

A review and update of the genus *Sapromyces* (Straminipila: Oomycota)

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ABSTRACT

Sapromyces—a freshwater saprotrophic genus of Oomycota, traditionally classified in the Leptomitales, more recently in the Rhipidiales—has received scant taxonomic attention since Sparrow's (1960) revised *Aquatic Phycomycetes*. Sparrow recognized the two species of *Sapromyces* well-established at that point, *S. elongatus* and *S. androgynus*; a third species, *S. indicus*, was included, but not incorporated in his key, apparently because information did not reach Sparrow in time to completely readjust text. Dick (2001) recognized these three species—providing nomenclatural information, but not distinguishing features. A goal of our investigation was to assess *S. indicus* Iyengar et al., and, accepting this species, include it in a revised key. We conclude that *Sapromyces* should indeed contain three species, *S. elongatus*, *S. androgynus* and *S. indicus*; a fourth possible species, *S. dubius* Fritsch, based on sparse, uncertain material (initially described, but not named, by Reinsch), is considered “doubtful.” *Sapromyces reinschii* (J. Schröt.) Fritsch is treated as a synonym of *S. elongatus*. Authorship of the binomial combination *Sapromyces elongatus* was incorrectly attributed; it should be *S. elongatus* (Cornu) Thaxt. Thaxter is sole author of *S. androgynus*. The original source (which of two publications?) of the basionym of *S. elongatus* (*Rhipidium elongatum*) required clarification. The generic name *Sapromyces* invited attention because of two preceding synonyms, and a possible later homonym. We report our find of *Sapromyces* in Alabama—a probable identity to species—and discuss aspects of morphology: Form and mode of growth, potential vegetative reproductive structures, and absence of antheridia. Published on-line www.phytologia.org *Phytologia* 97(2): 82-93 (April 1, 2015). ISSN 030319430.

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Although genera of particular groups of Oomycota (e.g., “water-molds” of the Saprolegniales, and plant pathogens of the Peronosporales) are well known and frequently investigated organisms, many other genera (especially in lesser known orders) have remained obscure. In recent times, though, some of these more poorly understood representatives have received at least a modicum of taxonomic study (e.g., Blackwell 2010, 2011; Blackwell et al., 2013, 2014; Pereira and Vélez, 2004). *Sapromyces*, considered here, is an incompletely known genus, receiving perhaps even less attention than certain other poorly known Oomycetes since it is fundamentally saprotrophic (i.e., not “problematic” as a parasite). *Sapromyces* has been considered a member of the Leptomitales (Kanouse, 1927; Sparrow, 1960), an order distinguished from the Saprolegniales (which they may generally resemble) by hyphae that are often distinctly constricted at intervals. Although fundamentally coenocytic (characteristic of Oomycetes generally)—and not as prone to form sporadic cross-walls, as encountered in members of the Saprolegniales (e.g., in association with sporangia)—members of the Leptomitales may develop restrictive plugs of “cellulin” granules, internally, associated with hyphal constrictions (cf. Sparrow, 1960; Alexopoulos, 1962; Dick, 1973), and thus form what may be termed “pseudo-cells” (segments that resemble and perhaps function as cell units). There is a trend in the Leptomitales to form oogonia which contain but a single oosphere. Associatedly, oogonial contents of members of the Leptomitales are often differentiated not only into ooplasm (which develops into the oosphere, or “egg,” as in Saprolegniaceae) but also (in distinction to Saprolegniaceae) into a surrounding periplasm, leaving little “free-space” between the oogonial wall and developing oosphere (cf. Alexopoulos, 1962, p. 150). In the Leptomitales generally (in connection with possession of periplasm) the oospore matures centripetally—in contrast to a typically centrifugal development of oospores of Saprolegniaceae (Dick, 1969).

Within the Leptomitales (cf. Sparrow, 1960), forms such as *Leptomit* and *Apodachlya* were classified in the Leptomitaceae (thallus relatively undifferentiated), whereas *Sapromyces*, *Rhipidium*, *Araiospora*, and *Mindenella*, were placed in the Rhipidiaceae (thallus comparatively differentiated). *Sapromyces* is distinguished, though, from other genera of Rhipidiaceae by a basal (attachment) pseudo-cell not strikingly morphologically differentiated from other thallus “cells.” Dick (2001) included genera of Rhipidiaceae (including *Sapromyces*, which can bear a superficial resemblance to *Leptomit*) in an expanded concept of the grouping, i.e., the Rhipidiales, in his subclass Rhipidiomycetidae; *Leptomit* and *Apodachlya*, retained in the Leptomitales, were transferred to subclass Saprolegniomycetidae. Dick’s (2001) separation, of these seemingly similar groups of pseudo-fungi into different subclasses, requires scrutiny, but is not greatly dissimilar to Sparrow’s (1976) placement of the Rhipidiaceae in the “Peronosporacean galaxy” and the Leptomitaceae in the “Saprolegnian galaxy.” Whereas certain molecular-genetic information (Sekimoto et al., 2007; Beakes and Sekimoto, 2009; Beakes et al., 2012) appears to support such a broad separation (e.g., of *Apodachlya* from *Sapromyces*), other data (Riethmüller et al., 1999; Lara and Belbahri, 2011) may suggest closer relationship. Beakes et al. (2014, p. 51 vs. p. 53) bring to light what seem to be, at least in part, conflicting molecular outcomes. Further resolution of molecular data, including additional sampling diversity of Oomycetes (as, for example, suggested by Beakes et al., 2014), is necessary to be confident of relationships between members of the Leptomitales and those of the Rhipidiales (and, for that matter, of genera within each order).

