

A review of genus *Megachytrium* Sparrow (Chytridiomycota) and its primary host *Elodea canadensis* (Monocotyledoneae, Hydrocharitaceae)

Will H. Blackwell and Martha J. Powell

Biological Sciences, The University of Alabama, Tuscaloosa, AL 35487, USA
wblackwell70@gmail.com

ABSTRACT

Megachytrium is affirmed to be a monotypic genus (*M. westonii* Sparrow, the only known species), distinct from other genera of Chytridiomycota. *Megachytrium* has a robust, ‘undulant,’ polycentric thallus with intermittent swellings that can develop into either sporangia (which may possess short, operculate discharge-tubes) or resting spores which function as prosperangia (giving rise to external sporangia). The posteriorly uniflagellate zoospores possess a distinct, central globule, and are clearly chytridiaceous in character. Relationships for *Megachytrium* have been suggested with several chytrid orders; among these, and based on where putatively related genera have been placed, the Cladochytriales seem the best suggestion for systematic placement—an ‘assignment,’ though, not yet confirmed by molecular-sequence or ultrastructural study. The only known host for *Megachytrium* for many years was water-weed, *Elodea canadensis*. ‘Alternative’ generic names for *Elodea* (e.g., *Anacharis*) have caused confusion; eventually, though, *Elodea* became confirmed as the correct name. In relatively recent times, *Megachytrium* was also found on decaying material of *Myriophyllum verticillatum*. Further collection and study of *Megachytrium*—i.e., developmental, ultrastructural and molecular investigations—should provide useful additions to knowledge of Chytridiomycetes. *Published online www.phytologia.org Phytologia 103(1): 5-9 (March 22, 2021). ISSN 030319430.*

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Megachytrium is a rarely found, chytridiaceous parasite of *Elodea canadensis* (water-weed). Unresolved questions remain concerning the systematic position of *Megachytrium* among Chytridiomycota, i.e., the order/family in which it should be placed. There has seemingly been no molecular (or ultrastructural) study by which to substantiate one suggested systematic placement versus another. There are long-standing questions concerning the correct generic name of its host; formal names other than *Elodea* have often appeared in the literature; it has also been uncertain whether *Elodea* is the only host, and the extent to which *Megachytrium* is primarily parasitic as opposed to being weakly parasitic or saprotrophic on senescent leaves. To date, there is only one known species of *Megachytrium*, *M. westonii* Sparrow. Concerning authentication of name *Megachytrium* (and its single species), two references (Sparrow; 1931, 1933) are sometimes given (e.g., Karling, 1977); it was necessary to determine which of these was, nomenclaturally, the validating publication. Sparrow’s (1943, 1960) later accounts of *Megachytrium* are extensive summaries of previous knowledge, some additional discussion being provided. It is surprising that *Megachytrium* has received little taxonomic attention and is relatively poorly known (doubtless related to limited collecting), since most putative relatives have received molecular, and other recent, study; it is further surprising because *Megachytrium* develops an extensive thallus-complex, overwhelming (potentially covering, pervading) the host-substrate with this (extra- then intra-matrical) thallus; its presence should be perceivable.

Money (2014) lamented that many organisms discussed in Sparrow’s (1960) ‘phycomycete’ compendium (still of enormous value to ‘chytridologists’) have been ‘lost’ to science—i.e., not found in

recent decades, or even since initial description. *Megachytrium* was selected by Money as an example of such a ‘lost’ taxon. Here, we seek to bring [attention to] *Megachytrium* ‘back to life.’ The purposes of our paper are: to review and update the taxonomic history of *Megachytrium*; to ascertain if taxa additional to *M. westonii* exist; to confirm the correct generic name of its host (*‘Elodea’*); to determine if other hosts (or substrates, if it is saprotrophic) have been found; and to assess systematic relationships, in the absence of molecular and ultrastructural data. Collection of this interesting genus should be encouraged; it may not be as rare as thought, and we discuss an additional report of its occurrence. To avoid name confusion, genus *Megachytrium* (here considered) should not be mistaken for *Macrochytrium* (cf. Blackwell and Powell, 2020), a different chytrid with a somewhat similar name.

