; *Rhizoclostratum* possesses an apophysis—often fusiform and transversely oriented (cf. Karling, 1977). In Sparrow’s (1960, see p. 405) key to genera of Rhizidiaceae, *Obelidium* is distinguished from *Rhizoclostratum* and *Asterophlyctis* by “Rhizoids arising from a...cuplike basal portion of the sporangium” in *Obelidium*, versus “Rhizoids arising from an apophysis” in *Rhizoclostratum* and *Asterophlyctis*. This “distinction” is problematic; not only does *Obelidium mucronatum* often possess an apophysis, but the rhizoids, though usually initiating development first, may give the appearance of having arisen from the apophysis (cf. Sparrow, 1938, p. 4 and fig. 14).

Zoospore discharge in these genera is considered subapical or lateral; however, two species of *Siphonaria* do not discharge in this manner, and discharge in *Rhizoclostratium* is often basal (Sparrow, 1960). Even habitat, presumed to involve chitin substrate, may not always be similar; *Rhizoclostratium* (Sparrow, 1960; Karling, 1967) generally inhabits insect exuviae, but *R. marinum* occurs on the alga, *Codium*—Karling (1977), though, questioned generic placement of *R. marinum*.

The supposed production of resting spores (in the above four genera) by sexual means (cf. Karling, 1945)—allegedly initiated in these genera by rhizoidal anastomosis—is somewhat unusual; the majority of chytrid resting spores are asexually produced. Resting spore formation in *Asterophlyctis* (Antikajian, 1949; Karling, 1967) may in fact be asexual, and resting spores are unknown in taxa described as *Obelidium*—however, further attempts at discovering rhizoidal anastomosis, and potential heterothallism, are worthy of pursuit. The four putatively related genera are apparently inoperculate. Considered of major significance in delimiting larger groupings of chytrids (cf. Sparrow, 1960), the presence or absence of an operculum is now understood to have more relevance at the generic level. Operculate genera may occur in predominantly inoperculate groups, and vice versa (cf. Powell et al., 2011). The lack of an operculum, thus, does not necessarily predict relationship. In brief, analysis of details of traits of the four genera suggests that little meaningful morphology remains by which to reliably establish generic distinction, or confirm relationship. These four genera probably are related, though, and additional features suggest this. The developing sporangium in these genera typically possesses a large primary nucleus (cf. Karling, 1967), persistent until almost the point of zoospore cleavage. There is also reasonable consistency in the observation that zoospores are released from the sporangium together (and begin movement) in a temporary vesicle, before dispersing individually (cf. Karling, 1967). A similar structural type of zoospore apparently occurs in these genera (Letcher et al., 2005). These additional morphological traits are not, though, confined to these four genera. A general molecular similarity can be asserted for these genera (cf. James et al., 2006), *Asterophlyctis* being perhaps the most distantly related among them. Other genera, however, play into the molecular picture as well; isolates identified as *Rhizoclostratium*,

Podochytrium and *Phlyctorhiza* positioned in the same clade as did *Siphonaria petersenii* and *Obelidium mucronatum* (James et al., 2006).

TAXONOMIC SYNOPSIS

OBELIDIUM Nowakowski. Cohn, Beitr. Biol. Pflanzen 2: 86, 1876.

Type of genus = Type of *Obelidium mucronatum* Nowak., 1876.

Thallus eucarpic, monocentric, chitinophilic, typically developing in an interbiotic or epibiotic fashion, apophysate or apophysis lacking. Sporangium usually extramatrical, occasionally partially or wholly intramatrical, inoperculate, often mucronate (i.e., with an apical spine-like process), differentiating from the encysted zoospore, typically with a large primary nucleus persisting until the onset of zoospore formation; sporangial wall remaining thin or exhibiting uniform or basal thickening (in the last case, becoming cup- or stalk-like at the base). Rhizoids robust or more delicate, extensively or more infrequently branched, with or without major rhizoidal axes, intra- or extra-matrical, rarely sparsely developed. Zoospores posteriorly uniflagellate (characteristic of Chytridiomycota), spherical to ellipsoid, each with a single obvious lipid globule (uniguttulate), typically released as a group (often in a temporary vesicle) through a subapical to lateral discharge pore before dispersing individually, movement hopping or occasionally amoeboid. Resting spores not seen. Saprophytic on shed or fragmented exoskeletal material, particularly insect exuviae.