HISTORICAL TAXONOMIC INFORMATION ON *SAPROMYCES*

Sapromyces Fritsch (1893) is the correct name for this genus of rhipidialean Oomycetes, because two prior names—*Naegelia* Reinsch (1878), and *Naegeliella* J. Schröt. (date usually given as 1893, although the separate of *Die Natürlichen Pflanzenfamilien* containing *Naegeliella* was probably published in 1892)—were both preoccupied (already employed for genera unrelated to *Sapromyces*, or to each other). Consequently, these similar names (*Naegelia* and *Naegeliella*), in application to *Sapromyces*, can only be interpreted as illegitimate synonyms. The genus *Sapromyces* is at present considered to contain three species (see Key, and Figs. 1-8), as is subsequently discussed.

In seeming nomenclatural complication, *Sapromyces* Sabin (1941, see Lit. Cited) was erected as the generic name for certain strains of bacteria of the Pleuropneumonia group found in sewage. Sabin’s (1941) name was accepted (Edward and Freundt, 1969), but soon rejected (Edward and Freundt, 1970) on grounds of prior existence of the Leptomitalean genus by the same name (*Sapromyces* Fritsch, 1893). It might seem that Edward and Freundt were correct in 1969, to the extent that a name published under one code of nomenclature (e.g., the “bacteriological” or “prokaryotic” code) is generally allowed to stand, regardless of an identical name recognized under another code (e.g., the “botanical code,” or its current name); however, their stance in 1970 could also be supported in that the bacteriological code may not consider such a bacterial name (i.e., a “later homonym” of a “fungal name”) legitimate. Regardless, Sabin’s (1941) name has no effect on Fritsch’s (1893) name.

Two species of *Sapromyces* were recognized by Coker and Matthews (1937), *Sapromyces androgynus* Thaxt. (1896) and *S. elongatus* (Cornu) Coker in Coker & V. D. Matthews (1937; see Lit. Cited). The source of the epithet “*elongatus*” (*Rhipidium elongatum* Cornu) was recognized by Coker and Matthews as Cornu (1872). These species, authorships, and publication dates were subsequently recognized by Sparrow (1960) and Dick (2001). In seeming contradiction, though, whereas Dick (2001) credited the combination *Sapromyces elongatus* to Coker in information provided on this species, he also credited the same combination (in the same publication)—when indicating typification of genus *Sapromyces*—to Thaxter (1896). As noted currently in *Index Fungorum* (online update), it was indeed Thaxter who first made the combination of Cornu’s “*elongatum*” with *Sapromyces*; the citation should thus properly be *Sapromyces elongatus* (Cornu) Thaxt., not (Cornu) Coker. Additionally, *Index Fungorum* lists the original publication of the epithet “*elongatum*” (i.e., *Rhipidium elongatum*) as Cornu,

1871 (a different publication than Cornu, 1872). Thaxter (1896) focused on Cornu's 1872 publication, but also cited Cornu (1871) in noting four species of *Rhipidium*—including *R. elongatum*, which Thaxter believed (based on information in Cornu) did not belong in *Rhipidium*; Thaxter considered that *R. elongatum* was more appropriately placed in genus *Sapromyces*. Adequate descriptive information of species (of “*Rhipidium*”) is provided in Cornu (1871), very similar to that presented by him in 1872. There is thus no reason not to regard Cornu's 1871 publication as the source of valid publication of *Rhipidium elongatum* (basonym of *Sapromyces elongatus*), and we so accept it herein.

Although *Sapromyces* (Fritsch, 1893) stands as the correct name of the genus, Fritsch did not employ the earliest available epithet (“*elongatum*” of Cornu) for the original species—using, rather, the binomial *Sapromyces reinschii* (J. Schröt.) Fritsch (based on *Naegeliella reinschii* J. Schröt. 1892/1893). Since “*reinschii*” is not the earliest epithet, *S. reinschii* has, by most authors, been regarded as a synonym of *Sapromyces elongatus*. As indicated, the correct combination—*Sapromyces elongatus* (Cornu) Thaxt.—was provided by Thaxter (1896, p. 326). It was in this publication that Thaxter (p. 329) described *Sapromyces androgynus* as a new species. In addition to recognizing *S. androgynus* and *S. elongatus*, Thaxter, perhaps surprisingly, also recognized *S. reinschii* (p. 326). Thaxter indicated that *S. androgynus* may be distinguished from *S. reinschii* by smaller stature, but provided no insight into a distinction between *S. reinschii* and *S. elongatus*. Equally perplexing, Dick (2001), though listing *S. reinschii* as synonym of *S. elongatus*, also listed *S. reinschii* under “excluded species.” A problem is that *S. reinschii* was based (Reinsch, 1878; Schröter, 1892/1893) only on asexual material (see Reinsch, 1878, re: species “1” of “*Naegelia*,” figs. 1-6 of his plate 15; see also our Figs. 9-10)—these specimens being, however, at least not inconsistent with *S. elongatus* (although sporangia of *S. reinschii*, as originally illustrated, exhibit a more consistently “whorled” pattern than is perhaps usually the case in specimens of *S. elongatus*). After reviewing original literature (Cornu, 1871, 1872; Reinsch, 1878), and although its disposition remains somewhat uncertain, we do not find sufficient evidence to consider *S. reinschii* a distinct species. Sparrow (1932) at first recognized *S. reinschii*, but later (1943) employed the earliest epithet, as correct for this species, i.e., *S. elongatus*. We therefore (albeit perhaps by default) regard *S. reinschii* as a synonym of *S. elongatus* (as in Coker and Matthews, 1937; Sparrow, 1960; Dick, 2001).