TAXONOMIC HISTORY OF *MEGACHYTRIUM*

There is apparent inconsistency in the literature on the date of validation of the name *Megachytrium* (cf. Hawksworth et al., 1983; Czeuczuga et al., 2005). This genus name and the species name *M. westonii* first appeared in the literature in Sparrow (1931), in what was intended by Sparrow as a preliminary note; Sparrow nonetheless provided (a purpose of his published note) a formal diagnostic description of the genus and also a diagnosis of the species. Although Sparrow did not include a Latin diagnosis for either (descriptions published only in English), these names stand as valid, since the rule requiring a Latin diagnosis did not become a requirement until January 1, 1935 (cf. ICNAFP). Sparrow (1933), in expanded discussion of *Megachytrium*, repeated (for convenience) the diagnoses for the genus and species—handy, but nomenclaturally irrelevant—the official date of original publication standing as 1931. Sparrow (1943) provided a full morphological account (to the extent of what was known) of *Megachytrium* in his first addition of *Aquatic Phycomycetes*; a similar account (minor adjustments in discussion) was given in his revised edition of this work (1960); in both, the figures illustrated are from his 1933 paper—showing the stout, branched, polycentric thallus, with (presumably operculate) sporangia, variable in shape. Sparrow’s (1933) figures are apparently the only illustrations of *M. westonii* drawn from nature. *Megachytrium* seems to have been known (at least through this time period) just from its original collecting site: ‘Fall Creek, Forest Home, Ithaca, New York’ (Sparrow 1931, 1933)—merely, more generally, listed later (Sparrow, 1943, 1960) as from the ‘United States.’ Sparrow (1933) briefly considered a congeneric relationship between *Protomyces radicolus* Zopf—a root-rot parasite of *‘Stiftia’* (= *Stiftia*, Asteraceae)—and *Megachytrium westonii*, but dismissed this idea after further examination of morphological/host evidence; *Protomyces* was eventually determined to be quite unrelated (not a chytrid, in fact). Sparrow, rightly, concluded that *Megachytrium* is monotypic (as he continued to do, 1943, 1960 and 1973); no additional taxa were noted by Longcore (1996), and we have found none published since that point.

MORPHOLOGY, LIFE CYCLE (descriptive information on genus and its one species combined)

Megachytrium has a coarse (‘mycelial’), polycentric, eucarpic thallus which was observed to be epibiotic on, and subsequently endobiotic in, its host (*Elodea*, ‘water-weed’)—of which it can be substantially destructive (causing discoloration and deterioration). The ‘hyphae’ of *Megachytrium* are tubular (contents finely granular, often refractive), occasionally septate (cross-walls thin), branched, sometimes somewhat ‘wavy’ in outline, and can be relatively broad (sizes, though, usually ranging from 3–7 µm in diameter). The thallus, often vacuolate, may become profuse; anastomosis between branches can occur, resulting in broader, ‘fused,’ hyphal areas and an ‘interlocking’ appearance; there is, however, no evidence of attenuation of hyphae into rhizoids. Subsphaeroidal or pyriform, swollen areas along the hyphae can develop into either sporangia or resting spores. The usually intercalary sporangia (sometimes ‘terminal’ on short, lateral branches) are spherical to ovate/ellipsoid or pyriform or clavate, often somewhat irregular, 15–50 µm long, 10–30 µm in diameter, potentially sub-apophysate, and a given sporangium can develop a short, variable discharge tube (sometimes merely papilla-like) which will typically form a small (3–5 µm), convex ‘operculum’ apically; the sporangial wall is thin, colorless and smooth; sporangial proliferation may occasionally occur. Zoospores are completely formed within the sporangium, and are chytridiaceous in