Species of *Obelidium*

(*Siphonaria petersenii* considered because of similarity in morphology)

A₁. Sporangium ovate, ellipsoid or spheroid, usually not or only the base embedded in host matrix, relatively thin-walled or wall becoming distinctly thickened and differentiated toward the base; spines (or similar pointed excrescences) one (apical) or a number (variously distributed), in any case borne on main body of sporangium, solid; zoospores mostly spheroidal; rhizoidal system usually well-developed, richly branched or with dominant trunks penetrating substrate..... B

B₁. Sporangium with one apical spine-like process (mucro) or, less commonly, two oppositely placed subapical processes; lateral sporangial spines lacking; sporangial base thin-walled or thickened and cup-, vase- or stalk-like; apophysis often present, sometimes obscure; sporangium and zoospores without special pigmentation..... C

C₁. Sporangial base thickened, cup-like, a pinched or stalk-like portion sometimes evident above the basal cup, the apical mucro prone to be elongate and spine-like; rhizoids usually similar in appearance, profusely branched, endobiotic or interbiotic.....*O. mucronatum* (1)

C₂. Sporangial base relatively thin-walled, not specially differentiated, the apical mucro usually pyramidal in form (though sometimes taper-tipped); rhizoids mostly endobiotic, with one or two main trunks extending into the substrate; secondary rhizoidal branches relatively sparse, often obscure in substrate.....*O. megarhizum* (2)

B₂. With a long apical and several lateral sporangial spines; sporangial base not thickened or cup-like; any stalk-like structure is beneath the sporangium, of rhizoidal origin, and not thickened; apophysis lacking; sporangium often with golden-orange pigmentation; zoospore lipid-globule often golden-red.....*S. petersenii*

A₂. Sporangium often obovate-oblong, main portion becoming uniformly thickened, lacking spines; two short lateral spines (barbs, with protoplasmic contents) borne oppositely on thin-walled, somewhat elongate, stalk-like portion of sporangium (this embedded in substrate); zoospores ellipsoidal; rhizoids delicate, sparse.....*O. hamatum* (3)

(1) *Obelidium mucronatum* Nowakowski. Cohn, Beitrag zur Biologie der Pflanzen 2: 86, 1876.

Type: Nowakowski's (1876) figs. 1-5, of Taf. V, accepted as the type.

Thallus typically interbiotic or epibiotic. Sporangium 20-56µm long, 7-20µm broad, broadly ovate or subspheroid to more narrowly elongate-ellipsoid, extramatrix or rarely intramatrix, without special color, with a single solid apical spine (mucro), less frequently with two (subapical, oppositely placed) spines; mucro simple, typically not more than one-third the sporangial height, refractive, often the first part of the

sporangium to differentiate; base of sporangial wall usually becoming thickened and cup-, vase- or funnel-like in appearance, 4-12 μ m broad; a stalk-like portion (immediately above the cup-like sporangial base) may also develop, this as much as 10 μ m long. Rhizoids intra- or extra-matrical, typically well-branched, often becoming extensively developed with finer branches spreading as much as 100 μ m; the primary rhizoidal axis occasionally enlarging proximally and bearing smaller, reduced branches; rhizoids rarely less branched, somewhat more delicate and sparsely developed. A small subsporangial apophysis usually present (but may be obscured by the cup-like sporangial base), developed from the inflated upper portion of the germ tube or the upper portion of the rhizoidal branches to which it is attached. Zoospores spherical to slightly ellipsoid, 2.5-3.5 μ m, with a flagellum ca. 20 μ m long and a colorless (but refractive) lipid globule, typically released *en masse* through a broad, subapical to lateral, circular exit pore before dispersing individually; a few zoospores may occasionally remain trapped inside the sporangium. Resting spores unknown. Thalli on exuviae of midges, other dipterans, and types of caddisflies. (**Fig. 1**)

Distribution: Reports (see Sparrow, 1960) from: Germany, Denmark, portions of Russia, and the United States (Michigan, Sparrow, 1938; Karling, Louisiana, 1948). Later reported: Karling (1967), New Zealand; Czeuczuga et al. (2005), Poland (Supraśl River).

