

The taxa of *Dictyomorpha* (Chytridiomycota, *in praesens tempus*)

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ABSTRACT

Dictyomorpha (initially known, among Chytridiomycetes, as *Pringsheimiella*), an endoparasite of types of ‘water molds’ (e.g. *Achlya*), is relatively unusual in being a heterothallic chytrid. As traditionally recognized, *Dictyomorpha* belongs to Family Olpidiaceae, Order Chytridiales. The genus was long considered monotypic, *D. dioica* the only taxon known. However, an additional variety (*D. dioica* var. *pythiensis*) was eventually described, seemingly based exclusively on occurrence in a different host (*Pythium*). Without explanation, this variety was subsequently elevated (different author) to species. We reviewed the two, putative taxa of *Dictyomorpha* in an attempt to determine whether varietal or specific status is preferable. Based on apparent morphological distinctions evident in existing literature and illustrations, the rank of species is supported, viz. *Dictyomorpha dioica* and *D. pythiensis*. We also consider whether *Dictyomorpha* should remain in Phylum Chytridiomycota, or, rather, if this genus is perhaps more appropriately placed in Phylum Cryptomycota (“Superphylum” Opisthosporidia). Published on-line www.phytologia.org *Phytologia* 99(1): 74-82 (Jan 19, 2017). ISSN 030319430.

KEY WORDS: *Achlya*, aquatic fungi, chytrid, *Dictyomorpha*, endoparasite, *Nucleophaga*, Olpidiaceae, Oomycetes, *Plasmophagus*, *Pringsheimiella*, *Pythium*, resting spores, *Rozella*, sporangia, zoospores.

Dictyomorpha (originally *Pringsheimiella*)—an endobiotic, single-celled genus producing small, posteriorly uniflagellate zoospores—has been considered a member of the Olpidiaceae; this family contains holocarpic forms (simple thallus converting, asexually, entirely to a sporangium), lacking rhizoids (i.e., lacking “vegetative” structures). Although the Olpidiaceae has traditionally been placed in Order Chytridiales (Class Chytridiomycetes), recent placements of some members have indicated other relationships (as will be discussed). The name *Dictyomorpha* (‘net-form’) would seem [incorrectly] to imply a ‘network’ or ‘multicellularity;’ mutual compression of zoosporangia in [sorus-like] clusters in the host (cf. Mullins, 1961; Karling, 1977)—resultant from multiple zoospore infections (cf. Couch, 1939; Karling, 1977)—imparts this illusion. *Dictyomorpha* should not be confused with *Dictyuchus* (name = ‘net-holder’), an unrelated genus [of Oomycetes] in which a single sporangium may contain a network of (its own) zoospore-cysts (cf. Blackwell and Powell, 1999). Karling (1977)—and previously Couch (1939), ref. *Pringsheimiella*—noted that, superficially, *Dictyomorpha* may resemble [perhaps be mistaken for] *Dictyuchus* (until one realizes that the “*Dictyuchus*-like” appearance of *Dictyomorpha* is the result of a combination of the morphology of *Dictyomorpha* and its host, e.g., *Achlya*—and not simply the consequence of morphological development of a single organism).

Dictyomorpha (for many years thought to contain only *D. dioica*) was known as a parasite of *Achlya* (A. “*flagellata*,” cf. Couch, 1939; Mullins, 1961); *D. dioica* is relatively distinct among Chytridiomycota in being heterothallic (apparently existing as morphologically similar, male and female strains). A new variety (*D. dioica* var. *pythiensis*) was later discovered in a species of *Pythium* (Sarkar and Dayal, 1988). *Dictyomorpha dioica* was thought to be morphologically uniform, in spite of recognition of this additional variety (see Sarkar & Dayal, 1988); however, this variety was eventually recognized as a species by Dick (2001) who provided no supporting evidence for his elevation of taxonomic level. The zoospores of *Dictyomorpha*—and its resting spores (these formed as the result of sexual reproduction, by motile gametes seemingly identical to zoospores)—bear resemblance to those of *Rozella*, cf. Mullins (1961). *Rozella* had been considered a genus of Chytridiomycota, but some species

are now classified elsewhere (discussed herein)—raising questions as to correct phylum placement of *Dictyomorpha*. Our study questions the uniformity of *Dictyomorpha*, examines potential taxa in the genus (their ‘rank’), and reconsiders relationships of this genus among Fungi and related organisms.