their features; they are spherical and approximately 5 μm in diameter; they develop a rather long, posterior, whiplash flagellum and typically exhibit a centrally placed, hyaline but refractive [lipid] globule; they are variable in number, and escape following dehiscence of the operculum; the zoospore germ-tube is branched, tips blunt and slightly swollen. Resting spores are usually intercalary, broadly ovoid, have a somewhat thickened wall, and are 20 by 15 μm ; resting spores exhibit truncated ends (flattened connections to other cells or other portions of the hypha) and usually possess globular contents; they were observed to function (without requiring a dormant period) as ‘prosporangia’—a resting spore germinates to produce an external sporangium, which tends to be smallish but usually possesses an operculum—the resting-spore wall is partially assimilated during sporangial production (post-germination resting spores are hyaline in appearance). Thallus development has not been extensively studied, remaining incompletely known (stages are difficult to observe within opaque host-tissue such as *Elodea*); such studies, though, can be useful to biological and systematic understanding of chytrids (Blackwell et al., 2006). It is not known, for example, precisely how the initially extramatrically-growing *Megachytrium* thallus gains entrance into its host when becoming intramatricial. It is known, though, that early growth within the host often follows a path corresponding to junctures of cell-walls [apparently through the middle lamella]; this suggested to Sparrow (1960) some sort of ‘pectin relationship’ [pectinase activity by *Megachytrium*?]. **Note on illustrations:** We here provide no illustration of *Megachytrium*, since this would involve merely copying drawings from other sources. For reference, see illustrations of *Megachytrium* in either Sparrow (1943; Fig. 25, A and B) or Sparrow (1960; Fig. 37, A and B). A useful, interpretive drawing of life-cycle features of *Megachytrium* is in Karling (1977; Plate 113, Figs. 1-6).

POSSIBLE SYSTEMATIC RELATIONSHIPS OF *MEGACHYTRIUM*

Sparrow (1931) suggested a possible systematic connection of *Megachytrium* to Hyphochytriomycetes (Hyphochytriales) such as *Hyphochytrium infestans*—based on general similarity of the polycentric thallus. Sparrow (1943) postulated *Megachytrium* might be an ‘operculate counterpart’ to [the inoperculate] *Hyphochytrium*; Sparrow (1960) recast this statement, i.e., that *Megachytrium* might be a ‘chytridiaceous counterpart of the anteriorly flagellate *Hyphochytrium*.’ His latter assessment presaged understanding that Hyphochytriomycetes—with an anterior, ‘insel-type’ of flagellum—were distinct from Chytridiomycetes, these possessing a posterior, ‘whiplash’ flagellum; see historical discussion (Blackwell and Powell, 2020) noting closer relationship of Hyphochytrids with ‘Pseudofungi’ (e.g., Oomycetes) than with true Chytridiomycetes. Sparrow (1943, 1960) placed *Megachytrium* in family Megachytriaceae (order Chytridiales) along with genera *Nowakowskiella* and *Septochytrium*—a grouping of chytridiaceous forms with polycentric thalli and allegedly operculate sporangia, occurring saprotrophically on ‘vegetable’ [cellulosic] debris (or possibly initially parasitically, e.g., *Megachytrium*). *Megachytrium* was distinguished in this group by thallus-branches which do not taper distally to the extent of forming rhizoids (see also Sparrow, 1973, p 103).

Karling (1977) did not believe that separation of polycentric genera with operculate sporangia from those with inoperculate sporangia was justified, and considered family Cladochytriaceae to include: *Cladochytrium*, *Physocladia*, *Nowakowskiella*, *Amoebocytrium*, *Polychytrium*, *Septochytrium*, *Megachytrium* and *Coenomyces*. The Cladochytriaceae were eventually recognized as an order, Cladochytriales (Mozley-Standridge et al., 2009); unfortunately, *Megachytrium* could not be found for study in that investigation; also, one or more genera of Cladochytriales were moved elsewhere, e.g. *Polychytrium*, to the Polychytriales (Longcore and Simmons, 2012); while other genera, e.g. *Endochytrium* (not included by Karling, 1977, in Cladochytriaceae), are now placed in the Cladochytriales (cf. Mozley-Standridge et al., 2009; Powell and Letcher, 2014)—a grouping presently including polycentric and monocentric members. *Megachytrium* does not belong in the Polychytriales (a chitinophilic assemblage); it is likely to belong to the Cladochytriales—a generally saprobic group, inhabiting decaying plant and algal (cellulosic) substrates—but this has not been substantiated by molecular or ultrastructural studies. Certain