Discussion: *Obelidium mucronatum* is a variable species (Sparrow, 1938). Karling (1967) felt that its variation might encompass other species of the genus (with which we disagree, as discussed under these species). A central part of the identity of *O. mucronatum*, as established by Nowakowski (1876), has been the solid apical spine (mucro or "spike") terminating the zoosporangium (cf. Nowakowski, Taf.5, fig.1). Sparrow (1937) informally described, and illustrated (figs. a-i of his text Fig. 5), specimens from Massachusetts (on caddisfly integument, "pond near Hyannis"), referring to them as "*Obelidium* (?) *mucronatum*;" these specimens, exhibiting the cup-like sporangial base of *O. mucronatum*, differed by lack of an apical mucro and by a characteristically more delicate rhizoidal system. After examining typical *O. mucronatum* from Michigan, Sparrow (1938) indicated that the non-mucronate (Massachusetts) specimens should not be included in this species, and possibly constituted a new species of *Obelidium*—which he declined to describe without further study. Later, Sparrow (1960) was more equivocal on the disposition of the non-mucronate

material—zoospore discharge was still not observed—and questioned its retention in *Obelidium*. Since no additional information is available on this non-mucronate taxon, no resolution can be made as to its identity, other than to affirm that it could doubtfully be included in *O. mucronatum*, or even in the genus *Obelidium*.

(2) *Obelidium megarhizum* Willoughby, Trans. Brit. Mycol. Soc. 44: 588, text-fig. 1 & pl. 37, 1961 (with Latin description).

Type: Willoughby: Herb. I.M.I. 85111

Thallus epibiotic or restrictedly interbiotic. Sporangium extramatrical or intramatrical at the base, ovoid or ellipsoid (occasionally narrowly so) or spheroid (often assuming a broadly ovate or spheroidal shape just prior to zoospore discharge), 11-40 μ m long, 6-35 μ m broad, uniformly relatively thin-walled, with no portion of the wall especially differentiated except for the single solid apical mucro; this mucro, often refractive and of generally pyramidal form, is 2.5-8 μ m long and 1.5-6 μ m broad at the base. Apophysis sometimes evident, 5.5-8.5 μ m in diameter. Rhizoids relatively coarse, with one or two dominant trunks ca. 2-6.5 μ m broad, which may extend as much as 160 μ m into the substrate; lateral rhizoidal branching (sometimes obscure in the chitinous substrate) is seemingly relatively sparse. Zoospores generally spherical, 3.5-4.5 μ m, sometimes relatively numerous, discharged subapically (through a circular pore, 5.5-15 μ m broad, formed by liquefaction of a portion of the sporangial wall), becoming active within a group prior to individual dispersal. Resting spore not seen. Isolated on termite wings from culture of submerged lake mud, and on purified shrimp chitin from culture of twigs and mud from edge of a river. (Figs. 2 and 5-11)

Distribution: England, Malham Tarn, Yorkshire, L. G. Willoughby (reported 1961); United States, North Carolina, Rutherford County, edge of Broad River, below Bill's Mountain, 3.1 mi. northeast on Hwy 64 from Hwy 9 intersection, collected by W. Blackwell and M. Powell (WB#266G), April 9, 2005.