In a detailed account of *Sapromyces*, Sparrow (1960) provided a key to the two species of the genus definitely established at that time, *S. elongatus* and *S. androgynus*. Sparrow seemingly accepted a third species (*Sapromyces indicus* M. O. P. Iyengar et al., 1955), but did not include it in his key, since it apparently did not come to light in time for a full account in the second edition of *Aquatic Phycomycetes*. Dick (2001) recognized *S. indicus*, but did not indicate its distinction from other species. A fourth possible species of *Sapromyces*, *S. dubius* Fritsch (1893), based on an unnamed species of Reinsch (1878)—designated by Reinsch as species “2” (of “*Naegelia*”)—was considered a synonym of *S. elongatus* by Coker and Matthews (1937). However, Sparrow (1943), though initially tentatively considering *S. dubius* a synonym of *S. elongatus*, later excluded *S. dubius* from *Sapromyces*, coming to believe that it represented a fragment of a *Rhipidium* species (Sparrow, 1960). Dick (2001) likewise excluded *S. dubius* from *Sapromyces*, but without comment on its identity. We concur to the extent of considering *S. dubius* questionable, and do not include it in our key. However, given the paucity of the original material, and Reinsch's sparse illustration (1878, figs. 7-11 of his plate 15; see also our Fig. 11), we are uncertain of its determination, and unable, with assurance, to either include it in or exclude it from *Sapromyces*. Perhaps future collections will resolve the disposition of “*Sapromyces dubius*.”

The situation now, virtually unchanged since Sparrow (1960), is that three species of *Sapromyces*—*S. elongatus*, *S. androgynus* and *S. indicus*—are recognized. Little information has accrued directly useful to solution of taxonomic problems in the genus. Because Sparrow, of necessity, hastily included *S. indicus* M. O. P. Iyengar et al. (1955) in the genus, what falls to our study (other than matters of nomenclature) is to evaluate *S. indicus*, and, if accepting its distinctiveness, include it in a revised key to species. Additionally, we present our find of *Sapromyces*—a new record in Alabama, adding

substantially to the geographic record in the USA (cf. Sparrow, 1960). Although not all structures of the life cycle were observed in these specimens, we indicate a probable determination to species. Particular aspects of morphology are discussed, that may contribute to a better understanding of *Sapromyces*.

TAXONOMIC SUMMARY

Sapromyces Fritsch, 1893 (Oomycota)

Naegelia Reinsch, 1878; non L. Rabenhorst, 1844 (Fungi incerti sedis)

Naegeliella J. Schröt., 1893; non C. Correns, 1892 (Orchidaceae)

Type species: Sapromyces elongatus (Cornu) Thaxt. (1896); based on *Rhipidium elongatum* Cornu (1871). Synonym: *Sapromyces reinschii* (J. Schröt.) Fritsch (1893); based on *Naegeliella reinschii* J. Schröt. (1892/1893); in turn based on an unnamed species of *Naegelia* described by Reinsch (1878, see pp. 289-291, 298, and figs. 1-6 of his plate 15), designated by Reinsch as species "1."

In addition to the relatively undifferentiated basal pseudo-cell, *Sapromyces* may be distinguished from genera of traditional Rhipidiaceae (and related Leptomitalean genera) by a combination of features, none perhaps singularly distinctive; these features include: An elongate growth form (obtained by predominantly terminal budding), and a sometimes umbel-like pattern of hyphal branching; hyphal segments that are often elongate, clavate, or sometimes more generally broadened; sporangia that are frequently pedicillate (a consequence of formation by constriction and budding), the sporangia often becoming elongate and cylindrical or more broadly ovate in form, and sometimes clustered or in apparent whorls on or near a hyphal tip; membrane surrounding the emerging zoospores typically rupturing rapidly to potentially free the zoospores; spiral rotation of an antheridial branch; attachment of the antheridium at or near the apex of the oogonium; and obpyriform to spherical oogonia, subject to external encrustation.

Key to Species of *Sapromyces* (with notes on distribution, collection and morphology)

1. Oospore wall merely roughened, uneven, or sometimes undulate or with low protuberances; mature sporangia often exceeding 80 μm in length; basal pseudo-cell from 115 to as much as 1200 μm long and which may constitute a significant proportion of the thallus, relatively thin-walled, often branching in a hapteroid fashion at the base; species androgynous or diclinous.
 2. Antheridial branches short, androgynous (borne on oogonial branches); oogonium obpyriform; basal "cell" 115-250 μm long.....*S. androgynus* Thaxt. (1896)
 2. Antheridial branches long, winding, diclinous (occurring on non-oogonial branches); oogonium spheroidal; basal "cell" 300-1200 μm long.....*S. elongatus* (Cornu) Thaxt. (1896)
1. Oospore wall distinctly reticulate; sporangia often less than 80 μm long; basal pseudo-cell 40-80 μm long, constituting a relatively small portion of thallus, thick-walled, pear- or vase-shaped, unbranched; species is diclinous.....*S. indicus* M. O. P. Iyengar et al. (1955)

For useful descriptive accounts of the three recognized species of *Sapromyces*, see Coker and Mathews (1937) and Sparrow (1960) for *S. elongatus* and *S. androgynus*, and Iyengar et al. (1955) for *S. indicus*; see also our illustrations (Figs. 1-8). An extensive nomenclatural listing and typification of these species is available in Dick (2001). Evaluation of literature (and illustrations) of *S. indicus* Iyengar et al. (1955) indicates that it is a distinct taxon, deserving recognition equal to *S. elongatus* and *S. androgynus*.

Distributional note: *Sapromyces indicus* was reported from fallen leaves in stream-water in the Kambakkam Hills, 60 miles north of Madras (Iyengar et al., 1955). Both *Sapromyces elongatus* and *S.*

androgynus are geographically widespread (Sparrow, 1960), being known, for example, from various locations in Europe and North America. Yet, confirmed reports are infrequent, particularly for *S. androgynus* (Sparrow, 1960, p. 886); this is not to suggest, though, that these forms may not be locally common (Thaxter, 1896, re: *S. androgynus*). The relative rarity of reports of *Sapromyces* is probably more a reflection of lack of collection than infrequency of occurrence. Reports are usually from twigs, leaves, or small fruits floating in shallow water. “Baits” (e.g., pear or apple) do not seem to have been used in some cases; if baiting were more often utilized, reports of *Sapromyces* would likely become more common. Czeżuga et al. (2007) considered both *S. androgynus* and *S. elongatus* rare, but by using baits of various fruits and seeds (in bodies of water in eastern Poland) they were able to isolate both species.

