Phytotaxa 399 (3): 209–238
https://www.mapress.com/j/pt/
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Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.399.3.5

Towards a phylogenetic classification of the Myxomycetes

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In memoriam Irina O. Dudka

Abstract

The traditional classification of the Myxomycetes (Myxogastrea) into five orders (Echinosteliales, Liceales, Trichiales, Stemonitidales and Physarales), used in all monographs published since 1945, does not properly reflect evolutionary relationships within the group. Reviewing all published phylogenies for myxomycete subgroups together with a 18S rDNA phylogeny of the entire group serving as an illustration, we suggest a revised hierarchical classification, in which taxa of higher ranks are formally named according to the International Code of Nomenclature for algae, fungi and plants. In addition, informal zoological names are provided. The exosporous genus *Ceratiomyxa,* together with some protosteloid amoebae, constitute the class Ceratiomyxomycetes. The class Myxomycetes is divided into a bright- and a dark-spored clade, now formally named as subclasses Lucisporomycetidae and Columellomycetidae, respectively. For bright-spored myxomycetes, four orders are proposed: Cribrariales (considered as a basal group), Reticulariales, a narrowly circumscribed Liceales and Trichiales. The dark-spored myxomycetes include five orders: Echinosteliales (considered as a basal group), Clastodermatales, Meridermatales, a more narrowly circumscribed Stemonitidales and Physarales (including as well most of the traditional Stemonitidales with durable peridia). Molecular data provide evidence that conspicuous morphological characters such as solitary versus compound fructifications or presence versus absence of a stalk are overestimated. Details of the capillitium and peridium, and especially how these structures are connected to each other, seem to reflect evolutionary relationships much better than many characters which have been used in the past.

Key words: *Amoebozoa, botanical and zoological nomenclature, Eumycetozoa, hierarchical classification, Myxogastrea*

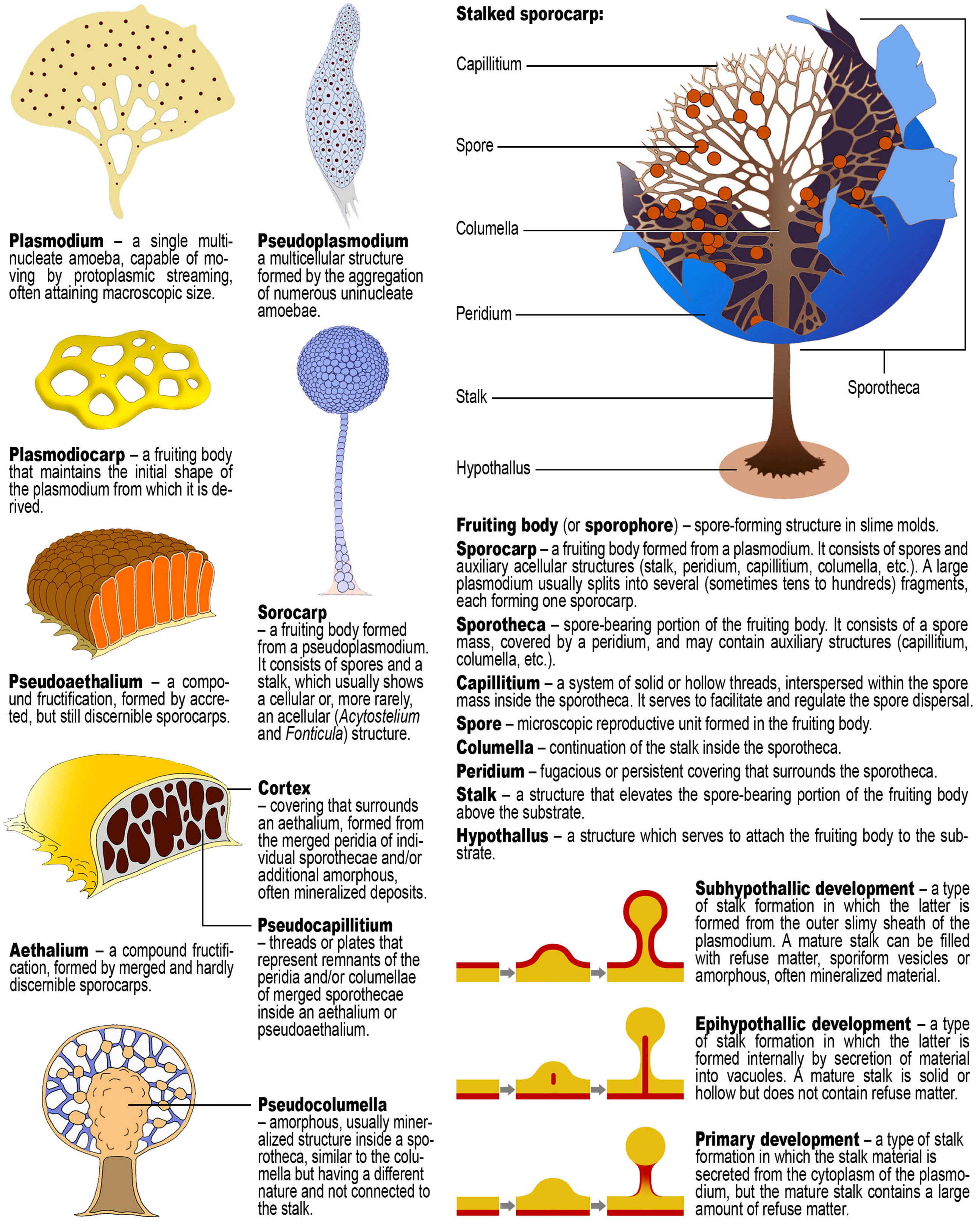
Introduction

Myxomycetes, or Myxogastrea, are a group of amoeboid eukaryotes which produce macroscopic fruiting bodies with a relatively complex structure (Fig. 1). In the current classification of living organisms, they are considered as a monophyletic taxon within the Amoebozoa (Adl *et al.* 2012, 2018, Ruggiero *et al.* 2015). First observations of myxomycetes date back into the 17th century (Pancovius 1656), but the first hierarchical classifications of these organisms were proposed much later (Chevalier 1826). The first classification based on comprehensible criteria was developed by Rostafiński (1875), who divided myxomycetes into two "subdivisions" based on color of the spore mass—the Amaurosporeae (dark-spored) and Lamprosporeae (bright-spored). This classification was further improved by Lister (1894, 1911, 1925) and Hagelstein (1944). An alternative approach, proposed by Massee (1892) and supported by Macbride (1922), Jahn (1928) and Martin (1960), recognized within the myxomycetes four or five orders (Echinosteliales, Liceales, Physarales, Stemonitales and Trichiales), based on several criteria, such as calcification of fruiting bodies and presence of a capillitium. Following the publication of the influential monograph of Martin and Alexopoulos (1969), the five order classification received worldwide recognition and was adopted in nearly all

Accepted by Wen-Ying Zhuang: 6 Mar. 2019; published: 27 Mar. 2019

subsequent monographs (Farr 1976, Nannenga-Bremekamp 1991, Neubert *et al.* 1993, 1995, 2000, Lado and Pando 1997, Ing 1999, Stephenson 2003), up to the most recent major treatment by Poulain *et al.* (2011).

All these classifications were based on a combination of morphological characters of the fructification, although plasmodium appearance and fruiting body development also were considered to some extent (Ross 1973). Myxomycetes are probably one of the last major groups of eukaryotes whose evolution has been studied using molecular methods. Thus, their hierarchical classification has never been revised in the light of phylogenetic data (Leontyev and Schnittler 2017, Lado and Eliasson 2017).



Plasmodium – a single multinucleate amoeba, capable of moving by protoplasmic streaming, often attaining macroscopic size.

Pseudoplasmodium a multicellular structure formed by the aggregation of numerous uninucleate amoebae.

Plasmodiocarp – a fruiting body that maintains the initial shape of the plasmodium from which it is derived.

Pseudoaethalium – a compound fructification, formed by accreted, but still discernible sporocarps.

Sorocarp – a fruiting body formed from a pseudoplasmodium. It consists of spores and a stalk, which usually shows a cellular or, more rarely, an acellular (*Acytostelium* and *Fonticula*) structure.

Cortex – covering that surrounds an aethalium, formed from the merged peridia of individual sporothecae and/or additional amorphous, often mineralized deposits.

Pseudocapillitium – threads or plates that represent remnants of the peridia and/or columellae of merged sporothecae inside an aethalium or pseudoaethalium.

Aethalium – a compound fructification, formed by merged and hardly discernible sporocarps.

Pseudocolumella – amorphous, usually mineralized structure inside a sporotheca, similar to the columella but having a different nature and not connected to the stalk.

Fruiting body (or **sporophore**) – spore-forming structure in slime molds.

Sporocarp – a fruiting body formed from a plasmodium. It consists of spores and auxiliary acellular structures (stalk, peridium, capillitium, columella, etc.). A large plasmodium usually splits into several (sometimes tens to hundreds) fragments, each forming one sporocarp.

Sporotheca – spore-bearing portion of the fruiting body. It consists of a spore mass, covered by a peridium, and may contain auxiliary structures (capillitium, columella, etc.).

Capillitium – a system of solid or hollow threads, interspersed within the spore mass inside the sporotheca. It serves to facilitate and regulate the spore dispersal.

Spore – microscopic reproductive unit formed in the fruiting body.

Columella – continuation of the stalk inside the sporotheca.

Peridium – fugacious or persistent covering that surrounds the sporotheca.

Stalk – a structure that elevates the spore-bearing portion of the fruiting body above the substrate.

Hypothallus – a structure which serves to attach the fruiting body to the substrate.