Discussion: Willoughby (1961) distinguished *Obelidium megarhizum* from *O. mucronatum* by the occurrence of one or two coarse, deeply penetrating, but sparingly branched, main rhizoidal trunks (as opposed to a spreading, more profusely branched rhizoidal system) and by the comparatively thin sporangial-wall base, not differentiated (not thickened and cup- or stalk-like) in comparison to

the rest of the sporangial wall. Karling (1967, 1977) indicated that these supposed *megarhizum*-features might fall within the variation of *O. mucronatum*. However, Karling's (1967) illustrations (e.g., his fig. 47) of putative rhizoidal identity between these species are not convincing; he did not deal with the other main distinguishing feature of *O. megarhizum*, i.e., the thin-walled sporangial base. Our observations of specimens of *O. megarhizum* from North Carolina support distinction of these species by the two traits suggested by Willoughby (1961). Additionally, the apical mucro in *O. megarhizum* does not typically attain the slender, elongate appearance often observed in *O. mucronatum* (and in *Siphonaria petersenii*). And, *O. megarhizum* is epibiotic (see also Willoughby's plate 37), or else more limitedly capable of interbiotic growth than *O. mucronatum*—consistent with Karling's (1967) notation, re: Willoughby's material, that rhizoidal axes were more strictly intramatrix in *O. megarhizum* than in *O. mucronatum*. The only interbiotic growth we observed in *O. megarhizum* was occasional extension of the subsporangial rhizoidal stalk beyond the chitinous substrate (Figs. 8, 9). Karling (1967) noted that Willoughby's (1961, fig. 1c) illustration of a "central vacuole" in a young thallus of *O. megarhizum* was probably the primary nucleus. A vacuole in a developing thallus is illustrated in our Figs. 9 and 11.

(3) *Obelidium hamatum* Sparrow, Proc. Amer. Phil. Soc. 78: 52, 1937
(with Latin description).

Type: Sparrow's (1937) figs. j-m of text Fig. 5 accepted as type.

Thallus relatively small; main body of sporangium mostly epibiotic, 10-12 μ m long, 8-9 μ m broad, obvoid or somewhat oblong to ovoid, developing a uniformly somewhat thickened wall; lower (non-zoosporogenous) portion of sporangium thin-walled, tapering and stalk-like, 8-12 μ m long by ca. 4 μ m broad, extending into host substrate, bearing two short, oppositely placed, lateral, barb-like branches (at or just above mid-portion). Rhizoids rather poorly developed, delicate and sparsely branched (even unbranched), extending farther into substrate from the acute basal tip of the stalk-like portion of the sporangium. Apophysis lacking. Zoospores often ellipsoid, ca. 4 μ m by 2 μ m, with a single lipid globule evident, discharged laterally (often at the base of the ovate portion of the sporangium), sometimes creeping and amoeboid in behavior on surfaces encountered. Resting spore not observed. On dipteran (e.g., midge) exuviae. (Fig. 3)

Distribution: The type locality, collection by Sparrow ("8-IX-34"), was "Clark's Pond," New Hampshire (Sparrow, 1937). Sparrow (1960) reported additional specimens (mostly empty sporangia) in samples of exuviae from Michigan (no specific locality given).

Discussion: Sparrow (1937) formally described *O. hamatum*, and continued to recognize it as a distinct species the following year (Sparrow, 1938). Sparrow (1960) later expressed doubt as to its relationship (even inclusion in *Obelidium*), though having observed additional (if limited), similar specimen material. Karling (1967) implied that variations seen in *O. mucronatum* might cast doubt on recognition of *O. hamatum*; he did not, however, clearly document why *O. hamatum* should not be distinguished from *O. mucronatum*, and his illustrations of variation in *O. mucronatum* (reference being to his figs. 25 and 46) do not resolve the issue. Karling appeared to suppose that spines on the sporangial stalk of *O. hamatum* might be either aborted or incipient rhizoidal branches (based on forms seen in *O. mucronatum*), but such was never demonstrated. Karling (1977) became more uncertain as to whether *O. hamatum* should be a distinct species, though seeming to retain it in *Obelidium*. Neither Sparrow (1960) nor Karling (1977) suggested where *O. hamatum* might be placed, if not included in *Obelidium*. Thus, we are left with this situation: *O. hamatum* is obviously morphologically distinct—uniformly thickening, obovate sporangium; thin-walled stalk with paired "barbs;" feebly developed rhizoidal system; more ellipsoidal zoospores (cf. Sparrow, 1937)—compared with other species of *Obelidium*; yet, it resembles *Obelidium* more than species of related genera. Hence, we recognize *O. hamatum* as a species of *Obelidium* until contrary evidence is available.