Our collection (Figs. 13-25). Our specimens of *Sapromyces* were obtained by baiting on small slices of pear in a water collection (containing floating twigs and privet fruit) from a stagnant feeder creek to Northwoods Lake; Northport, Tuscaloosa Co., Alabama (collection WB#302). This collection adds significantly to an already geographically broad (if not necessarily common) distribution of the genus *Sapromyces* in the United States, Canada, Central America, Europe, Asia and Australia (cf. Sparrow, 1960). Most USA collections are northern. Records from the southeastern USA are sparse; Sparrow (1932) reported a probable (but sterile) collection of *S. reinschii* (= *S. elongatus*) from North Carolina by J. N. Couch; we find no previous report of *Sapromyces* from Alabama. Because of a predominantly asexual state, it was not possible to definitively determine our specimens to species; however, their morphology—combination of the ovate form of sporangia (cf. Emerson, 1958, his fig. VII, 3; and our Figs. 13-15, 17) and extensive, flocculent thallus, with the smooth, rounded form of apparent, young oogonia—is more consistent with *Sapromyces elongatus* than *S. androgynus* or *S. indicus*. The fact that antheridial branches were not observed (as they probably would have been in a monoecious form like *S. androgynus*) is possibly indicative not only of a diclinous condition (as in *S. elongatus*), but of an organism that may occur in distinct sexual strains (i.e., that is possibly heterothallic, cf. Sparrow, 1932, in discussing “*S. reinschii*”)—and, thus, that is potentially dioecious (occurring as distinct male and female “plants”). Specimens in our collection, remaining in a de facto vegetative state, eventually degenerated in water culture in spite of attempts at culture transfer. Additional finds of *S. elongatus* could confirm its heterothallic nature; however, the fact that Bishop (1940) noted “latent maleness” (ability to eventually initiate antheridial formation) in certain female strains of “*Sapromyces reinschii*” (= *S. elongatus*), maintained in culture, would suggest that homothallism (and monoecism) cannot be entirely ruled out in this species, under all culture or environmental conditions. Also, Sparrow (1960, p. 860) noted that some strains of *S. elongatus* remained sterile, regardless of exposure to other, sexual strains. The fact that sporangia in our specimens maintained an ovate, “juvenile” form (e.g., our Fig. 14)—never fully elongating (cf. Emerson, 1958, his fig. VII, 2) and never observed to form zoospores—could indicate that our specimens represent not only an asexual strain, but one that is predominantly “vegetative” as well.

Unusual Aspects of Morphology (Our specimens): Some hyphal pseudo-cells observed were swollen (Figs. 16, 18, 19) and possessed large, refractive granules (cf. Dick, 1973; see our Fig. 19); these hyphal units can assume odd, uneven shapes (Figs. 18, 19), and could detach from the thallus (or else the thallus may fragment into segments or “pieces,” Fig. 18). Such features suggest not only a depauperate state of the thallus (in less than optimal environmental conditions), but also potential vegetative reproduction by “gemmae” (asexual reproductive bodies). The production of possible vegetative reproductive bodies in *Sapromyces* has seemingly not been previously reported. Additionally, the fact that structures which were apparently oogonia (Fig. 22) initiated formation, but did not develop further (remaining juvenescent), suggests the possibility (discussed, in part, above) that the presence of a male (antheridial) strain of this species may be required in the micro-environment for continued oogonial development (and subsequent oosphere and oospore formation)—a supposition somewhat supported by information in Bishop, 1940 (extending work begun by Jordon, in Weston, 1938), and Sparrow (1960, pp. 859-861). *Sapromyces* is difficult to culture through its life cycle. Emerson (1958) reported a lack of success in determining conditions, in pure culture, that would successfully induce gametangial formation. Gleason and Unestam

(1968), studying terminal respiration (cytochromes) of various Leptomitales, also noted difficulties in culturing *Sapromyces* (*S. elongatus*) under certain conditions (e.g., reduced oxygen tension levels). We suspect that difficulties we encountered in maintaining water cultures (substrate added) over a period of time possibly arose from previous environmental depletion, e.g., reduced oxygen levels, in the initial, natural collection (and thus specimens, already stressed, which were unable to recover satisfactorily).

Growth Form: Growth form is of general interest in genera of the traditional Leptomitales. The terms “monopodial” and “sympodial” were often used to describe thallus patterns. Sparrow (1960) considered *Sapromyces* and *Apodachlya*, for example, to be monopodial (growing by supposed dominance of a main axis). However, Thaxter (1896) seemed to indicate that *Apodachlya* could be sympodial; certainly, *Apodachlya* is more prone to lateral branching than some other Leptomitalean forms (cf. Dick, 1973). Fitzpatrick’s illustration (1930, p. 176) of *Sapromyces androgynus* also suggests possible sympodial growth (e.g., growth by overtopping by lateral braches). Iyengar et al. (1955, p. 143) indicated that thallus growth of *S. indicus* could be sympodial, which seems odd, since they also indicated (p. 140) that its “growth is always terminal.” The problem with terms like monopodial and sympodial (perhaps more clearly used in connection with higher plants and kinds of algae) is that such are difficult to apply with certainty to organisms such as leptomitalean Oomycetes (e.g., *Sapromyces*), which often grow in a somewhat irregular fashion, by an almost yeast-like budding or “pinching,” from a small, usually distal, “papilla-like,” segment of cytoplasm, isolated just beyond a point of constriction—see Dick, 1973, p. 155, fig. 3 of his plate I; compare also our Figs. 12 and 7, and 25 and 17. It can be difficult to say if this budding is strictly terminal (precisely apically polar), or somewhat to one side or other of the “cell” apex—bearing on how “straight” the hyphal filament will ultimately be. In our specimens of *Sapromyces*, a branch or sporangium could be terminal (Figs. 14, 15), both terminal and to the side of the hyphal apex (Figs. 13, 20, 23), or arise at the sides of the apex with no clear terminal structure (Fig. 21). The pattern can be obscured (e.g., in *Sapromyces elongatus*) by multiple budding from an apex, resulting sometimes in an umbel- or whorl-like appearance of sporangia or branches (see descriptive information in Sparrow, 1960, p. 884; and Reinsch, 1878, figs. 1, 2 of his Plate 15; and our Figs. 9 and 24). It becomes more difficult to decipher such in a form like *Rhipidium*, with numerous, almost brush-like branches arising from the surface of a broadened, flattened or irregular apex of a specialized basal cell (cf. Fitzpatrick, 1930, p. 179). It is more meaningful to discuss whether budding of branches or sporangia is generally (not precisely) from the apical (“polar”) region of a “cell” (as in *Sapromyces*, *Araiospora* and, more obscurely, *Rhipidium*) or whether this may also occur from a lateral position; Dick (1973, re: figs. 1, 2 of his Plate I) used the term “nonpolar” for such lateral bud-branching, as in *Apodachlya* (seen rarely in *Sapromyces*, cf. Iyengar et al., 1955, their fig. 12; our Fig. 6). Polar vs. nonpolar development of branches of members of Leptomitales should not be confused with a bipolar development of germinating zoospores of various genera (e.g., *Sapromyces*, *Rhipidium*, *Aqualinderella*; cf. Emerson and Weston, 1967). In any event, growth form (branching pattern) of the Leptomitales is a suitable subject for future study.