Subhypothallic development – a type of stalk formation in which the latter is formed from the outer slimy sheath of the plasmodium. A mature stalk can be filled with refuse matter, sporiform vesicles or amorphous, often mineralized material.

Epihypothallic development – a type of stalk formation in which the latter is formed internally by secretion of material into vacuoles. A mature stalk is solid or hollow but does not contain refuse matter.

Primary development – a type of stalk formation in which the stalk material is secreted from the cytoplasm of the plasmodium, but the mature stalk contains a large amount of refuse matter.

FIGURE 1. Illustrated glossary for morphological traits of myxomycetes and related taxa.

Myxomycetes show a higher within-group genetic divergence than true fungi, higher animals, or vascular plants (Fiore-Donno *et al.* 2012, Pawlowski *et al.* 2012, Adl *et al.* 2014, Kretzschmar *et al.* 2016). The internal transcribed spacer (ITS) region, often used for barcoding and as a source of phylogenetic information in fungi and plants, was found to be too polymorphic even for phylogenetic studies at the level of genera (Martin *et al.* 2003, Fiore-Donno *et al.* 2011). The 18S rRNA gene, coding the RNA of the small ribosomal subunit (SSU), evolves more slowly (Vogt and Braun 1976, Fiore-Donno *et al.* 2005, 2008, 2010, Wikmark *et al.* 2007), but its divergence is still high (Fiore-Donno *et al.* 2018). In many eukaryotic taxa, including the myxomycetes, this gene is represented by several to many hundreds of extrachromosomal copies, the so-called mini-chromosomes (Torres-Machorro *et al.* 2010) or rDNA (Johansen *et al.* 1992). This greatly facilitates the amplification of DNA and helps to obtain sequences from scanty or limited material. Moreover, with rare exceptions, 18S rDNA sequences are homogeneous, since one of the parental ribotypes is usually eliminated in crosses during plasmodial development (Ferris *et al.* 1983, Feng and Schnittler 2015), and this enhances sequence readability. Finally, in contrast to protein-coding genes, where the variation is relatively evenly distributed and found mostly at the third base of a triplet, 18S rDNA sequences show a pattern of alternating conservative and extremely variable sections according to the secondary structure of the rRNA (see Fig. 4 in Fiore-Donno *et al.* 2012). This greatly helps in the identification of target regions for primers and sequence alignment.

A disadvantage 18S rDNA shares with virtually all markers investigated thus far for myxomycetes is that universal primers, able to amplify this gene for all species of myxomycetes, are still unknown (Schnittler *et al.* 2017). Another problem for higher-level classification is created by the occurrence of group I introns in this part of genome (Feng and Schnittler 2015). The evolution of these units of parasitic DNA was most likely shaped by horizontal gene transfer and thus their presence does not occur in parallel with the evolution of the host organism (Schnittler and Feng 2016). The presence of this numerous introns makes complete 18S rDNA sequences unpredictable in size and difficult to obtain. Only the first ca. 600 positions are free of introns. The information from such a small section is sufficient for barcoding (Schnittler *et al.* 2017, Feng and Schnittler 2017) but is inadequate to resolve deeper evolutionary relationships.

Despite these problems, 18S rDNA remains the most widely applied phylogenetic marker in studies of myxomycetes (Fiore-Donno *et al.* 2005, 2008, Leontyev *et al.* 2014a, b, 2015, Walker *et al.* 2015, Wrigley de Basanta *et al.* 2015). Alternative markers (Supplementary file 4) include the protein elongation factor 1 alpha, EF1A (Fiore-Donno *et al.* 2011, Feng *et al.* 2016, Shchepin *et al.* 2016), the internal transcribed spacers ITS1 and ITS2 (Martin *et al.* 2003, Fiore-Donno *et al.* 2011) and the mitochondrial cytochrome C oxidase subunit 1 gene, COI (Rundquist and Gott 1995, Feng and Schnittler 2015, Shchepin *et al.* 2016).

A first effort to elucidate phylogenetic relationships in myxomycetes was made by Fiore-Donno *et al.* (2005), using partial 18S rDNA and EF1A sequences for eleven species of myxomycetes which represented all five orders. The results from this study indicated that the myxomycetes are a monophyletic group which splits into two basal clades. The first clade includes the Liceales and Trichiales, which have brightly colored spores (including red, orange, purple, yellow and olive). Melanin, if present at all, occurs in very low concentrations (Kalyanasundaram 1994). The second clade contains the Echinosteliales, Stemonitidales and Physarales, which, except for the genus *Echinostelium*, have dark (different tints of brown to black) spores pigmented by abundant melanin. The separation of orders on the basis of the presence of a capillitium, lime deposits or epihypothallic sporocarp development (Raunkiær 1888–89, Torrend 1907, Yachevskiy 1907, Ross 1973) was not supported by molecular phylogenies.

Applying zoological nomenclature, Cavalier-Smith (2013) was the first to name the two basal clades of endosporous (i.e., forming spores within multispored sporocarps) myxomycetes, recognizing two superorders within his subclass Myxogastria. The superorder Lucisporidia (bright-spored myxomycetes) included the Liceales and Trichiales, while Columellidia (dark-spored myxomycetes, often possessing a columella) encompassed the Echinosteliales, Stemonitidales and Physarales. This classification has much in common with the systems of Rostafiński (1875) and his followers, but contrasts with the currently accepted classifications which recognize four or five equidistant orders (Martin and Alexopoulos 1969, Nannenga-Bremekamp 1991, Poulain *et al.* 2011, Lado and Eliasson 2017).

As such, the system of myxomycetes is in need of revision (Leontyev and Schnittler 2017). This paper presents a first effort to revise it, assuming that each taxon should correspond to a monophyletic clade. Since both taxon coverage and the number of available markers are still rather limited, we consider our proposal as a starting point for further studies directed towards a natural system for the Myxomycetes.

Materials and methods

Additional data sources.—Full 18S rDNA sequences remain unavailable for a large fraction of species and even genera of myxomycetes. However, for some of these taxa partial sequences of the same or other genes may already have been studied and used in published phylogenies (Supplementary file 4). To consider these data, we have used all accessible papers presenting molecular phylogenies of dark- and bright-spored myxomycetes (Fiore-Donno *et al.* 2005, 2008, 2009, 2010, 2011, 2012, 2013, 2018, Nandipati *et al.* 2012, Liu *et al.* 2015, Miller *et al.* 2017), together with studies of single families, genera or species, for example the Echinosteliaceae (Kretzschmar *et al.* 2016, Reticulariaceae (Leontyev *et al.* 2014a, b, 2015), *Perichaena* (Walker *et al.* 2015), *Didymium* (Wrigley de Basanta *et al.* 2015, 2017, García-Martín *et al.* 2018), *Kelleromyxa* (Erastova *et al.* 2013) and *Lepidoderma* (Shchepin *et al.* 2016). These data were used to determine the position in our classification of those genera, for which no full 18S rDNA sequences are available so far.

Principles of the proposed classification.—The proposed classification represents a compromise between the multi-step architecture of phylogenetic cladograms and the number of levels in a taxonomic hierarchy, which should be limited due to practical reasons. We tried to retain all currently recognized taxa except for cases where they appear clearly poly- or paraphyletic. To facilitate comparisons with published monographs, we have included in the proposed classification all genera accepted as valid in the nomenclatural database of Lado (2005–2018). For complementary information about authorities and protologues of names or synonyms see Lado and Eliasson (2017).

The nomenclature of the “slime molds”, including myxomycetes, is covered by the International Code of Nomenclature for algae, fungi and plants (ICN), since this name is specifically mentioned in Preamble 8 of this code (Turland *et al.* 2018). In contrast, the International Code of Zoological nomenclature (ICZN) does not mention slime molds or myxomycetes (Ride *et al.* 1999). A transfer of the Myxomycetes to zoological nomenclature would cause nomenclatural instability, since the two Codes have different nomenclatural starting points, and numerous homonyms (Ronikier and Halamski 2018). At the same time, myxomycetes constitute a group within the Amoebozoa, and most recent papers dealing with the molecular phylogeny of myxomycetes (e.g. Cavalier-Smith 2013) follow ICZN concerning name endings and taxonomic ranks. In this paper, for taxa from family to class, we provide formal names according to the ICN (indicated by “B”), but add as well informal names corresponding with ICZN (marked by “Z”). The rank superorder, used in zoological nomenclature, is not used by the ICN; therefore, we provide only informal zoological names for this rank.

Some of the names introduced below (Meridermatales, Meridermataceae and Reticulariales) were already mentioned in a publication of Leontyev (2015) but without providing diagnoses and giving IDs for repositories of fungal names. According to ICN (art. 38, 42), names published in this way are considered as *nomina nuda.* Therefore, the abovementioned publication has no influence on the first valid publication of these names herein.

Phylogenetic analyses.—To illustrate the proposed classification with a first comprehensive phylogeny including all major groups of myxomycetes (Fig. 2), 139 full-length 18S rDNA nucleotide sequences of myxomycetes were retrieved from the GenBank Nucleotide database (www.ncbi.nlm.nih.gov/genbank, Supplementary files 2, 3). The tree of myxomycetes was rooted with six species of dictyostelids, which were also retrieved from the GenBank. Sequences were aligned with MAFFT 7.2.2 (Katoh and Sandley 2013) using the E-INS-i option (Katoh *et al.* 2005) and default gap penalties resulting in 26225 positions of the alignment. Five runs of this software produced identical alignments.