other cellulose-inhabiting genera have been determined to belong to the Cladochytriales, e.g. *Cylindrochytridium* (Steiger et al., 2011), and eventual placement of *Megachytrium* in Cladochytriales would not be surprising. Another order of Chytridiomycetes, the Rhizophlyctidales (cf. Letcher et al, 2008; Powell and Letcher, 2014), cannot however yet be ruled out. Various members of Rhizophlyctidales are capable of growing on diverse substrates (including cellulosic ones). Sporangial discharge-papillae of *Rhizophlyctis rosea* (the correct name, vs. *Karlinga rosea*; see Blackwell and Powell, 1999) are said to often be ‘endo-operculate;’ these bear some resemblance to the ‘operculate,’ short discharged-tubes of *Megachytrium* (occurring on fundamentally intercalary sporangia). The terminal sporangia of *Rhizophlyctis rosea* can come to ‘appear’ intercalary due to emergence of [enlarging] ‘rhizoidal thalli’ at several points on the sporangium—this ‘morphology,’ though, represents only a superficial similarity to *Megachytrium*. It is probable that *Megachytrium* will be confirmed (by molecular analysis) as a member of the Cladochytriales.

THE HOSTS OF MEGACHYTRIUM

Questions have surrounded the generic name of water-weed, ‘*Elodea canadensis*,’ host-plant of *Megachytrium*. Names other than *Elodea* have been used. Sparrow (1943) noted this host as *Anacharis canadensis*, but in 1960 referred to it as *Elodea canadensis*—thus utilizing different generic names for the same host. Fassett (1940) employed the name *Anacharis*—listing, though, an alternative name, *Philotria*. Small (1933) favored the name *Philotria*. Still other generic names have been used, e.g., *Udora* and *Apalanthe*. Adding to uncertainty is that *Elodea* is confusable with ‘look-alike’ genera (e.g., *Egeria* and *Hydrilla*). Geographically, ‘*Elodea*’ is an ‘American’ plant, with a number of species. However, none of the historical revisions or monographs (New World) completely resolved the correct generic name. Over time, *Elodea* became adventive (among other places) in the British Isles; Simpson (1984) there took up the question of which species were present—three were found in Britain; two of these occurred in Ireland as well. Simpson (1986) also sought out the proper generic name. One problem leading to name-proliferation was that flowers of *Elodea* could be bisexual or unisexual—plants could have perfect flowers or could be dioecious or polygamodioecious (see also Fernald, 1950). Certain extra names arose from not realizing that *Elodea*, in fact, encompassed this variation. Simpson (1986) also determined that *Elodea* was *not* an illegitimate name (earlier homonyms *not* being validly published) and that Michaux (1803, *Flora Boreali-Americana*) is author of the now-accepted name, *Elodea* (the earliest legitimate name for ‘water-weeds’). Fernald (1950) indicated that the name *Elodea* was proposed for conservation, but we find no evidence this name was conserved.

For 75 years (1931-2005) it was assumed that *Elodea canadensis* (by whatever name) was the only host for *Megachytrium*. The only certainly known location for *Megachytrium* during this time frame may have been where Sparrow (1931) initially found this chytrid—Fall Creek, Ithaca, New York—i.e., the ‘type locality;’ it was surely unrecorded outside the United States. However, in a broad study, Czczuga et al. (2005) reported *Megachytrium westonii* from ‘Jarosówka Spring,’ Poland, on fragments of *Elodea canadensis* (doubtless adventive) and *Myriophyllum verticillatum* (water milfoil); since they gave no indication that their find of *Megachytrium* might represent a new species (no descriptive information/illustrations provided), there are no grounds to suggest otherwise. In any case, the find by Czczuga et al. denoted a second occurrence of *Megachytrium* and a second host (*Myriophyllum*)—indicative that *Megachytrium* is not as host-specific as perhaps thought. The title of their paper (‘Aquatic fungi growing on dead fragments of submerged plants’) suggests *Megachytrium* can be saprotrophic (as well as parasitic). The find by Czczuga et al. (2005), though apparently only the second formally-documented occurrence of *Megachytrium*, nonetheless offers encouragement to any wishing to collect additional specimens of this genus. It also underscores the importance of traditional, broad-based surveys of the fungal flora—from a variety of aquatic habitats. The distribution of *Megachytrium*, if not abundant, now appears at least potentially broad.

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