Perhaps worthy of further comment—without necessarily implying special phylogenetic meaning—is the supposedly distinguishing growth pattern of *Sapromyces*. This growth form, while fundamentally elongate and distinctly “hyphal” (generally resembling *Leptomitus* and *Apodachlya*, for example), nonetheless involves a basal (attachment) “cell” (as in *Rhipidium*, *Araiospora* and *Mindeniella*). However, this basal unit in *Sapromyces*, though present (e.g., see our Fig. 1), is not distinctly specialized (as compared, for example, with that in *Rhipidium* and *Araiospora*, cf. figs. 66–68 in Fitzpatrick, 1930). The thallus of *Sapromyces* could perhaps be viewed as somewhat intermediate (as regards the breadth of cells and presence or degree of specialization of a basal cell) between seemingly relatively undifferentiated, “filamentous” (or “myceliar”) forms of the Leptomitaceae (*Leptomitus* and *Apodachlya*) and more differentiated or reduced (“monocentric”) forms of the Rhipidiaceae (*Rhipidium*, *Araiospora*, *Mindeniella*, and *Aqualinderella*). Emerson and Weston (1967) suggested that a gradational series of forms appears to exist within the Leptomitales—in which *Sapromyces* might represent a connecting link (cf. Dick, 1973, p. 146) between more “typical” representatives of respective families of

the original order (see also Iyengar et al., 1955, p. 143). However, the reality of *Sapromyces* as an actual connecting link between Leptomitaceae and Rhipidiaceae is yet to be confirmed; more data are needed to justify such a conclusion. Presently, we may simply observe the interesting series of thallus forms within the traditional grouping, Leptomitales, with *Sapromyces* representing a putative, quasi-intermediate form. In any event, this is a group of organisms that invites further comparative morphological and developmental study—in addition, of course, to further ultrastructural and molecular investigations.