GBlocks 0.91b (Talavera and Castresana 2007) was then used to select only well-aligned conservative positions for the study, allowing gaps (parameter “Allowed Gap Positions”) for half of the sequences for a certain alignment position. The number of positions considered as well aligned and used to build a tree was defined by the proportion of sequences displaying the same base in flanking positions of conservative blocks. The respective parameter (“Minimum Number of Sequences for a Flank Position”) was tested for values between 50% and 85% with an increment of 5%. For each alignment, a Maximum Likelihood (ML) tree was reconstructed with IQ-Tree 1.5.5 (Nguyen *et al.* 2015) with the optimum substitution model chosen by ModelFinder according to BIC tests (Kalyaanamoorthy *et al.* 2017). Tree topologies were compared with each other using rSPR 1.3.0 software with subtree-prune-and-regraft distances (Whidden *et al.* 2013). The alignments with the lowest threshold under which the tree topology was stabilized (75%; Supplementary file 1) were used to construct phylogenies. Visual examination of the alignment confirmed that these thresholds indeed removed most “gappy” and poorly aligned positions while preserving well-aligned conservative blocks. In the resulting alignment, from 1105 nucleotide sites 684 (61.9%) were informative, 318 (28.8%) were constant.

FIGURE 2. Maximum Likelihood phylogeny of Myxomycetes. The tree was inferred from full 18S rRNA gene sequences using IQ-Tree 1.5.5 with 1000 ultrafast bootstrap replicates under the SYM+R6 model.

Phylogenetic analyses were carried out with both ML and Bayesian inference (BI). ML was run on IQ-Tree with 1000 replicates of ultrafast bootstrap (Minh *et al.* 2013) and with the optimal substitution model chosen with ModelFinder according to BIC tests (SYM+R6). BI was computed with MrBayes 3.2.1 (Huelsenbeck and Ronquist 2001, 2012) using one cold and three heated Monte Carlo Markov chains in two simultaneous runs with the evolutionary model set to GTR+G4+I. The number of generations, sample frequencies and burn-in ratio were set to 50 million, 1000 and 0.25, respectively. Convergence of MCMC chains was assessed (1) by checking the standard deviation of split frequencies for independent runs (around 0.01 after 25% of generations); (2) by estimating effective sample sizes of all parameters and LnL which were several times larger than generally accepted minimum of ESS = 200 for independent MCMC runs and for combined run information; and (3) by inspecting the shape of trace plots for all parameters and LnL. Clade confidence scores resulting from BI analysis were transferred to the ML tree using IQ-Tree (it implements an algorithm that, similar to 'sumt' command in MrBayes, counts the proportion every taxon bipartition appears in Bayesian trees).

An Approximately Unbiased test (AU) (Shimodaira 2002) of competing phylogenetic hypotheses was carried out. For this, a tree with loosely constrained topology was optimized under SYM+R6 model in IQ-Tree using the same alignment as for the optimum ML tree. The optimized tree was compared with the optimum ML tree using the AU test with 10000 RELL bootstrap replicates.

Results

All already published phylogenies (see citations above and Supplementary file 4), together with our phylogeny of the class Myxomycetes (Fig. 2), contradict the traditional classification with five equidistant orders, underlining the need for a new classification of myxomycetes. The main differences between the proposed and the currently used classification are given below.

(1) To reflect the evolutionary relationships among the main branches within Eumycetozoa, we recognize three classes within this phylum: Dictyosteliomycetes, Ceratiomyxomycetes (=Protosporangiida: *Ceratiomyxa*, *Clastostelium* and *Protosporangium*) and Myxomycetes (the latter now including only endosporous species).

(2) We provide a more elaborated and precise system of ranks at the level of family and higher, including the categories of subclass (two taxa at this level), superorder (four taxa) and order (nine taxa).

(3) For several taxa we propose emendations and/or re-erections. The circumscription of the orders Cribrariales, Liceales, Physarales, Stemonitidales and Trichiales, and the families Stemonitidaceae, Reticulariaceae and Dianemataceae is emended, while the families Amaurochaetaceae, Lamprodermataceae and the genus *Licaethalium* are re-erected and emended. If a new circumscription of a taxon is used, we provide an emended description for it; otherwise, the description is limited to relevant morphological characters.

(4) To indicate phylogenetic relationships which are not reflected by the currently used classification, we propose three new orders (Clastodermatales, Reticulariales and Meridermatales) and a one new family (Meridermataceae). In addition, we provide informal zoological names for some taxa where these have not been published (Clastodermatida, Cribrariida, Amaurochaetidae).

In our phylogeny, several branches, including Liceaceae, Dianemataceae, Trichiaceae, Echinosteliales, Amaurochaetaceae, Lamprodermataceae, Didymiaceae and Physaraceae, received support values below 0.9/90. However, in phylogenies of myxomycete subgroups, where more informative sites in alignments can be retained than for the myxomycetes as a whole, these taxa received usually higher support values and were often reproduced in independent analyses; therefore, we have included these in our classification.

Several large "classical" genera are already known to be para- or polyphyletic (e.g., *Licea*, *Hemitrichia, Physarum, Perichaena* and *Trichia*) and need to be revised, based on phylogenetic data. However, molecular data are currently available for only a small fraction of the ca. 1000 accepted morphospecies (Lado 2005–2018), and even more species can be expected if a biological species concept is applied (Feng *et al.* 2016, Walker and Stephenson 2016). For this reason at this level of knowledge, we do not provide formal descriptions of genera. Genera which are are clearly not justified in the light of molecular phylogenies are excluded from the classification (indicated by square brackets).

• **PHYLUM EUMYCETOZOA** L.S. Olive, The Mycetozoans: 4 (1975) (Z)
According to Kang *et al.* (2017) we limited this phylum to the monophyletic group formed by the Myxomycetes, Dictyosteliomycetes and Ceratiomyxomycetes. This excludes all other fruiting members of the Amoebozoa. A detailed classification is proposed only for the class Myxomycetes.

•• **CLASS DICTYOSTELIOMYCETES** Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXV (2001), previously proposed by D. Hawksw., B. Sutton & Ainsw., *Ainsworth & Bisby's Dictionary of the Fungi*, 7th Edn (Slough): 121 (1983), but *nom. inval.*, Art. 39.1 (Melbourne). (B); **DICTYOSTELEA** Lister (1909) emend. L.S. Olive (1970) (Z)
Twelve genera are currently accepted, with nine of them described in 2018 (Sheikh *et al.* 2018). These are *Acytostelium* Raper, Mycologia 48(2): 179 (1956); *Cavenderia* S. Baldauf, S. Sheikh & Thulin, in Sheikh *et al.*, Protist 169(1):19

(2018); *Coremiostelium* S. Baldauf, S. Sheikh, Thulin & Spiegel, in Sheikh *et al.*, Protist 169(1):24 (2018); *Dictyostelium* Bref., Abh. Senckenberg. Naturf. Ges. 7: 85 (1870); *Hagiwaraea* S. Baldauf, S. Sheikh & Thulin, in Sheikh *et al.*, Protist 169(1):22 (2018); *Heterostelium* S. Baldauf, S. Sheikh & Thulin, in Sheikh *et al.*, Protist 169(1):11 (2018); *Polysphondylium* Bref., Untersuch. Gesamtgeb. Mykol. Inst. 6: 5 (1884); *Raperostelium* S. Baldauf, S. Sheikh & Thulin, in Sheikh *et al.*, Protist 169(1):22 (2018); *Rostrostelium* S. Baldauf, S. Sheikh & Thulin, in Sheikh *et al.*, Protist 169(1):10 (2018); *Speleostelium* S. Baldauf, S. Sheikh & Thulin, in Sheikh *et al.*, Protist 169(1):22 (2018); *Tieghemostelium* S. Baldauf, S. Sheikh & Thulin, in Sheikh *et al.*, Protist 169(1):23 (2018); *Synstelium* S. Baldauf, S. Sheikh & Thulin, in Sheikh *et al.*, Protist 169(1):24 (2018). The enigmatic genus *Coenonia* Tiegh., Bull. Soc. Bot. France 31: 304 (1884), known from only a single collection, also may belong to this class (Sheikh *et al.* 2018).

•• CLASS CERATIOMYXOMYCETES D. Hawksw., B. Sutton & Ainsw., *classis nov.*, previously proposed by the same authors in *Ainsworth & Bisby's Dictionary of the Fungi*, 7th Edn (Slough): 257 (1983) but *nom. inval.*, Art. 39.1 (Melbourne) (B); **CERATIOMYXEA** (Z).

Mycobank MB 826861 (validation), MB 90066 (orginal name)

Typus. *Ceratiomyxa* J. Schröt., in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1: 16 (1889)

Description. Organisms with a complex, usually sexual life cycle, which includes amoeboflagellates, plasmodia and protosteloid fructifications. Meiosis is completed before spore wall maturation, and the spores are often multinucleate. The amoeboflagellate stage is short-lived: spore germlings may divide shortly after germination to produce more amoeboflagellates, which do not divide further (Spiegel *et al.* 2018) but convert into obligate amoebae or start to form a plasmodium (probably after syngamy). Amoeboflagellates are covered with a coat of fine hairs that are branched at the apex; the third microtubular rootlet of their flagellar apparatus consists of only two microtubules (which are, in contrast, numerous in Myxogastria, see Spiegel 1990, Shadwick *et al.* 2009). Plasmodia small (<1 mm) to extensive (>1 m), reticulate; lacking regular shuttle streaming. Individual fructifications are protosteloid, consist of one, two, four or eight spores, seated at the top of a relatively long stalk, straight to bent at several articulations. Spores smooth, spherical, ovoid or obconical, containing one, two or four nuclei. Individual sporocarps may arise separately on a substrate, or on a common layer of extracellular slime, which may be smooth, poroid or dissected into variously branched pillars.

To keep botanical and zoological nomenclature more congruent, and taking into account that the name *Ceratiomyxa* was published much earlier than *Protosporangium*, we propose to use the name Ceratiomyxea instead of Protosporangiida (this order includes the same taxa, Kang *et al.* 2017) as the zoological counterpart for Ceratiomyxomycetes.