Tentative placement:

Siphonaria petersenii Karling, Amer. J. Bot. 32: 580, 1945 (with Latin diagnosis).

Type: Karling's (1945, see reference above) figs. 1-26, p. 582, accepted as the type.

Thallus inter- epi- or intra-biotic. Sporangium 10-36 μ m long, 5-20 μ m broad, usually ovate or ellipsoid (rarely transversely elongated) or elongate-pyriform, typically extramatrical, often somewhat golden or orange in color, with a long (as much as 15 μ m) slender, unbranched, solid apical spine and 3-12 variously placed lateral spines (these usually somewhat shorter, simple or occasionally bifurcate); sporangial wall

not becoming thickened; sporangial base not specially differentiated. Rhizoids mostly intramatrical, directly connected to sporangial base, at first monoaxial but soon branching and tending to spread in a robust manner (often 80 μ m into the substrate), the ultimate branches fine. Apophysis lacking. Zoospores spheroidal, 3-3.5 μ m, a single, often golden-red lipid globule evident; zoospore discharge subapical, communal (in a vesicle) before individual dispersal. Resting spores result from a sexual process initially involving rhizoidal anastomosis, spherical to oval or somewhat angular, 6 to 15 μ m, reddish-brown, the thickened wall often bumpy or with low spines. Numerous thalli may develop on exuviae of dipterans such as mayflies. (Fig. 4)

Distribution: Reported from New York, Connecticut, and the type locality in Brazil (Karling, 1945, Flores Nabuco, Amazonas).

Discussion: Were it not for its lateral sporangial spines, *Siphonaria petersenii* (Karling, 1945) resembles *Obelidium mucronatum*. There is similarity in growth form, substrate preference, sporangial shape, and the spreading, well-branched rhizoidal system. An apophysis is not present in *S. petersenii*, whereas *O. mucronatum* is considered apophysate; however, the apophysis in *O. mucronatum* may be obscure, or even lacking (Sparrow, 1938). The subapical discharge of zoospores in *S. petersenii* is similar to *O. mucronatum* (not to the apical or basal discharge of other *Siphonaria* species, cf. Sparrow, 1960); both have a similar zoospore type (Letcher et al., 2005). In a study incorporating ultrastructural and molecular data (Vélez et al., 2011), including a relatively limited number of taxa, *O. mucronatum* and *S. petersenii* paired very closely. However, in James et al. (2006)—including more taxa, but focusing on molecular data—the relationship of these two species was less conclusive; each ultimately paired more closely with other taxa. Further molecular resolution will be required if these species are to be formally placed in the same genus. Resting spores have been observed (Karling, 1945) in *Siphonaria petersenii*, but not in taxa described as *Obelidium*; it is uncertain if this represents a real difference, or that resting spore stages (perhaps uncommon if involving heterothallism) have not yet been encountered in *Obelidium*. Were *Obelidium* species and *Siphonaria petersenii* placed in the same genus, a morphologically logical unit would result (for taxa with spiny sporangia). Although sporangia of *Asterophlyctis irregularis* bear tapered, peg-like projections, other morphological features (e.g., basal or subbasal zoospore discharge) do not suggest inclusion in *Obelidium*.