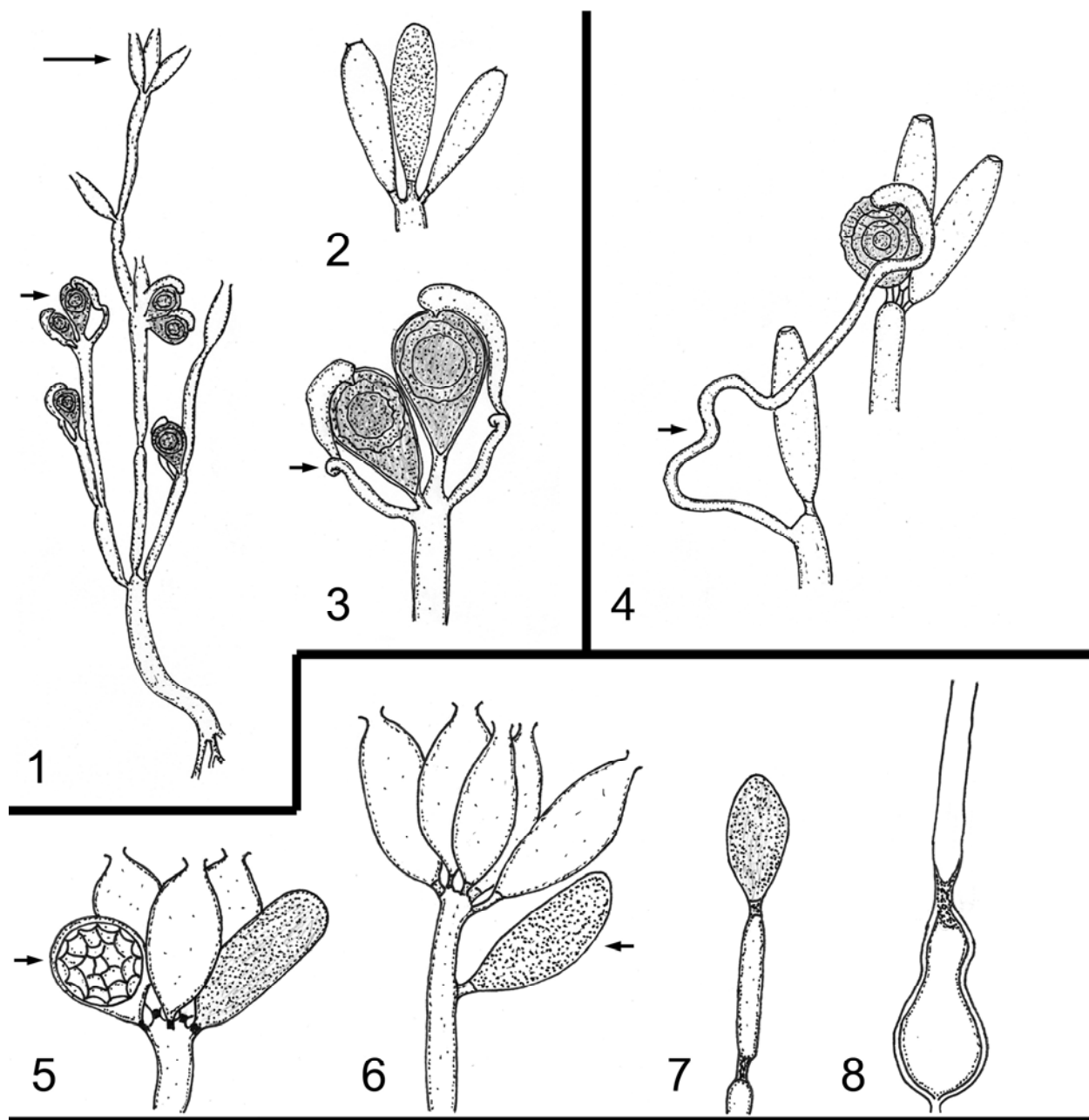
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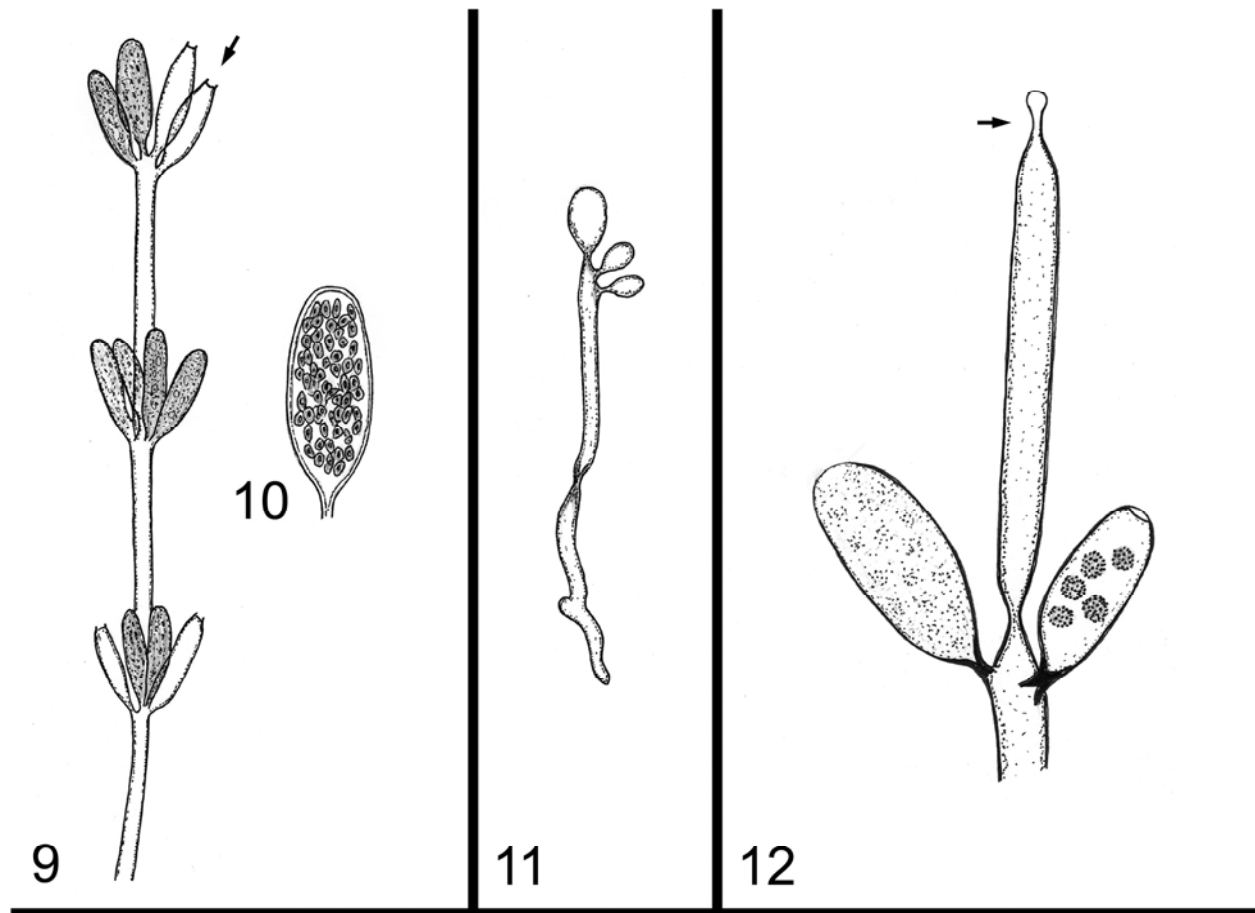
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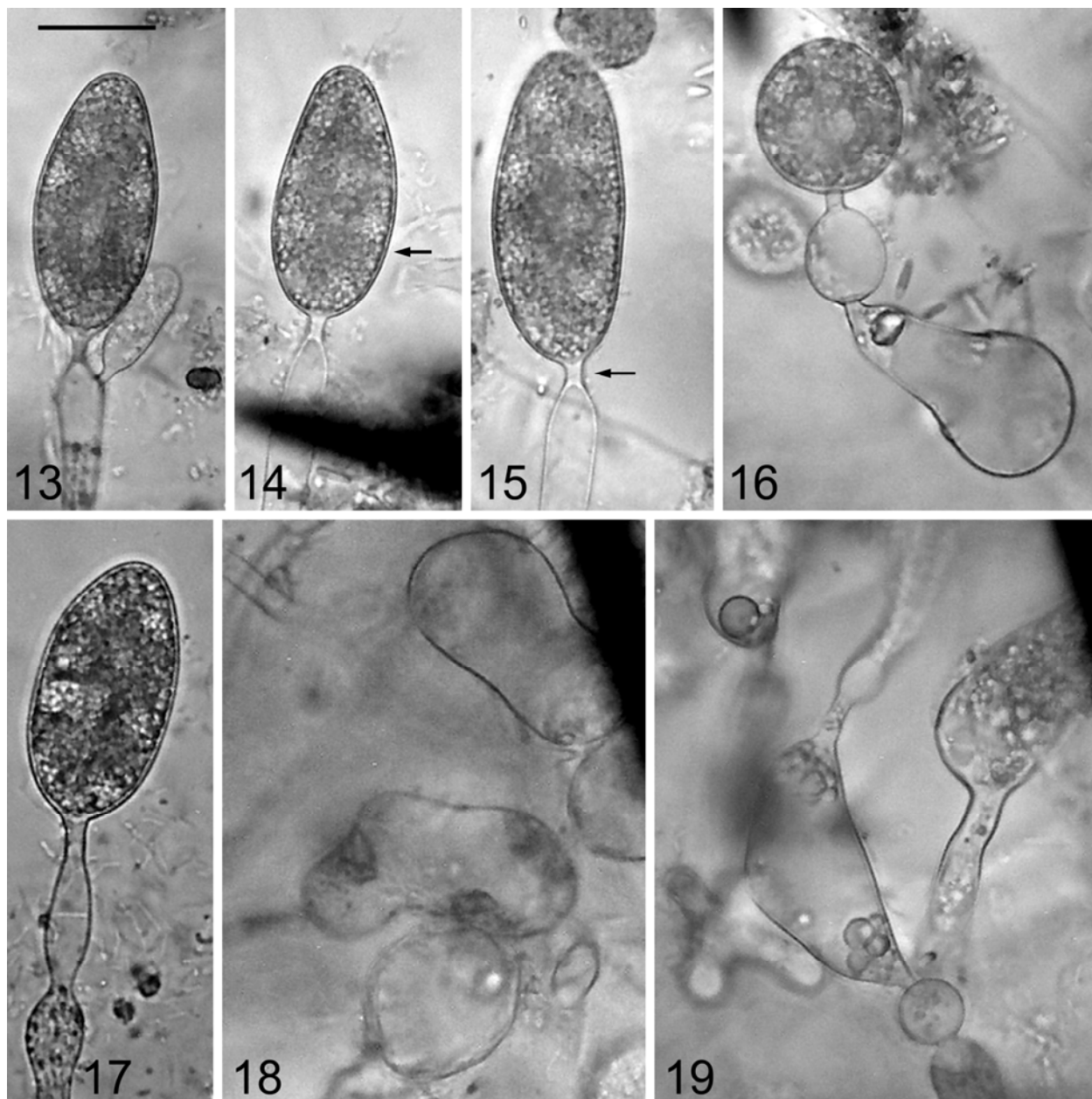
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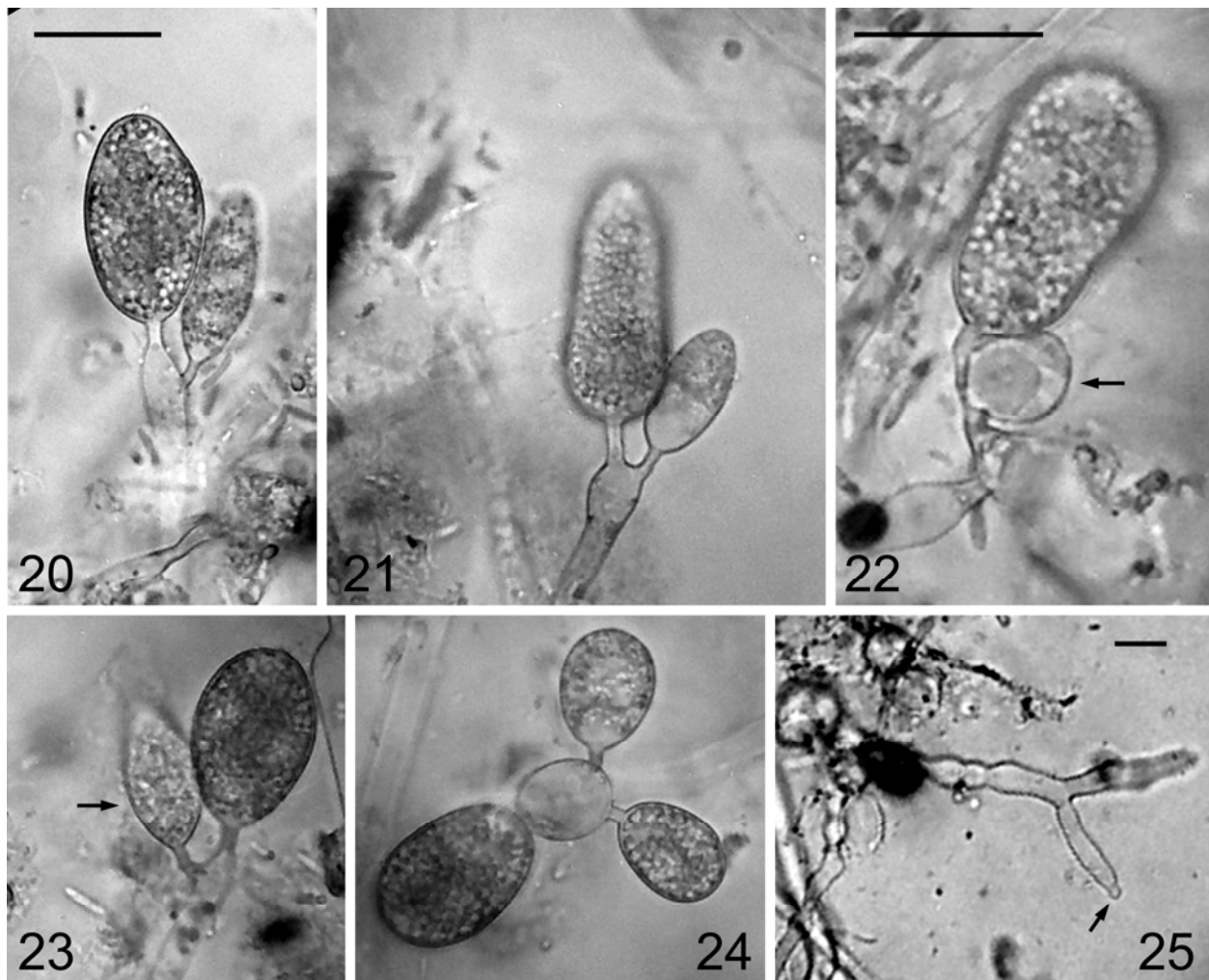
Figs. 1-3: *Sapromyces androgynus* (after Thaxter, 1896): Fig. 1, thallus with sex organs (short arrow), and (mostly emptied) sporangia (long arrow); basal pseudo-cell of thallus relatively undifferentiated, but branched ("holdfast-like") at its base. Fig. 2, "pedicelled" sporangia. Fig. 3, two oogonia and attached antheridia on same parent branch; note characteristic twist (arrow) of antheridial "stalk." **Fig. 4:** *Sapromyces elongatus* (after Sparrow, 1960): antheridium arising from different hyphal branch than oogonium; antheridial "stalk" (arrow) long and winding. **Figs. 5-8:** *Sapromyces indicus* (after Iyengar et al., 1955): Fig. 5, sporangial cluster and an oogonium (arrow); oospore wall, in oogonium, reticulate. Fig. 6, sporangia terminal, but one (arrow) formed from lateral budding. Fig. 7, branch (with sporangium) the result of development by hyphal constriction and budding. Fig. 8, thick-walled, pear-shaped basal "cell."