Currently, this group includes three genera: *Ceratiomyxa* J. Schröt., in Engler & Prantl, Nat. Pflanzenfam. 1(1): 16 (1889); *Clastostelium* L.S. Olive & Stoian., Trans. Brit. Mycol. Soc. 69(1): 83 (1977); and *Protosporangium* L.S. Olive & Stoian., J. Protozool. 19(4): 563 (1972).

•• CLASS MYXOMYCETES G. Winter, Rabenh. Krypt.-Fl., ed. 2, 1(1): 32 (1880) ["1884"] (B); Myxogastres Fr. (1829), Syst. mycol. 3: 67 (1829) ut subordo; Myxogasteres Schröt., in Engler and Prantl, Nat. Pflanzenfam. 1(1): 8 (1889); Endosporeae Rostaf., Vers. Syst. Mycetozoen 2 (1873) ut "cohors"; Myxogastromycetidae G.W. Martin, in Ainsworth, Ainsworth & Bisby's Dictionary of the Fungi, 5th Edn (Kew): 497 (1961), *nom inval.* Art. 39.1; Myxogastromycetes M. Locquin, Numéro spécial Bull. Soc. Linn. Lyon 1: 235 (Feb. 1974) *nom. inval.* Art. 36.1, as "Myxogastromycetes (Fr.) Schröter"); **MYXOGASTREA** Cavalier-Smith, Microbiol. Rev. 57: 971 (1993) (Z); Myxogastria Cavalier-Smith, Eur. J. Protist. 49(2): 146 (2012) [2013] as "Myxogastria L.S. Olive, 1970", *nom. inval.* Art. 36.1. See detailed nomenclature of the group name in Lado and Eliasson 2017.

This group unites the sporocarpic (endosporous, myxogastric) Eumycetozoa with fructifications containing two (*Echinostelium bisporum*) to millions of spores and a more or less durable peridium. In contrast to the traditional circumscription (Macbride 1922, Martin and Alexopoulos 1969), the genus *Ceratiomyxa* is excluded.

••• Subclass Lucisporomycetidae Leontyev, Schnittler, S.L. Stephenson, Novozhilov & Shchepin, *subcl. nov.* (B); **Lucisporinia** (Z); = Lucisporidia Cavalier-Smith (2013) ut superordo; Lamprosporae Rostaf. (1873) pro parte

Mycobank MB 823237

Typus. *Trichia* Haller, Hist. stirp. Helv. 3:114 (1768).

Ethymology. *Lux* (Latin), light; *spore* (Greek), seed, spore; due to the bright color of the spore mass.

Diagnosis. Stalk absent or subhypothallic (an elevated hypothallus—a 'hypothallic stalk', occurs in *Tubifera microsperma*). A columella, understood as a continuation of the stalk into the sporotheca, is absent (a tubular columella-like structure occurs in *Tubifera casparyi*). Capillitium, if present, tubular, richly ornamented or nearly smooth, not connected to the tip of the stalk, sometimes merge with the peridium, forming funnel-shaped junctions. Spores colored in tints of brownish, yellow, orange, red, violet or olivaceous. The largest clade containing *Cribraria vulgaris*, *Reticularia lycoperdon*, *Licea castanea* and *Trichia varia* but not *Echinostelium minutum*, *Clastoderma debaryanum, Meriderma carestiae*, *Stemonitis fusca* and *Physarum viride*.

The subclass unites the so-called bright-spored myxomycetes, spores of which are not noticeably melanised. This group, known as Lucisporidia (Cavalier-Smith 2013), have no published botanical name. In an attempt to parallelize botanical and zoological nomenclature we propose the name Lucisporomycetidae as the botanical analogue of the Lucisporidia. This name is descriptive and is not formed from the name of an included genus, as allowed by ICN, art. 16.1.

•••• Superorder Cribrariidia (Z)

Typus. *Cribraria* Pers., Neues Magazin Bot. 1: 91 (1794).

Description. Stalk subhypothallic (or similar to that in Echinosteliales, Clark and Haskins 2014). Columella and capillitium absent. Peridium perforated or nearly intact, encrusted with calcium-containing structures, the so-called dictydine granules (Stephenson *et al.* 2004, Lado and Eliasson, 2017, Wang *et al.* 2017). Spores often collapse when dry. The largest clade containing *Cribraria vulgaris* and *Lindbladia tubulina* but not *Reticularia lycoperdon*, *Licea castanea* and *Trichia varia*.

In the phylogenies of Fiore-Donno *et al.* (2013, 2018) and the one in Fig. 2, the genera *Cribraria* and *Lindbladia* appear as a sister group to all other bright-spored myxomycetes, which is in our proposal reflected by the rank of a superorder.

••••• Order Cribrariales T. Macbr., N. Amer. Slime-Molds, Ed. 2 (New York): 199 (1922), excl. Liceaceae et Reticulariaceae; **Cribrariida** (Z)

Description. With the character of the superorder.

This order, proposed by T. Macbride, was re-erected to emphasize the separate position of the Cribrariaceae among all taxa traditionally accommodated within the Liceales *sensu lato*.

•••••• Family Cribrariaceae Corda, Icon. Fung. 2: 22 (1838) (B); **Cribrariidae** (Z)

With the character of the order.

••••••• *Cribraria* Pers., Neues Mag. Bot. 1: 91 (1794)

The genus appears clearly monophyletic, but may include species of *Lindbladia*.

••••••• *Lindbladia* Fr., Summa veg. Scand. 449 (1849)

Lindbladia seems to be most closely related to *Cribraria argillacea* (see discussion). Detailed investigations are needed to provide arguments for or against placing it in a genus of its own.

••••••• *Licaethalium* Rostaf., Vers. Syst. Mycetozoen 4 (1873)

One species of *Reticularia* (*R. olivacea*) shows very deviating partial 18S rDNA sequences, which branch together with the Cribrariaceae (Leontyev *et al.* 2015). This affiliation is also supported by the olive pigmentation of the spore mass, the verrucose spores and black color of immature fructifications, characteristic of both *R. olivacea* and *Lindbladia*. Since *R. olivacea* no longer can be treated within the genus *Reticularia*, we propose to re-erect the generic name *Licaethalium*, already proposed in the monograph of Rostafiński (1875). Two more species (*R. liceoides* and *R. simulans*) show a close similarity with *R. olivacea* in terms of most morphological characteristics and have even been considered as varieties of the latter (Lister 1896, Nannenga-Bremekamp 1973). Both are good candidates to be transferred to the genus *Licaethalium*. *Licea synsporos*, which possesses olivaceous verrucose spores joined in clusters and covered by a translucent peridium, may also represent a species of *Licaethalium*.

•••• Superorder Trichiidia (Z)

Typus. *Trichia* Haller, Hist. Stirp. Helv.: 114 (1768).

Description. Capillitium present or secondarily lost, tubular, filled with gas, richly ornamented, covered with warts, spines, rings, spirals, or nearly smooth. Peridium solid; not containing dictydine granules. Spores do not collapse when dry. The largest clade containing *Reticularia lycoperdon*, *Licea castanea* and *Trichia varia* but not *Cribraria vulgaris* or *Lindbladia tubulina*.

This group includes all bright-spored taxa except for members of the Cribrariaceae, which lack a capillitium. Therefore, the synapomorphy of Trichiidia may be the presence of a tubular capillitium (Leontyev *et al.* 2014c). In the Trichiidia this structure may have evolved independently from that present in the dark-spored myxomycetes (see Fig. 3 below). If this holds true, capillitia in the Lucisporomycetidae and Columellomycetidae are not homologous.

A capillitium appears in some species of the family Reticulariaceae (*Alwisia* and *Lycogala*), Dianemataceae (*Dianema* and *Calomyxa*) and most of Trichiaceae. Its secondary loss occurs in taxa forming very small sporocarps or plasmodiocarps (*Licea*, *Alwisia morula, Perichaena liceoides*), and in taxa with pseudoaethalia (*Dictydiaethalium* and *Tubifera*) and aethalia (*Reticularia*).

••••• **Order Reticulariales** Leontyev, Schnittler, S.L. Stephenson, Novozhilov & Shchepin, *ordo nov.* (B); **Reticulariida** (Z)

Mycobank MB 823241

Typus. *Reticularia* Bull., Herb. France 7(78–84): pl. 326 (1787–88).

Diagnosis. Capillitium usually absent; if present, connected to the peridium with funnel-like junctions connected to outer space in mature (*Alwisia bombarda, A. lloydiae* and *Tubifera casparyi*) or immature (*Lycogala*) sporocarps; ornamented with warts, blunt spines or rings. Spores reticulate; ornamentation formed by simple ridges. The largest clade containing *Reticularia lycoperdon*, *Tubifera ferruginosa* and *Lycogala epidendrum* but not *Licea castanea* or *Trichia varia*.

The new circumscription of the order (Leontyev *et al.* 2014a) includes the genera *Alwisia*, *Lycogala, Tubifera* and *Reticularia*. The first two of them possess a true capillitium (McHugh and Reid 2008, Leontyev *et al.* 2014b, c, Leontyev 2016), and this is reflected in the emended description of the group.

•••••• **Family Reticulariaceae** Chevall., ex Corda, Icon. Fung. 5: 22 (1842), excl. *Dictydiaethalium* Rostaf. (B); **Reticulariidae** (Z)

With the character of the order.