TAXONOMIC HISTORY OF *DICTYOMORPHA* (Figures 1 - 20)

Dictyomorpha was described as a genus of Chytridiales (Mullins, 1961). Illustration (Fig. 1) of [what turned out to be] sporangia of this organism [in its host, *Achlya*] is, however, traceable to Pringsheim (1860, specimens from Germany). Pringsheim, though, provided no legitimate name for this organism, incorrectly interpreting the motile cells he observed (his plate 22, fig. 5 and plate 23, fig. 3) as a stage (antherozoids) in the life-cycle of *Achlya* [unrelated genus of Oomycetes]. *Achlya* and other Saprolegniaceae do not possess flagellated gametes. Motile cells [actually zoospores] figured by Pringsheim are uniflagellate (flagellum at or toward one pole), Figs. 1,3. Zoospores of *Achlya* and other Saprolegniaceae are biflagellate (*Achlya* is laterally biflagellate). Motile cells do not seem to have been illustrated by Cornu (1872); however, the organism seen by him (similar to that illustrated by Pringsheim) was placed in Cornu’s new genus, *Woronina* (non-chytridiomycetous organism—classified in the Plasmodiophoromycetes, e.g., Alexopoulos, 1962). Sparrow’s (1943, fig. 44A) illustration of the organism seen by Cornu (1872) matches generally with that illustrated by Pringsheim (1860). Couch (1939)—noted in Sparrow (1943)—described ‘Pringsheim’s organism,’ not as a Plasmodiophoromycete, but more correctly as a chytridialean genus—under his proposed name, *Pringsheimiella* (acknowledging Pringsheim’s illustration). Couch (1939), based on collections in North and South Carolina, accurately described zoospores of *Pringsheimiella* as posteriorly uniflagellate. Couch, realizing that *Pringsheimiella* had been known just in its asexual phase, determined *P. dioica* (then the only taxon) to be heterothallic—among the first members of the Chytridiales shown to be so—male and female strains necessary for sexual reproduction (and production of resting spores, Figs. 11-12). Couch noted potential physiological (not morphological) differences between certain strains. Sparrow (1960) recognized *Pringsheimiella* Couch (1939). Mullins (1961) was uncertain that the organisms seen by Pringsheim (1860) and Couch (1939) were the same; however, Karling’s (1977) illustration of this organism compares well with those of Couch and Pringsheim. There is little doubt that Pringsheim’s fig. 1, plate 23, is of sporangia (in *Achlya*) of what would be described as *Pringsheimiella* (Couch, 1939) and *Dictyomorpha* (Mullins, 1961). Mullins was concerned that Pringsheim didn’t observe [the zoospore as having] the lipid body of chytrid zoospores; however, certain of Pringsheim’s illustrations (plate 23, fig. 3) suggest this feature.

Mullins (1961) reviewed the taxonomy/nomenclature of *Pringsheimiella* Couch (1939), concluding the generic name was preoccupied; Mullins indicated that “*Pringsheimiella*” was employed by Höhnelt, in “1919” in vol. “17” of Ann. Mycol., as the name of an alga. Nielsen and Pedersen (1977) noted that Höhnelt’s use of this algal name was actually in 1920 (vol. 18). Regardless, because of Höhnelt’s prior usage, *Pringsheimiella* Couch (1939) is a later homonym (illegitimate). Mullins (1961) supplied a legitimate, substitute name *Dictyomorpha* [*nomen novum*] for *Pringsheimiella* Couch. Mullins re-collected *Dictyomorpha* (Highlands, NC area) and restudied the life cycle—providing additional description and illustrations (including zoospore variation, see Fig. 9), and depositing slide material (additional to that of Couch, re: *Pringsheimiella*) in the UNC herbarium. Still, only one species was recognized in *Dictyomorpha*; this species, named *D. “dioica”* by Mullins (1961), would seem to have been transferred from *Pringsheimiella* (*P. “dioica”*; Couch, 1939). One might assume this species name would be cited “*Dictyomorpha dioica* (Couch) Mullins”—and it is so cited by Karling (1977) and Dick (2001). However, *Index Fungorum* currently (correctly we believe) lists the citation as “*Dictyomorpha dioica* Couch ex Mullins”—doubtless because Couch (1939) provided no Latin diagnosis when he described genus *Pringsheimiella* and species *P. dioica* (relegating Couch to having ‘proposed’ the epithet “*dioica*” rather than legitimately publishing it). Mullins (1961) provided a combined, Latin genus/species

description for *Dictyomorpha/D. dioica*, validating both. Authorship of the name *D. dioica* could, in fact, be cited as either “Couch ex Mullins” or “Mullins” (cf. *International Code...*, Article 46.5).