Figs. 9-10: “*Sapromyces reinschii*” (after Reinsch, 1878; this “species” probably = *S. elongatus*; however, based on only asexual material, the identity of *S. reinschii* has been difficult to confirm): Fig. 9, thallus segment with apparently “whorled” or “umbel-like” arrangements of zoosporangia; these clustered, often stalked (“pedicillate”) sporangia arise by a simple budding process from a generally terminal (terminal at least at the point in time at which the sporangia arose) portion of a hyphal branch. Fig. 10, sporangium with incipient zoospores still contained within; zoospores will eventually be released from a generally circular, apical (initially papilla-like) opening in the apex of the sporangium; this apical “aperture” (see fig. 9, arrow) seems generally consistent in genus *Sapromyces* (compare, for example, fig. 9 with figs. 1, 4, 6 and 12). **Fig. 11:** “*Sapromyces dubius*” (after Reinsch, 1878), a doubtful species of *Sapromyces*; the exact taxonomic disposition of *S. dubius* remains uncertain (it was considered by Sparrow, 1960, to represent a fragment of a *Rhipidium* species, but this is likewise difficult to confirm). **Fig. 12:** Constriction/budding growth in *Sapromyces elongatus* (after Dick, 1973); see sub-terminal constriction (arrow), with small bud of protoplasm arising distally beyond (which will form the next hyphal pseudo-cell, or else a sporangium; compare with the resultant growth by budding in fig. 7, *S. indicus*).