••••••• *Alwisia* Berk. & Broome, J. Linn. Soc., Bot. 14:86 (1873) emend. Leontyev, Schnittler, G. Moreno, S.L. Stephenson, D.W. Mitchell & C. Rojas, Mycologia 106(5): 938 (2014)

The genus *Alwisia* was erected for *A. bombarda* but later included in *Tubifera*. Together with three species described as new to science, *A. bombarda* forms a separate branch in molecular phylogenies and can therefore be maintained as a genus of its own (Leontyev *et al.* 2014a, b). The position of *Alwisia* causes this genus to appear closest to the last common ancestor of the family. In addition, the threads in *A. bombarda* and *A. lloydiae* seem to represent an ornamented, tubular capillitium (Leontyev *et al.* 2014b, c); its presence may be an ancestral trait shared by all members of the superorder Trichiidia.

••••••• *Lycogala* Adans., Fam. pl. 2: 7 (1763)

This is a clearly circumscribed genus, but the delimitation of species within *Lycogala epidendrum* s.l. remains difficult. Partial 18S rDNA sequences show a high molecular diversity (Leontyev *et al.* 2014c) and seem to confirm the assumption of Ing (1999) that this represents a species complex. The traditional circumscription of the fruiting bodies of *Lycogala* as aethalia and its tubular threads as pseudocapillitium was criticized on the basis of ontogenetic studies (McHugh and Reid 2008) and comparative morphology (Leontyev *et al.* 2015). If the tubules in *Lycogala* turn out to be a true capillitium, this would be the second genus of the order Reticulariales, after *Alwisia*, with such a structure.

••••••• *Reticularia* Bull., Herb. France 7(78–84): pl. 326 (1787–88)

Under this genus we only maintain the species with brownish and reticulate spores (*R. lycoperdon, R. splendens, R. jurana* and probably also *R. intermedia* and *R. lobata*) that represent a monophyletic cluster, sister to *Lycogala* (Leontyev *et al.* 2015). We propose to transfer the olive-spored species with verrucose spores to the family Cribrariaceae, uniting them under the generic name *Licaethalium*. The position of species with verrucose, yellowish (*R. aurea*) or brownish spores (*R. rubiginosa*) remains unclear, but they are likely to assume a position outside the family Reticulariaceae. *Reticularia aurea* may represent an aberrant form of *Dictydiaethalium* (R. Cainelli, pers. comm.)

••••••• *Tubifera* J.F. Gmel., Syst. nat., ed. 13, 2(2): 1472 (1792) emend. Leontyev, Schnittler & S.L. Stephenson (2015)

Comparison of partial 18S rDNA in *Tubifera ferruginosa* led to the description of several new species (Leontyev and Fefelov 2012, Leontyev *et al.* 2015). *Tubifera microsperma* and *T. dimorphotheca* seem to remain within the genus, while *T. bombarda* is transferred to *Alwisia*. *Tubifera dictyoderma* and *T. casparyi*, together with several species awaiting description, may better be accommodated in separate genera (Leontyev 2016). The position of *T. papillata* remains unclear.

••••• **Order Liceales** E. Jahn, in Engler and Prantl, Nat. Pflanzenfam. Ed. 2, 2: 319 (1928), excl. Cribrariaceae, Reticulariaceae (B); **Liceida** (Z)

Emended description. Capillitium absent; if present (*Listerella*) connected to the peridium but not opened outwards in mature sporocarps; ornamented with rings. Peridium opening by preformed furrows. Spores warted or nearly smooth, often with a pale area.

The traditional order Liceales, which included the families Reticulariaceae and Cribrariaceae, cannot be maintained (Eliasson 2017). However, the group which includes the genus *Licea* at its core appears distinctly enough to be considered as an order.

•••••• **Family Liceaceae** Chevall., Fl. gén. env. Paris 1: 343. 1826; **Liceidae** (Z)

With the character of the order.

••••••• *Licea* Schrad., Nov. gen. pl. 16 (1797), incl. *Listerella*. This genus is clearly polyphyletic and in need of revision. According to molecular data, *L. variabilis* has to be considered as a member of the family Dianemataceae. *Licea synsporos* is very similar to "*Reticularia*" *liceoides* and may belong to the family Cribrariaceae (see comment under *Licaethalium*). Several species of *Licea* with yellow spores may show closer affinities to *Perichaena*, simply representing miniature forms which lack a capillitium (Eliasson 2017). A revised genus *Licea* may unite only species in which the peridium opens by preformed furrows, forming a lid or polygonal plates, and possessing relatively dark, smooth or minutely punctate (SEM) spores, often with a pale area.

••••••• [*Listerella* E. Jahn, Ber. Deutsch. Bot. Ges. 24(10): 540 (1907)]

The enigmatic genus *Listerella* with the single species *L. paradoxa* has a capillitium, in contrast to habitually similar species of *Licea*. However, several examples of the presence or absence of a capillitium within species of one genus (Leontyev *et al.* 2014c, Eliasson 2017) suggest that this character is insufficient to warrant the separation of this taxon into a separate genus.

••••• **Order Trichiales** T. Macbr., N. Amer. Slime-moulds, ed. 2, 237 (1922) (B); **Trichiida** (Z)

Emended description. Capillitium present or absent (*Dictydiaethalium*, *Perichaena liceoides* and *"Licea" variabilis*), free or connected to the peridium, but in the latter case not opened outwards in mature sporocarps; ornamented with rings, cogs, reticula, spines or spirals. Spores warted or reticulate, the reticulum may be formed by compound ridges (nearly parallel, fasciculate, often coalescing ridges, which leave small meshes in-between).

•••••• **Family Dianemataceae** T. Macbr., N. Amer. Slime-moulds, ed. 2, 237 (1922), incl. *Dictydiaethalium*, *Prototrichia* and *Licea variabilis* (B); **Dianematidae** (Z)

Emended description. Capillitial or pseudocapillitial structures, if present, often directed from the bottom to the upper surface of the fructifications. Capillitial threads single or sparsely branched in a narrow angle, thin, with hollows hardly visible, ornamented or nearly smooth. Spores thick-walled (visible in optical section as two lines somewhat distant from each other), ornamented by narrowly conical spines or, more rarely, by a fragmentary or complete reticulum.

Our phylogeny fully supports the conclusions of Fiore-Donno *et al.* (2013) relating to the inclusion of *Dictydiaethalium*, *Prototrichia* and *Licea variabilis* into this family.

••••••• *Calomyxa* Nieuwl., Amer. Midl. Naturalist 4:335 (1916)

The single studied species of this small genus shows close affinities to *Dianema* but may still represent a separate genus (Fiore-Donno *et al.* 2013).

••••••• *Dianema* Rex, Proc. Acad. Nat. Sci. Philadelphia 43:397 (1891)

Two species of this genus, *D. nivale* and *D. inconspicuum*, form a monophyletic branch related to *Calomyxa*, *Dictydiaethalium*, *Prototrichia* and *Licea variabilis* (Fiore-Donno *et al.* 2013).

••••••• *Dictydiaethalium* Rostaf., Vers. Syst. Mycetozoen 5 (1873)

This genus shows closer affinities to *Dianema* and does not branch with all other genera of the family Reticulariaceae where it has traditionally been included (Martin and Alexopoulos 1969).

••••••• *Prototrichia* Rostaf., Sluzowce monogr. suppl. 38 (1876)

Despite the presence of some morphological characters which unite this genus with the family Trichiaceae (stalked sporocarps and capillitial threads ornamented with spirals), a molecular phylogeny assigns *Prototrichia* to the family Dianemataceae (Fiore-Donno *et al.* 2013).

•••••• **Family Trichiaceae** Chevall., Fl. gén. env. Paris 1: 322. 1826, *sensu* Martin & Alexopoulos (1969), incl. Arcyriaceae and Perichaenaceae (B); **Trichiidae** (Z)

Description. Capillitial threads not having a consistent direction, sometimes attached to the bottom of the sporotheca but not clearly directed towards its top; simple or branching at wide angles, sometimes anastomosing and forming a net, relatively thick, with hollows clearly visible, ornamented by well developed rings, cogs, spines, reticula or spirals. Spores thin-walled, verrucose or reticulated, in the latter case mostly with compound ridges.

The separation of the Trichiaceae into two or three related families, including Arcyriaceae or Perichaenaceae, has always been problematic. Morphological characters used for this separation, including the presence/absence of spiral bands on the capillitium and its birefringence (Nannenga-Bremekamp 1982), do not occur exclusively within monophyletic branches. If the family will be split, a first monophyletic clade may unite species of *Hemitrichia* and *Trichia* which have stalks filled with spore-like cells (Fiore-Donno *et al.* 2013); a second clade is formed by the genera *Arcyria* and *Arcyodes*, and a third clade includes all the remaining members of the family Trichiaceae.

••••••• *Hemitrichia* Rostaf., Vers. Syst. Mycetozoen 14 (1873), incl. *Trichia decipiens*

In the future this genus may be emended to include other species with a hollow stalk that is filled with spore-like cells (e.g., *Trichia decipiens*).

••••••• *Arcyria* F.H. Wigg., Prim. fl. holsat. 109 (1780), incl. *Arcyodes, Hemitrichia imperialis*

A clearly circumscribed clade which can be seen as a separate family. *Hemitrichia imperialis* is conspecific or at least very close to *A. stipata* (Schnittler *et al.*, unpubl. results) based on partial 18 rDNA sequences. The rare *Hemitrichia abietina* [*A. abietina* (Wigand) Nann.-Bremek.] assumes a position closer to *Hemitrichia* in Fiore-Donno *et al.* (2013) and Fig. 2, but closer to *Arcyria* in Fiore-Donno *et al.* (2018).

••••••• [*Arcyodes* O.F. Cook]

This genus with the single species *A. incarnata* branches within *Arcyria* (Fiore-Donno *et al.* 2013) and should be included in this genus.

••••••• *Perichaena* Fr., in Fries & Lindgren, Symb. gasteromyc., fasc. 2, 11 (1817)

This paraphyletic genus is currently underrepresented in molecular investigations. At least some species show affinities to *Trichia* (e.g., *P. longipes*, Walker *et al.* 2015), while others may form a separate genus, sister to *Trichia* (*P. corticalis*, *P. depressa* and *P. luteola*, Fiore-Donno *et al.* 2013).