Pursuant to Mullins (1961), *Dictomorpha* was still thought to contain only *D. dioica*, without sub-specific taxa, until Sarkar and Dayal (1988), based on material from India, described *D. dioica* var. *pythiensis* (see our Figs. 15-20)—occurring in *Pythium aphanidermatum*—automatically creating *Dictyomorpha dioica* var. *dioica* [not mentioned by Sarkar and Dayal]. While attempts by Sarkar and Dayal to infect hosts (including *Achlya*) other than *Pythium aphanidermatum* with *D. dioica* var. *pythiensis* were unsuccessful—var. *pythiensis* being apparently host-specific—they indicated a “close morphological similarity” between their variety and typical *D. dioica*, noting no consistent morphological differences; they felt, therefore, that var. *pythiensis* could not be justified as a new species. Since host specificity was nonetheless considered important in deciphering entities within the Olpidiaceae (Sparrow, 1960; Mullins and Barksdale, 1965), Sarkar and Dayal (1988) deemed varietal recognition appropriate. As noted by Sarkar and Dayal, Mullins and Barksdale (1965) demonstrated an increased host range for *Dictyomorpha dioica* [i.e., var. *dioica*]; successful infections included a total of eight identified (and two unidentified) species of *Achlya* (primarily in Subgenus *Achlya*)—including the original host (*A. flagellata*)—and also, *Thraustotheca clavata*; *Pythium* was not included in their investigation. Questionable evidence from early literature (Pringsheim, 1860) suggested that *D. dioica* may have occurred in *Saprolegnia* (cf. Mullins, 1961); however, *Saprolegnia* isolates tested (Mullins and Barksdale, 1965) were immune to such infection. The “*Saprolegnia*” identified by Pringsheim (1860, his plate 22) was apparently a mixture of *Achlya* and *Dictyuchus* (the latter not involving *Dictyomorpha*).

In a nomenclatural summary, Dick (2001)—placing *Dictyomorpha* in Family Rozellopsidaceae, Order Rozellopsidales (Order “*insertae sedis*”)—recognized two species, “*Dictyomorpha dioica* (J. N. Couch) J. T. Mullins” and “*Dictyomorpha pythiensis* (N. Sarkar & R. Dayal) M. W. Dick, stat. nov.” Proper author citation of *D. dioica* [i.e., Couch ex Mullins] has already been discussed. Of concern is Dick’s (2001) recognition of var. *pythiensis* (Sarkar & Dayal, 1988) at species level, since Dick offered no justification for this status change (no distinguishing features of the taxa were noted). As we mentioned, Sarkar and Dayal had recognized “*pythiensis*” as a variety of *D. dioica* (not a separate species) because “*pythiensis*” was based, by them, on host specificity—occurring in *Pythium*, not *Achlya*—rather than on morphology. There was thus a need to determine if there are in fact morphological differences between the two alleged taxa within *Dictyomorpha*.

AT WHICH RANK SHOULD THE TAXA OF *DICTYOMORPHA* BE RECOGNIZED?

The question hence remains: Should the two ‘entities’ (var. *dioica* and var. *pythiensis*) within *Dictyomorpha dioica* be considered varieties (Sarkar and Dayal, 1988) or species (Dick, 2001)? Dick presented no evidence for his decision to recognize *Dictomorpha dioica* and *D. pythiensis* as distinct species. If there is no reliable difference between these ‘taxa’ other than host occupied (implied by Sarkar and Dayal, 1988), varietal status would be (at most) the appropriate taxonomic category. Even if this ‘host difference’ is accompanied by only one, minor, morphological difference, varietal status is perhaps still preferable. But if there is separation of taxa by host infected *and* by several morphological differences, species recognition should be considered. Reexamination of literature (including illustrations) was essential to this determination, since living material is not currently available; future collection of *Dictyomorpha* is obviously important to further understanding of the genus.

Comparison of illustrations of [what eventually came to be known as] *Dictyomorpha dioica* in Pringsheim (1860), Couch (1939), Mullins (1961), Karling (1977) and Sarkar and Dayal (1988)—reference our Figs. 1-20—suggests (in addition to occurrence in mutually exclusive hosts) that morphological differences do exist between “var. *dioica*” and “var. *pythiensis*.” Eight (8) potential differences we noted in these illustrations—not always congruent with statements in text of the articles—