Figs. 13-15, 17: Representative photographs of generally apical sporangia, seen in our collection of *Sapromyces* (tentatively identified as *S. elongatus*); note characteristic, “young,” ovate form of sporangium (e.g., Fig. 14, arrow), and absence of zoospore development, indicative of retention of juvenescent state (probably in response to depleted conditions of original habitat). Characteristic constriction (e.g., Fig. 15, arrow) beneath sporangium, results in “pedicelled” appearance; more or less solid area in constriction (Figs. 14, 15) constitutes “plug” of cellulose. Fig. 17, shows consequence of growth by successive constriction and budding (cf. figs. 7, 12), characteristic of *Sapromyces*; as seen (figs. 7, 17), this may result in production of a sporangium. **Figs. 16, 18, 19:** pseudo-cells of thallus may form unusual, irregular shapes; these may contain large, refractive granules (Fig. 19, bottom and top of cell occupying left-center of photo); such “cells” are possible “gemmae” (vegetative reproductive bodies), separating by thallus fragmentation (Fig. 18). Scale bar (in Fig. 13) = 20 μ m for Figs. 13-19.



Figs. 20-25: Additional photographs of our specimens of *Sapromyces*, illustrating features of interest. Although sporangia were often seen to be solitary and terminal (figs. 14, 15), a number of branches of the thallus may exhibit one to several sporangia at or near the tip, these sometimes occurring in an apparently whorled pattern (Fig. 24, seen more or less in cross-section; see also fig. 9). When, for example, two sporangia are present, a sporangium may be terminal, and a second, lateral to it on the apex (see Figs. 20; 23, arrow; see also Fig. 13); or neither sporangium may quite attain an apical position (Fig. 21). Variation is evident in sporangial shape, from oblate-spheroid when young, to ovate, elliptic or obovate at a later stage (compare all sporangial photographs). Sporangial bases are often constricted, and may become plug-like (even darkened), cf. figs. 5, 12, 13 and 23. In addition to occurrence of sporangia at the sometimes almost “shouldered” apex of a hypha (see figs. 13, 20, 21), an oogonial initial can be observed to occur at the base of a sporangium; this oogonial initial (Fig. 22, arrow) may be distinguished by an almost spherical shape, relatively thin wall, and presence of two distinct regions within (the inner area can develop into ooplasm, the outer into periplasm). Fig. 25: branched thallus with constrictions; see small, terminal constriction and bud of protoplasm (arrow) by which growth occurs (compare with fig. 12). Scale bar (in Fig. 20) = 20 μ m for Figs. 20, 21, 23, 24; bar in Fig. 22 = 20 μ m; in Fig. 25 = 20 μ m.