••••••• *Trichia* Haller, Hist. stirp. Helv. 3: 114 (1768), incl. *Cornuvia, Metatrichia, Oligonema*

The genus seems to be better defined in a broader sense, including the genera *Cornuvia*, *Oligonema* and *Metatrichia*, which together form the clade "*Trichia*" in the phylogeny of Fiore-Donno *et al.* (2013).

••••••• [*Cornuvia* Rostaf.]

The single species (*C. serpula*) clusters with species of *Trichia* (Fiore-Donno *et al.* 2013). Its deviating capillitium might have been overvalued in traditional classifications. At least one species of *Trichia* (*T. brevicapillata*) is known to have very short capillitial threads, similar to the situation in *Cornuvia* and species of the genus *Oligonema*.

••••••• [*Metatrichia* Ing]

The genus *Metatricha* was erected on the basis of its double peridium with a cartilaginous outer layer and fascicle-stalked fructifications (Ing 1964). However, these characters are as well known for several species of *Trichia* (*T. botrytis*, *T. sordida*). On the other hand, *M. floripara* has solitary fructifications, and this applies as well to a form of *M. vesparium* which shows a different partial 18S rDNA sequence (Feng and Schnittler 2017). In 18S rDNA phylogenies species traditionally recognized within *Metatrichia* branch within those of the genus *Trichia* Fiore-Donno *et al.* 2013, Walker *et al.* 2015).

••••••• [*Oligonema* Rostaf.]

The same comment as made for *Cornuvia* applies here.

LUCISPOROMYCETIDAE INCERTAE SEDIS

For the genera listed below, no molecular data are available.

••••••• *Arcyriatella* Hochg. & Gottsb., Nova Hedwigia 48(3–4): 485 (1989)

A genus close to *Arcyria*, its single species may be an *Arcyria* with compound fructifications.

••••••• *Calonema* Morgan, J. Cincinnati Soc. Nat. Hist. 16(1): 27 (1893)

Similar comments as for *Cornuvia* apply. The capillitium, deviating from that of all other Trichiaceae, may be overvalued and does not justify the maintenance of a separate genus.

••••••• *Minakatella* G. Lister, J. Bot. 59:92 (1921)

An enigmatic pseudoaethalioid genus with an uncertain position.

••••••• *Trichioides* Novozh., Hoof & Jagers, Mycol. Progress 14 (1018): 2 (2015)

A newly erected genus for a single species (*T. iridescens*). Its iridescent peridium, as well as the melanized spores and capillitium, resemble those found in the dark-spored myxomycetes, but the ornamentation, branching and orientation of the capillitium resemble those found in *Prototrichia*, while the spores are punctulate and possess a rather large pale area, similarly to what occurs in *Licea* s. str. (Novozhilov *et al.* 2015).

••• **Subclass Columellomycetidae** Leontyev, Schnittler, S.L. Stephenson, Novozhilov & Shchepin, *subcl. nov.* (B); **Columellinia** (Z); = Columellidia Cavalier-Smith Eur. J. Protist. 49: 146 (2013) ut superordo; Fuscisporidia Cavalier-Smith Eur. J. Protist. 49: 146 (2013) *sensu* Kretzschmar *et al.* J. Eukar. Microbiol. Dec.: 5 (2015).
Mycobank MB 823236

Typus. *Stemonitis* Gled., Meth. fung. 140 (1753).

Ethymology. *Columella* (Latin)—small pillar; due to the supposed ancestral presence of a columella within the sporotheca.

Diagnosis. Stalk present or secondarily lost, epihypothallic, , subhypothallic or primary ("third type" according to Clark and Haskins 2014). Collumella solid, present or secondarily lost. Capillitium present (reduced to absent in some species of the genus *Echinostelium* and *Echinosteliopsis*), solid, smooth, branched and anastomosed, always connected to the columella. Spores rarely hyaline, more commonly melanised (brown to black). The largest clade containing *Echinosteliopsis oligospora* (see Fiore-Donno *et al.* 2018), *Echinostelium minutum*, *Clastoderma debaryanum, Meriderma carestiae*, *Stemonitis fusca* and *Physarum viride* but not *Cribraria vulgaris*, *Reticularia lycoperdon*, *Licea castanea* and *Trichia varia*.

This group unites the so-called dark-spored myxomycetes with a capillitium connected to a true columella, congruent to the Collumellidia (Cavalier-Smith 2013), or Fuscisporidia *sensu* Kretzschmar *et al.* (2016); whereas Fuscisporidia *sensu* Cavalier-Smith (2013) excludes Echinosteliidia. Most species have a well-developed capillitium and brown to black spores, but the capillitium may be absent in some species of *Echinostelium* and *Echinosteliopsis*, the spores sometimes are nearly colorless (*Echinostelium*, *Echinosteliopsis*) or relatively pale (*Stemonitopsis hyperopta*). The absence of a capillitium and melanin may represent primary conditions, since the Dictyosteliomycetes and Ceratiomyxomycetes have no capillitium and seemingly no melanin (although a detailed investigation is needed to see if it appears in traces). However, Kretzschmar *et al.* (2016) suggested the possibility of a secondary loss of melanin in *Echinostelium* and *Clastoderma*, although this appears less likely with the recent inclusion of *Echinosteliopsis* (Fiore-Donno *et al.* 2018).

The botanical name Stemonitomycetidae I.K. Ross (1973) has in a strict sense the priority over Columellomycetidae: the order Stemonitidales is included in both subclasses. However, since the principle of priority does not apply above the rank of family (ICN art. 16.1), we can avoid the name, proposed by Ross, because it is based upon a different taxonomic concept (including only species with epihypothallic stalk development). To parallelize botanical and zoological nomenclature, in a similar way as for the bright-spored myxomycetes, we propose Columellomycetidae as the first proposed name matching the taxomic concept proposed herein and the botanical counterpart to Columellidia.

•••• **Superorder Echinosteliidia** (Z)
Typus. *Echinostelium* de Bary, in Rostafiński, Vers. Syst. Mycetozoen 7 (1873)

Description. Capillitium, if present, scanty, poorly branched. Stalk granular, with intermediate development (Clark and Haskins 2014), consisting of a moderately thin outer layer, composed of slime and condensed cytoplasmic material with fibers secreted just under it. Spores hyaline or melanised. The largest clade containing *Echinostelium minutum* and *Barbeyella minutissima* but not *Clastoderma debaryanum, Meriderma carestiae*, *Stemonitis fusca* and *Physarum viride*.

In the phylogeny of Kretzschmar *et al.* (2016), the genera *Echinostelium*, *Barbeyella* and *Clastoderma* form a group sister to the dark-spored myxomycetes (Stemonitidia). In contrast, in a phylogeny, presented herein (Fig. 2), *Clastoderma* branches together with members of the superorder Stemonitidia but not with Echinosteliidia, with similar support of the corresponding clade. Independently, Fiore-Donno *et al.* (2018) found the same topology in a phylogeny based on 18S rRNA and EF1A genes. We cannot ignore this result and thus separate *Clastoderma* from the Echinosteliales, although the hypothesis on the monophyly of both taxa could not be rejected by the Approximately Unbiased test and additional studies are needed with broader sampling of *Clastoderma* and *Echinostelium* to clarify the relationships between these taxa. The few-spored *Echinosteliopsis oligospora* might as well deserve a higher-rank-taxon on its own (Fiore-Donno *et al.* 2018).

••••• **Order Echinosteliales** G.W. Martin, Mycologia 52(1): 127 (1961) ["1960"] (B); **Echinosteliida** (Z)
Description. With the character of the superorder.

•••••• **Family Echinosteliaceae** Rostaf. ex Cooke, Contr. Mycol. Brit.: 53 (1877) (B); **Echinostelidae** (Z)
With the character of the order.

••••••• *Barbeyella* Meyl., Bull. Soc. Bot. Genève 6:89 (1914)

Barbeyella minutissima is the only species of the family characterized by dark spores. As shown by morphological (Schnittler *et al.* 2000) and molecular (Kretzschmar *et al.* 2016) characters, the closest species in *Echinostelium* is *E. arboreum*. It shares with *Barbeyella* the peridial platelets, which develop as a derivate of funnel-like invaginations of the peripheral ends of the capillitial threads. It is noteworthy that the same funnel-shaped ends of the capillitium also occur in *Meriderma*, a genus which forms a basal clade within the dark-spored myxomycetes (Fiore-Donno *et al.* 2012).

••••••• *Echinostelium* de Bary, in Rostafiński, Vers. Syst. Mycetozoen 7 (1873), incl. *Semimorula* (?)

Probably the basal genus of the subclass Columellomycetidae. *Echinostelium bisporum* has been initially accommodated within the "protosteloid myxogastrids" (Spiegel 1990). The phylogenies of Kang *et al.* (2017) and Fiore-Donno *et al.* (2018) showed its relationship to other species of *Echinostelium*. The stalkless genus *Semimorula* E.F. Haskins, McGuinn. & C.S. Berry may branch within *Echinostelium* (Fiore-Donno *et al.* 2009, 2018, Kretzschmar *et al.* 2016).

••••••• [*Semimorula* E.F. Haskins, McGuinn. & C.S. Berry, Mycologia 75(1):153 (1983)]

See comments for *Echinostelium*.