include: **1.** Shape of zoosporangium—“*dioica*,” typically spherical (Figs. 1-2), except as altered by mutual compression; “*pythiensis*,” generally oval (Figs. 17-18). **2.** Sporangial discharge “tube”—“*dioica*,” merely a papilla (Figs. 6-7); “*pythiensis*,” occurring as an actual (sometimes somewhat elongated) tube (Figs. 16-18). **3.** Number of sporangia in host cell—“*dioica*,” often numerous (Fig. 1); “*pythiensis*,” ranging from one to eight, illustrated (Sarkar and Dayal, 1988) as six or fewer (Figs. 17-18). **4.** Location of sporangia in host—“*dioica*,” occurring in vegetative (often distal/apical) portions of host-hyphae (Figs. 1,2,6); “*pythiensis*,” occurring at various points in vegetative hyphae and, notably, in oogonia (Figs. 17-18). **5.** Sporangial wall—“*dioica*,” relatively thin and pliable (Fig. 7); “*pythiensis*,” firmer and more definite in shape (Figs. 17-18). **6.** Zoospores—“*dioica*,” illustrated (cf. Fig. 3) as typically somewhat elongated (Pringsheim, 1860) or irregular (spherical to elongate, e. g., Mullins, 1961; Karling, 1977); “*pythiensis*,” illustrated (cf. Fig. 15) as essentially spherical (Sarkar and Dayal, 1988, though stated by them to be elongate). **7.** Resting-spore outer wall—“*dioica*,” roughened, undulate, reticulate, or obscurely spiny (Figs. 11-14); “*pythiensis*,” more distinctly spiny (Fig. 20), although the spines are typically small. We note that Karling (1977) illustrated (see, for example, fig. 36 of his plate 8) the outer resting-spore wall of ‘typical’ *D. dioica* as more obviously (though still minutely) spiny than did either Couch (1939) or Mullins (1961). **8.** ‘Extra’ structure (‘compartment’) surrounding the already double-walled resting spore(s)?—“*dioica*,” one to several resting spores contained (often loosely) in a sometimes thick-walled, polygonal to square or rounded, extra ‘cell’ or ‘compartment’ (Figs. 11,12,14) produced by the host (illustrated: Couch, 1939; Mullins, 1961; Karling, 1977); “*pythiensis*,” no extra ‘host compartment’ surrounds resting spores, though host-hyphae may form septa (Fig. 20) in response to infection (cf. Sarkar and Dayal, 1988).

Certainly, not all characters are distinguishable between “*dioica*” and “*pythiensis*.” For example: Zoosporangial, and resting-spore, diameters of “*dioica*” were indicated (respectively) to be 15 to 20 μm , and 15 to 17 μm (Mullins, 1961); for *pythiensis*, these same parameters were (respectively) observed at 12 to 20 μm , and 14.95 to 18.95 μm (Sarkar and Dayal, 1988). Regardless of precise form, the small zoospores of the two taxa are also of similar dimensions (ca. 3 μm ; cf. Couch, 1939; Mullins, 1960; Sarkar and Dayal, 1988). The resting spores (other than degree of ‘spiny’ appearance of the outer wall) are not only similar between the two taxa of *Dictyomorpha*, but reminiscent as well of the resting spores of *Rozella* (to which *Dictyomorpha* may be related; cf. Mullins, 1961, p. 386, last paragraph).

Characters (whether potentially distinguishing or not) perceived through study of literature are subject to further investigation should live material of *Dictyomorpha* become available. Regardless, sufficient morphological differences seem evident in various illustrations—in consort with delimitation by host infected—to support recognition of the varieties of *Dictyomorpha dioica*—*D. dioica* var. *dioica* and *D. dioica* var. *pythiensis* (Sarkar and Dayal, 1988)—as separate species (Dick, 2001, although Dick gave no explanation for this change in taxonomic status). We thus accept (duly noting here proper authorship) two species within *Dictyomorpha*: *D. dioica* J. N. Couch ex J. T. Mullins (1961) and *D. pythiensis* (N. Sarkar & R. Dayal) M. W. Dick (2001). We cannot, though, concur with Dick’s inclusion of *Dictyomorpha* in the Rozellopsidaceae (Rozellopsidales); this category contains biflagellate forms, e.g., *Rozellopsis*. Zoospores of *Dictyomorpha* are definitely uniflagellate (Couch, 1939; Mullins, 1961; Karling, 1977; Sarkar and Dayal, 1988), cf. Figs. 3,8,9,15.

POSSIBLE SYSTEMATIC RELATIONSHIPS OF GENUS *DICTYOMORPHA*

Dictyomorpha—traditionally placed in the order Chytridiales [class Chytridiomycetes, phylum Chytridiomycota]—was considered a member of the family Olpidiaceae (simple, holocarpic forms lacking rhizoids). The Olpidiaceae included such seemingly similar genera as: *Olpidium*, *Olpidiomorpha*, *Rozella*, *Plasmophagus*, *Nucleophaga* and *Sphaerita* (cf. Sparrow, 1960; Karling, 1977). But molecular information has shed new light upon relationships of some Olpidiaceae. For example, certain species of *Olpidium* place within the clade of Zygomycetes (James et al., 2006); and, species of both *Rozella*