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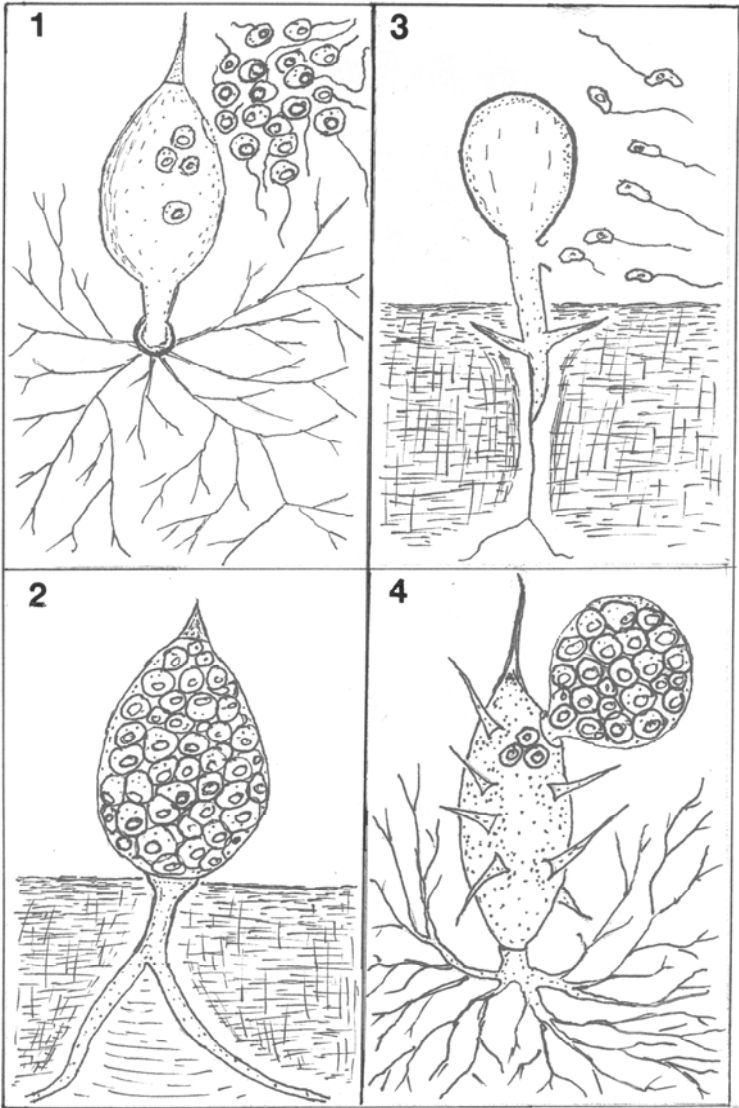
Figs. 1-4 (facing page).

Fig.1. Thallus of *Obelidium mucronatum*. Sporangium showing apical spine (mucro) and lower, stalk-like portion subtended by cup-like base; branching rhizoidal system seen extending out below this base. Spherical zoospores released, from subapical discharge pore, seen as they disperse individually (several remain trapped in sporangium).

Fig.2. *Obelidium megarhizum*. Sporangium assuming ovate form as its protoplast has undergone cleavage to form zoospores. Rhizoidal axis evident below sporangium; two prominent trunks penetrate substrate.

Fig.3. *Obelidium hamatum*. Obovate sporangium has released ellipsoid zoospores at junction with thinner-walled stalk (bearing two lateral "barbs") terminating in a sparse rhizoidal system.

Fig.4. *Siphonaria petersenii*. Ellipsoid sporangium (with spines), releasing zoospores in a vesicle. Rhizoidal system joining non-thickened sporangial base.



Figs.5-11 (facing page).

Obelidium megarhizum (photomicrographs, North Carolina specimens, on chitin):

Fig. 5. Epibiotic sporangia.

Fig. 6. Rounded sporangium with cleaved zoospores.

Fig. 7. Sporangium after zoospore release; discharge pore (arrow) subapical to mucro.

Fig. 8. Limited interbiotic growth by extension of rhizoidal stalk (white arrow); a main rhizoidal trunk (dark arrow).

Fig. 9. Interbiotic cluster (rhizoidal stalk, arrow); vacuole in lower portion of largest sporangium.

Fig. 10. Ellipsoid sporangium.

Fig. 11. Developing, ovate sporangium; vacuole evident.