•••• **Superorder Stemonitidia** nom. typif. pro Fuscisporidia Cavalier-Smith (2013), *non sensu* Kretzschmar *et al.* (2016) (Z); Amaurosporeae Rostaf. (1873) pro parte.
Typus. *Stemonitis* Gled., Methodus fungorum exhibens: 140 (1753).
Description. Capillitium always present, abundant, rarely to intensively branched and anastomosed. Stalk granular, fibrous or amorphous, epihypothallic, subhypothallic or primary, the last type occurs in *Clastoderma*. Spores melanised. The largest clade containing *Clastoderma debaryanum*, *Meriderma carestiae*, *Stemonitis fusca* and *Physarum viride* but not *Echinostelium minutum* and *Barbeyella minutissima*.

This is the core group of the dark-spored myxomycetes, characterized by spores appearing usually dark in mass, rarely pale brown or pinkish (*Stemonitopsis hyperopta*). This corresponds with the occurrence of melanin as a spore pigment. A stalk, reinforced with granular matter, as present in *Clastoderma*, may be ancestral for this group; in the Meridermatales and Stemonitales the development of the stalk is clearly epihypothallic and the stalk extends usually into a true columella, but in many Physarales the epihypothallic stalk is replaced by a subhypothallic one (see Fig. 3).

••••• **Order Clastodermatales** Leontyev, Schnittler, S.L. Stephenson, Novozhilov & Shchepin, *ordo nov.* (B**);**
Clastodermatida (Z)
Mycobank MB 823238

Typus. *Clastoderma* A. Blytt, Bot. Zeitung (Berlin) 38: 343 (1880).

Diagnosis. Stalk present, probably of the "third type" (Clark and Haskins 2014), filled with granular material at its basal part. Columella present, gradually turning into the capillitium. Capillitial threads branched and anastomosed, merging at the periphery to form plate-like swellings. Peridium fugacious. Lime absent. Spores pale brown. The largest clade containing *Clastoderma debaryanum* but not *Meriderma carestiae*, *Stemonitis fusca* and *Physarum viride*.

A hollow stalk filled with granular material unites this family with the Echinosteliales, thus supporting the phylogeny of Kretzschmar *et al.* (2016). However, a well-developed capillitium with anastomosing branches separates *Clastoderma* from the Echinosteliales, which is supported by our 18S rDNA phylogeny (Fig. 2) and by the two-gene phylogeny of Fiore-Donno *et al.* (2018). The homogenous upper portion of the stalk, connected to the capillitium in *C. debaryanum*, may represent an initial epihypothallic stalk, while the lower part seems to form via the intermediate way as in Echinosteliales. The plate-like swellings, which in contrast to capillitial funnel-like ends in *Barbeyella* are separated from the evanescent peridium (Frederick *et al.* 1986), represent another unique character of the order Clastodermatales.

•••••• **Family Clastodermataceae** Alexop. & T.E. Brooks, Mycologia 63(4):926 (1971) (B); Clastodermatidae (Z)
With the character of the order.

••••••• *Clastoderma* A. Blytt., Bot. Zeitung (Berlin) 38: 343 (1880)

Molecular data are available only for the type species (*C. debaryanum*). The monophyly of the genus remains doubtful.

••••• **Order Meridermatales** Leontyev, Schnittler, S.L. Stephenson, Novozhilov & Shchepin, *ordo nov.* (B); **Meridermatida** (Z)
Mycobank MB 823239

Typus. *Meriderma* Mar. Mey. & Poulain, in Poulain, Meyer & Bozonnet, Myxomycètes: 551 (2011)

Diagnosis. Stalk fibrose, epihypothallic. Columella gradually turning into the capillitium. Capillitial threads forming funnel-shaped ends which merge to the peridium. Peridium persistent, splitting into fragments which remain attached to the ends of capillitium. Lime absent. Spores dark brown to black. The largest clade containing *Meriderma carestiae*, *M. fuscatum* and *M. cribrarioides* but not *Stemonitis fusca* and *Physarum viride*.

This order includes the genus *Meriderma* as its core, but other species such as *Comatricha pseudoalpina* (Schnittler, unpubl. results) and *Collaria rubens* (Fiore-Donno *et al.* 2012) may be related.

•••••• **Family Meridermataceae** Leontyev, Schnittler, S.L. Stephenson, Novozhilov & Shchepin, *fam. nov.* (B); **Meridermatidae** (Z)
Mycobank MB 823240

Typus. *Meriderma* Mar. Mey. & Poulain, in Poulain, Meyer & Bozonnet, Myxomycètes: 551 (2011)

Description. With the characters of the order.

••••••• *Meriderma* Mar. Mey. & Poulain, in Poulain, Meyer & Bozonnet, Myxomycètes: 551 (2011)

The connection of peridium and capillitium, which is typical for *Meriderma* (Poulain *et al.* 2011), seems to be an ancient character of the dark-spored myxomycetes and is also displayed within the Echinosteliales (*Barbeyella minutissima* and *Echinostelium arboreum*).

••••• **Order Stemonitidales** T. Macbr., N. Amer. Slime-moulds, ed. 2, 22, 148 (1922), as "Stemonitales", excl. *Colloderma, Diacheopsis*, *Elaeomyxa, Lamproderma* (B); **Stemonitida** (Z)
Emended description. Stalk fibrose or amorphous, epihypothallic. Columella present, gradually turning into the capillitium. Capillitial threads attached to the columella but not attached to the peridium and usually not forming funnel-shaped ends, merging with the peridium (the 'peridial platelets' of *Symphytocarpus* spp. may be an exception). Peridium usually fugacious. Lime absent. Spores brown to black in mass.

As circumscribed herein, the traditional order Stemonitidales includes several taxa that need to be transferred to the order Meridermatales (genus *Meriderma*, see above) or to the family Lamprodermataceae (genera *Colloderma, Diacheopsis, Elaeomyxa* and *Lamproderma*), now included in the order Physarales (see below). Therefore, the traditional order Stemonitidales should be reduced in species content to form a monophyletic unit. This excludes all taxa with a persistent peridium, whereas the remaining members of a monophyletic order Stemonitidales possess an evanescent peridium, with a few exceptions such as *Stemonitopsis typhina* or *Comatricha alpina*.

•••••• **Family Stemonitidaceae** Fr., Syst. Mycol. 3(1): 75 (1829), excl. *Amaurochaete*, *Brefeldia*, *Colloderma*, *Comatricha*, *Diacheopsis*, *Elaeomyxa*, *Enerthenema*, *Lamproderma*, *Paradiacheopsis*, *Stemonaria* and *Stemonitopsis* (B); **Stemonitidae** (Z)
Emended description. Stalk hollow, corneous, with the basal part slightly to clearly translucent. Capillitium arising from the columella, branching and anastomosing. Capillitial threads usually forming a surface net.

Only three genera remain in this family, the delimitation of which is preliminary due to the lack of molecular data. In our phylogeny *Lamproderma cacographicum*, unlike other species of *Lamproderma*, forms an unsupported branch that is sister to the Stemonitidaceae. If multigene phylogenies will support an isolated position of this species, a separate genus within Stemonitidaceae should be erected.

••••••• *Macbrideola* H.C. Gilbert, Stud. Nat. Hist. Iowa Univ. 16(2): 155 (1934)

This genus is traditionally circumscribed by its hollow stalk, spherical to ovate sporothecae and the absence of a capillitial surface net. Based on morphology, these characters seem to be ancestral for the family, and the phylogeny of Fiore-Donno *et al.* (2012) confirms this.

••••••• *Stemonitis* Gled., Meth. fung. 140 (1753)

The core genus of the family Stemonitidaceae, encompassing species with cylindrical sporothecae and a capillitium profusely branched and anastomosed with a formation of pronounced surface net.

••••••• *Symphytocarpus* Ing & Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C. 70(2): 218 (1967)

Under this genus pseudoaethalioid species are grouped, but compound fructifications occur in many myxomycete taxa and are certainly a product of parallel evolution (see Fig. 3 below). Detailed molecular investigations are needed to determine in which cases such forms should be accommodated in a genus of their own or included in the closest genus with simple sporocarps.

•••••• **Family Amaurochaetaceae** Rostaf. ex Cooke, Contr. Mycol. Brit. 52 (Jan.-Jul. 1877) (B); **Amaurochaetidae** (Z)

Emended description. Stalk solid, composed of recognizable fibers, with the basal part opaque. In aethaliate forms the pseudocapillitium represents, at least in part, remnants of the stalks and therefore shows a similar structure. Capillitium arising from the columella, branching, anastomosing or composed of free threads. A surface net is usually absent, fragmentary or inseparable from the internal net.

Several family names can be chosen for this group, based on molecular data (Fiore-Donno *et al.* 2008). The name Comatrichaceae, previously published by Locquin, Syn. gen. fung. (Paris):1 (1972), is a *nom. inval.* (see ICN art. 39.1). Three other applicable family names were published simultaneously in one treatment of Cooke (1877), based on "tribes" of Rostafiński (1873), as Amaurochaetaceae, Brefeldiaceae and Enerthemataceae. Most characteristic for the family as a whole seems to be the first of these names ("amauro" = dark, "chaete" = mane, referring to the dark capillitial treads).

••••••• *Comatricha* Preuss, Linnaea 24:140 (1851)

As currently circumscribed, this genus is probably not monophyletic; *Comatricha nigricapillitia* may be closer to the genus *Enerthenema* (Fiore-Donno *et al.* 2008).

••••••• *Stemonaria* Nann.-Bremek., R. Sharma & Y. Yamam., in Nannenga-Bremekamp, Yamamoto & Sharma, Proc. Kon. Ned. Akad. Wetensch., C. 87(4):450 (1984)

No molecular data are available thus far for this genus, but its morphology, including the fibrous stalk, supports a position within the family Amaurochaetaceae. Within this family, it may or may not represent a separate genus.