(Karpov et al., 2014) and *Nucleophaga* (Corsaro et al., 2014) have relationships within phylum Cryptomycota (superphylum Opisthosporidia). Bearing, as it does, morphological similarity (of zoospores and resting spores) to *Rozella* (cf. Mullins, 1961; Karling, 1977), *Dictyomorpha* could conceivably place in the Cryptomycota, rather than the Chytridiomycota; just how closely *Dictyomorpha* is related to *Rozella*, remains to be determined. We do note that in *Dictyomorpha*, in contrast to *Rozella*, the sporangial walls are readily distinguishable from the wall of the host (cf. Mullins, 1961, p. 386). However, only molecular/genetic analysis will answer ultimate questions of generic and phylum relationships. The puzzle of the systematic relationship of *Dictyomorpha* is, in fact, quite similar to that of *Plasmophagus* (Blackwell et al., 2016). Unfortunately, these obligately parasitic organisms are not generally available in culture collections—nor may they typically be cultured in the absence of their hosts (cf. Mullins, 1961; Mullins and Barksdale, 1965; re: *Dictyomorpha dioica*)—rendering molecular analysis elusive. Future collecting of such organisms—so that molecular analyses will have at least the possibility of being performed—is essential to ultimate resolution of systematic problems. There is continuing need for broad surveys of “hydromycoflora”—such as that of Czczuga (1995) in north-east Poland—to “enrich our knowledge of biology of many aquatic fungi species.” *Dictyomorpha dioica* was indeed found by Czczuga, in one of 31 lakes sampled (the host for this organism, however, was not indicated).

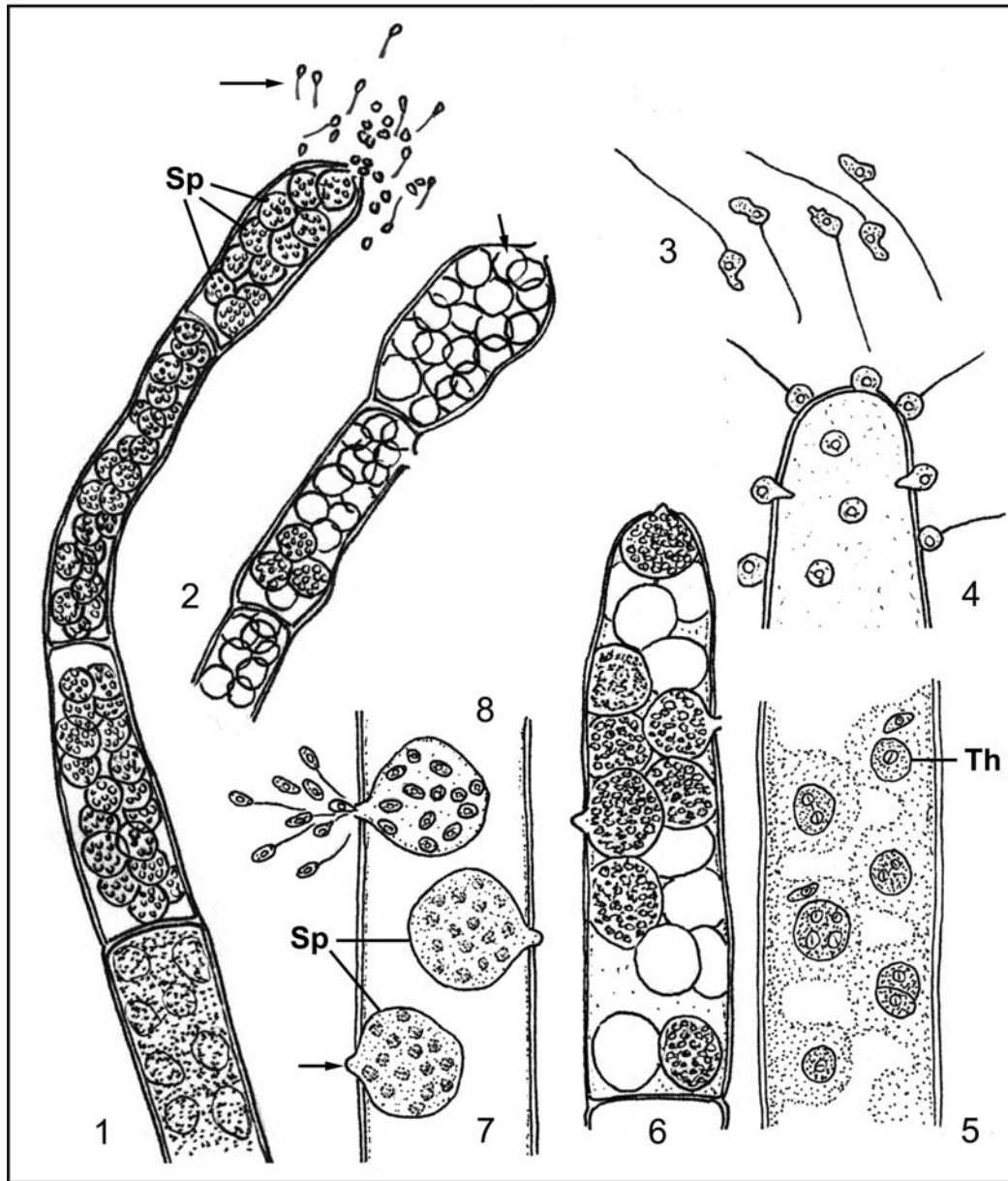
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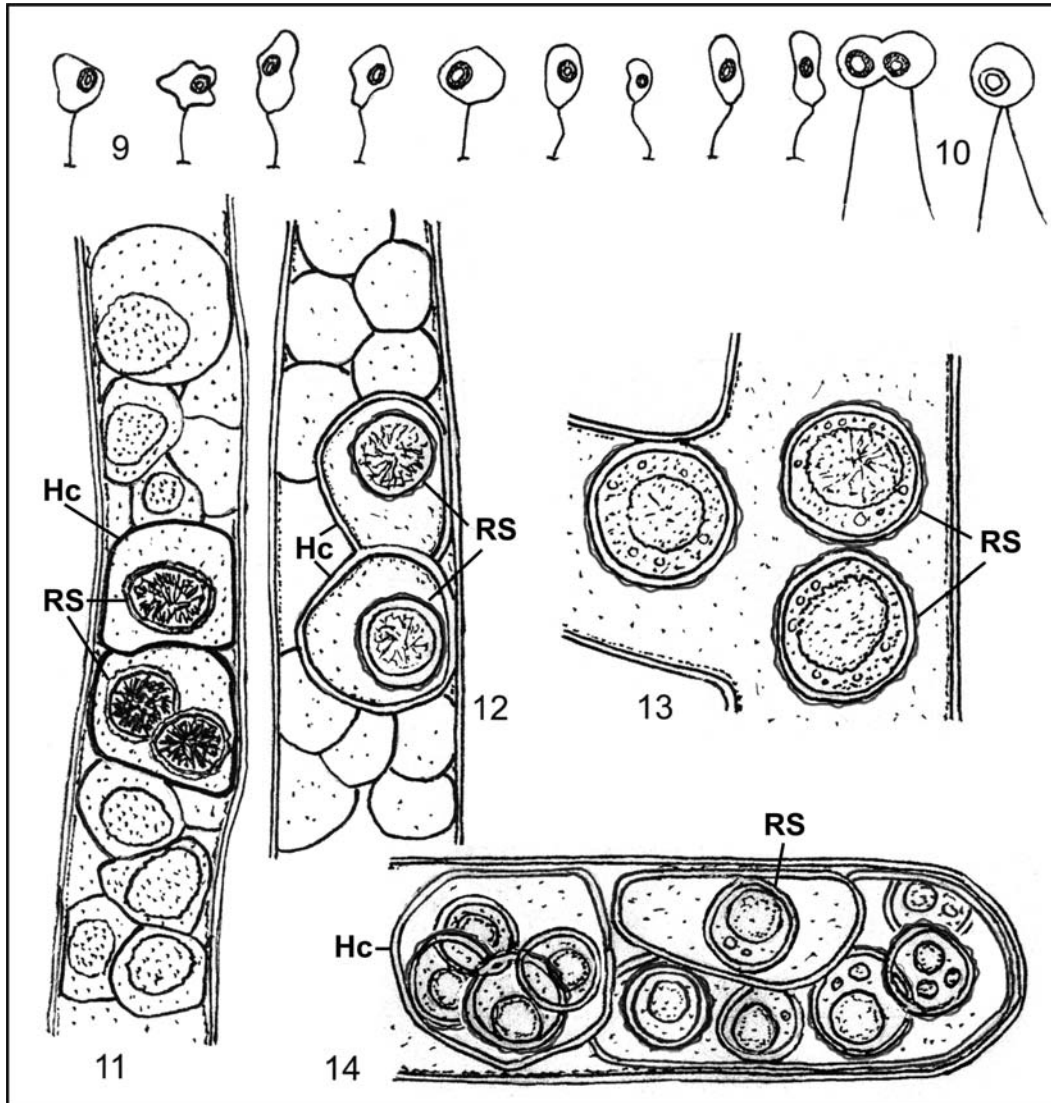
LITERATURE CITED

- Alexopoulos, C. J. 1962. *Introductory Mycology* (2nd ed.). Wiley; New York, London and Sydney.
- Blackwell, W. H., P. M. Letcher and M. J. Powell. 2016. Reconsideration of the inclusiveness of genus *Plasmophagus* (Chytridiomycota, *posteris traditus*) based on morphology. *Phytologia* 98: 128-136.
- Blackwell, W. H. and M. J. Powell. 1999. Taxonomic summary and reconsideration of the generic concept of *Dictyuchus*. *Mycotaxon* 73: 247-256.
- Cornu, M. 1872. Monographie des Saprolegniées; étude physiologique et systématique. *Ann. Sci. Nat. Bot.*, Sér. 5, 15: 1-198, pls. 1-7.
- Corsaro, D., J. Walochnik, D. Venditti, K. D. Müller, B. Hauröder and R. Michel. 2014. Rediscovery of *Nucleophaga amoebae*, a novel member of the Rozellomycota. *Paristol. Res.* 113: 4491-4498.
- Couch, J. N. 1939. Heterothallism in the Chytridiales. *J. Elisha Mitchell Soc.* 55: 409-414, pl. 49.
- Czczuga, B. 1995. Hydromycoflora of thirty-one lakes in Elk Lake District and adjacent waters with reference to the chemistry of the environment. *Acta Mycol.* 30: 49-63.
- Dick, M. W. 2001. *Straminipilous Fungi*. Kluwer Academic; Dordrecht, Boston and London.
- Höhnelt, F. von. 1920. Mykologische fragmente. *Annales Mycologici* 18: 71-98.
- Index Fungorum (currently updated online database of fungal names). “www.indexfungorum.org”
- International Code of Nomenclature for algae, fungi, and plants. 2012. IAPT, Melbourne Code. “www.iapt-taxon.org/nomen/main.php”
- James, T. Y., P. M. Letcher, J. E. Longcore, S. E. Mozley-Standridge, D. Porter, M. J. Powell, G. W. Griffith and R. Vilgalys. 2006. A molecular phylogeny of the flagellated fungi (Chytridiomycota) and description of a new Phylum (Blastocladiomycota). *Mycologia* 98: 860-871.
- Karling, J. S. 1977. *Chytridiomycetarum Iconographia*. J. Cramer; Vaduz, Liechtenstein; and Lubrecht & Cramer; Monticello, New York.

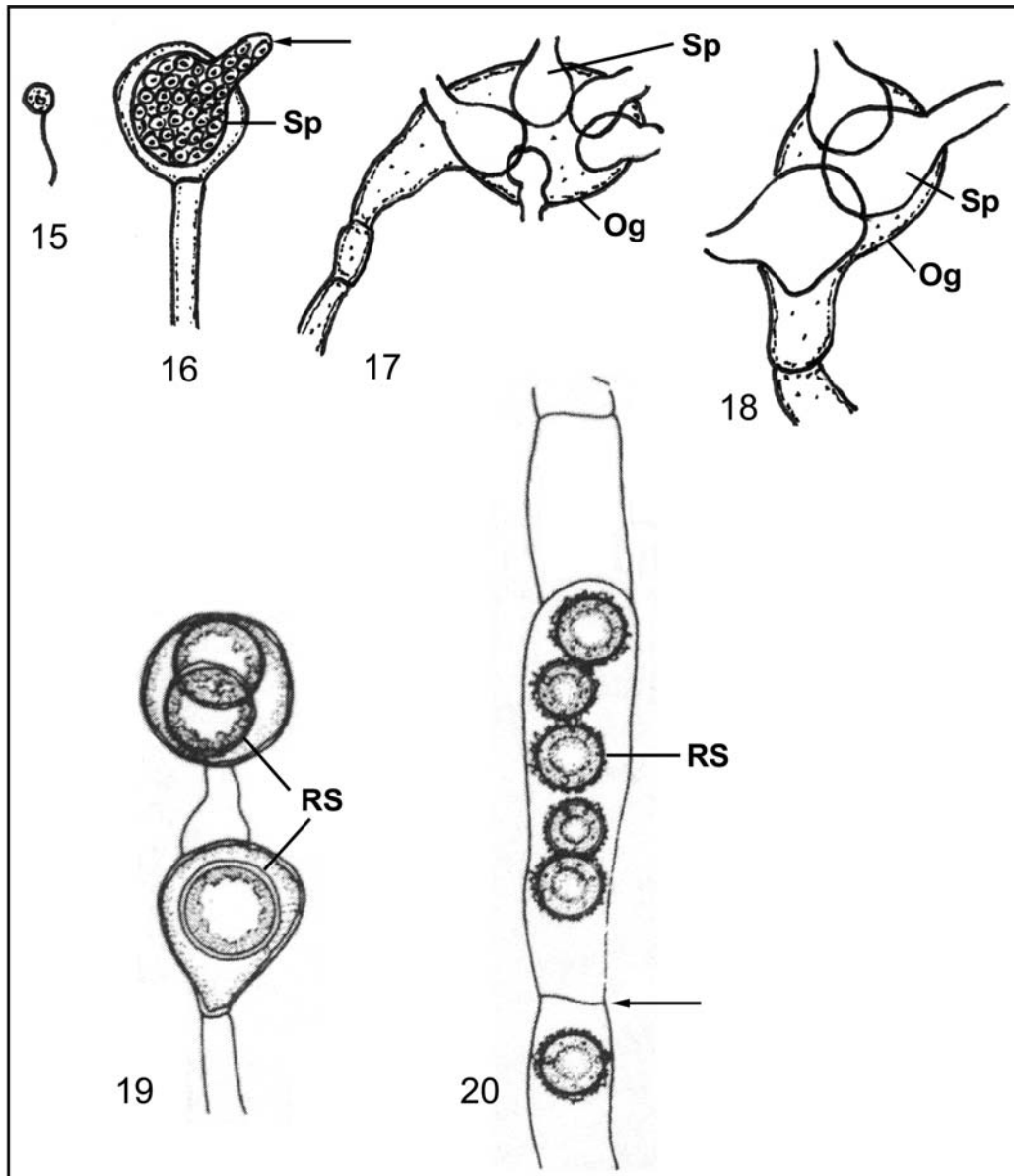
- Karpov, S. A., M. A. Mamkaeva, V. V. Aleoshin, E. Nassonova, O. Lilje and F. H. Gleason. 2014. Morphology, phylogeny, and ecology of the aphelids (Aphelidea, Opisthokonta) and proposal for the new superphylum Opisthosporidia. *Front. Microbiol.* 5: 112. doi: 10.3389/fmicb.2014.00112.
- Mullins, J. T. 1961. The life cycle and development of *Dictyomorpha* gen. nov. (formerly *Pringsheimiella*), a genus of the aquatic fungi. *Amer. J. Bot.* 48: 377-387.
- Mullins, J. T. and A. W. Barksdale. 1965. Parasitism of the chytrid *Dictyomorpha dioica*. *Mycologia* 57: 352-359.
- Nielsen, R. and P. M. Pedersen. 1977. Separation of *Syncoryne reinkei* nov. gen., nov. sp. from *Pringsheimiella scutata* (Chlorophyceae, Chaetophoraceae). *Phycologia* 16: 411-416.
- Pringsheim, N. 1860. Beiträge zur Morphologie und Systematic der Algen. IV. Nachträge zur Morphologie der Saprolegnieen. *Jahrb. Wiss. Bot.* 2: 205-236, pls. 22-25.
- Sarkar, N. and R. Dayal. 1988. A new variety of *Dictyomorpha dioica* (Couch) Mullins. *Proc. Nat. Acad. Sci. India* 58 (Sec. B, III): 403-406.
- Sparrow, F. K. 1943. *Aquatic Phycomycetes, Exclusive of the Saprolegniaceae and Pythium*. Univ. Michigan Press, Ann Arbor; Humphrey Milford, London; and Oxford Univ. Press.
- Sparrow, F. K. 1960. *Aquatic Phycomycetes*, 2nd revised edition. Univ. Michigan Press, Ann Arbor.



Figs. 1-8: *Dictyomorpha dioica*. 1: Sporangia (Sp), generally spherical in form, in host (*Achlya*); zoospores released at tip of host filament (arrow). 2: Discharged sporangia (arrow). 3: Variable (often elongate) shape of posteriorly uniflagellate zoospores. 4: Zoospores infecting host (*Achlya*) by their apical ends. 5: Young thalli (Th) developing in host. 6: Maturing, and also empty, sporangia inside apical portion of host hypha. 7: Maturing sporangia (Sp); note exit-papilla (arrow). 8: Mature sporangium; zoospores released, through papilla, laterally from host filament. Figs. 1-3 after Pringsheim (1860), 4-5 after Mullins (1961), 6 after Couch (1939) and Mullins (1961), 7-8 after Mullins (1961).



Figs. 9-14: *Dictyomorpha dioica*. **9:** Range of zoospore form. **10:** 'Zoospores' fusing, as gametes, to form zygote. **11-14:** Resting spores (RS) in various maturation stages (in hyphae of host, *Achlya*); note 'extra cells' ('host compartments' = Hc), each surrounding one to several resting spores (Figs. 11, 12, 14); wall of 'host compartments' sometimes thickened (12); outer resting-spore wall roughened, reticulate or 'undulate' (11-12), sometimes sub-spiny (13). Figs. 9-10 after Mullins (1961), 11-12 after Couch (1939), 13 after Mullins (1961), 14 based generally on Couch (1939) and Karling (1977), among others.



Figs. 15-20: *Dictyomorpha pythiensis*. **15:** Zoospore. **16:** Sporangium (Sp) in host (*Pythium*), exit-tube forming (arrow). **17-18:** Emptied sporangia (Sp) in host oogonium (Og); sporangia generally oval, exit-tubes persistent. **19:** Resting spores (RS) in host oogonia. **20:** Resting spores (RS), inside host hypha, exhibiting minutely but distinctly spiny walls; special 'host compartments' (potentially enclosing resting spores) lacking, but extra hyphal septa may form (arrow). Figs. 15-20 after Sarkar and Dayal (1988).