••••••• *Stemonitopsis* (Nann.-Bremek.) Nann.-Bremek., Nederlandse Myxomyceten (Zutphen) 203 (1975)

Stemonitopsis is unusually variable for several characters such as the color of the spore mass, spore ornamentation and duration of the peridium, therefore this genus may not represent a monophyletic taxon. Some taxa, such as the common *S. typhina*, that have a persistent peridium, show extremely deviating partial SSU sequences Fiore-Donno *et al.* 2012, Feng and Schnittler 2017), and due to long-branch attraction, the systematic position of these species cannot be ascertained.

••••••• *Amaurochaete* Rostaf.

The phylogeny of Fiore-Donno *et al.* (2012) places this aethalioid genus within the family; morphological evidence comes from the fibrous structure of the remnants of columellae and capillitium.

••••••• *Brefeldia* Rostaf.

A second aethalioid genus placed in the family Amaurochaetaceae by the phylogeny of Fiore-Donno *et al.* (2012); the columellae and stalks are too severely reduced to determine if they are fibrous or hollow.

••••••• *Enerthenema* Bowman

A genus currently circumscribed by the capillitium arising from a funnel-like disk at the apex of the columella. However, *Comatricha nigricapillitia*, lacking the funnel-like disk, may be closely related to *Enerthenema* (Fiore-Donno *et al.* 2012).

••••••• *Paradiacheopsis* Hertel.

The genus is separated from *Comatricha* by a stalk composed of twisted fibers, whereas in most members of the latter genus the fibres are parallel. However, this feature does not apply to some species, like *Paradiacheopsis longipes* (Leontyev *et al.* 2012). Only one species (*P. solitaria*) was included in the phylogeny of Fiore-Donno *et al.* (2012), and it appears to be related to *Comatricha nigra*.

••••• **Order Physarales** T. Macbr., N. Amer. Slime-moulds, ed. 2, 22 (1922), incl. *Colloderma, Diacheopsis*, *Elaeomyxa,* and *Lamproderma* (B); **Physarida** (Z)

Emended description. Stalk epihypothallic or subhypothallic, often filled with amorphous material. Columella truncate, not grading into the capillitium, sometimes partially or completely reduced. Capillitial threads branched and anastomosed, often attached to the peridium but not forming funnel-shaped ends (*Badhamia* may represent an exception). Peridium persistent, iridescent. Spores brown to black in mass.

In the phylogeny of Fiore-Donno *et al.* (2012), the corresponding clade includes the traditional order Physarales but also limeless forms, such as members of the genus *Lamproderma*. A unifying character may be the persistent but separating peridium (not evanescent as in the Stemonitidales but also not attached to the capillitium as is the case in the Meridermatales). Additional unifying characters may be (i) the weakly melanised capillitial tips, (ii) iridescence of the peridium (present in *Lamproderma*, as well as in most of the poorly calcified members of the Physaraceae and Didymiaceae), (iii) a tendency towards a calcified peridium (already present in the form of separate crystals in some species of *Lamproderma*), and (iv) the more or less abrupt branching of the columella in the middle of the sporotheca (present in some species of *Lamproderma* and most columellate members of the Physaraceae and Didymiaceae; however, *Physarum penetrale* has a columella reaching the top of sporotheca). It is noteworthy, that (v) nivicolous species are abundant among both the traditional Physarales and *Lamproderma* spp., but these are mostly absent in the true Stemonitidales (Poulain *et al.* 2011).

•••••• **Family Lamprodermataceae** T. Macbr., N. Amer. Slime-Moulds, Edn 2 (New York): 189 (1899) (B); **Lamprodermatidae** (Z)

Emended description. Fructifications without lime on the peridium, or lime present as a solitary, needle-like crystals (‘splinters’). Stalk epihypothallic. Capillitial threads dichotomously branching and anastomosing; lime nodes absent.

••••••• *Lamproderma* Rostaf., incl. *Diacheopsis* Meyl., *Colloderma* G. Lister, and *Elaeomyxa* Hagelst.

It is possible that this large genus is best circumscribed to include *Diacheopsis*, *Colloderma* and *Elaeomyxa*, but it cannot be ruled out that splitting it into several new genera will be a better solution when detailed molecular data become available.

In our phylogeny, *Lamproderma cacographicum* has an unsupported position within the Stemonitidaceae, while *L. scintillans* forms the most basal clade of the Physarales. If such a position is supported by future multigene phylogenies, both species must be transferred to separate genera.

••••••• [*Colloderma* G. Lister, J. Bot. 48:312 (1910)]

This genus is most likely not monophyletic, since the two sequenced species (*C. oculatum* and *C. robustum*) appear on different branches within the clade “*Lamproderma*” of Fiore-Donno *et al.* (2012). Both may be better accommodated in an enlarged genus *Lamproderma*.

••••••• [*Elaeomyxa* Hagelst., Mycologia 34(5):593 (1942)]

The single sequenced species branches within the clade “*Lamproderma*” and does not form a separate clade (Fiore-Donno *et al.* 2012).

••••••• [*Diacheopsis* Meyl., Bull. Soc. Vaud. Sci. Nat. 57:149 (1930)]

Most, if not all, taxa of the genus *Diacheopsis* seem to represent sessile forms of *Lamproderma* (Schnittler *et al.* 2012). In at least one case, sequences of a *Diacheopsis* were found to be identical to a species of *Lamproderma* (Fiore-Donno *et al.* 2012).

••••••• [*Collaria* Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C. 70(2): 208 (1967)]

This genus probably does not represent a natural group; at least one species (*C. rubens*) should be placed in the family Meridermataceae, while the taxonomic position of the others remains unclear.

•••••• **Family Didymiaceae** Rostaf. ex Cooke, Contr. Mycol. brit. 29 (1877) (B); **Didymiidae** (Z)

Description. Lime deposits usually present on the peridium and stalk, rarely found in the capillitium. Stalk, if present, subhypothallic. Capillitium thread-like, dichotomously branching and anastomosing but rarely forming a network, without lime nodes.

Several species within the traditional family Didymiaceae assume in our phylogeny an unresolved position within Physarales (see comments below).

••••••• *Diderma* Pers., Neues Mag. Bot. 1: 89 (1794)

Further investigations are needed to verify if the traditional separation between *Diderma* (granular lime) and *Didymium* (crystalline lime) is justified. At least one species of *Didymium* (*D. anellus*) is nested within the *Diderma* clade (Fiore-Donno *et al.* 2012). In our 18 rDNA phylogeny (Fig. 2), two studied species of *Diderma* and *D. anellus* occur at an unresolved position within Physarales. The study of Nandipati *et al.* (2012), focusing on the Physarales, gave a clearer picture.

••••••• *Didymium* Schrad., Nov. gen. pl. 20 (1797)

A detailed monographic study is needed to determine whether or not the majority of the species of *Didymium* form a monophyletic group. In our phylogeny, the seven analyzed species of the genus form three branches, with the first clustering with *Diderma* (*D. anellus*), the second branching together with *Protophysarum*, and the third branching together with *Mucilago*.

••••••• *Lepidoderma* de Bary, in Rostafiński, Vers. Syst. Mycetozoen 13 (1873)

As now circumscribed, this genus is probably not monophyletic (Schnittler, unpubl. results). The stalked species *L. tigrinum* seems to be closer to *Diderma* than to the other species of *Lepidoderma*, which are mostly plasmodiocarpic. In our phylogeny, *L. carestianum* assumes an unresolved position within Physarales, but in Nandipati *et al.* (2012) it is clearly placed within Didymiaceae.

••••••• *Mucilago* Battarra, Fungi arimin. 76 (1755)

Mucilago may be only an aethalioid form of *Didymium* and thus might not deserve generic rank. However, in the phylogeny of Nandipati *et al.* (2012), it occurs as a separate clade. The position of *M. crustacea* in our phylogeny also seems to support a separate genus.

•••••• **Family Physaraceae** Physaraceae Chevall., Fl. gén. env. Paris (Paris) 1: 332 (1826) (B); **Physaridae** (Z)

Description. Lime deposits usually present in the peridium, stalk and capillitium. Stalk, if present, subhypothallic. Capillitium hollow, forming a three dimensional network; capillitial tubes are filled with lime, either concentrated in the nodes or evenly distributed throughout the tubes.

For this family, our 18S rDNA phylogeny of all myxomycetes (Fig. 2) does not show sufficient resolution. We therefore based our classification on published phylogenies limited to the order Physarales (Fiore-Donno *et al.* 2008, 2010, Nandipati *et al.* 2012).

••••••• *Craterium* Trentep., in Roth, Catal. bot. 1:224 (1797)

At least some species assigned to this genus show affinities with *Physarum*. In the phylogeny of Nandipati *et al.* (2012), *C. minutum* appears as a separate clade, sister to *Leocarpus*.

••••••• *Leocarpus* Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 3:25 (1809)

More molecular data are needed to determine the systematic position of this monotypic genus. Species belonging to different genera, especially *Diderma miniatum* and *Physarum listeri*, share with *Leocarpus* the stiff, smooth, shining, colored, triple peridium, composed of an inner membranous wall (the true peridium), a solid layer of lime, and an outer pigmented layer. Another specific character of *Leocarpus*, the duality of its capillitium (some tubes are filled with lime, others are free of lime), seems to be unique within the Physaraceae.

••••••• *Fuligo* Haller, Hist. stirp. Helv. 3:110 (1768)

Transitional forms, such as *Fuligo cinerea*, connect this usually aethalioid genus to *Physarum.* Therefore, *Fuligo* may not constitute a monophyletic unit but simply accommodate these aethalioid forms. This is supported by our phylogeny, where two species of *Fuligo* branch within *Physarum*. However, other published data show that *Fuligo septica* may form a rather separate branch in a phylogeny of the Physarales (Nandipati *et al.* 2012). The position of *F. aurea* (= *Erionema aureum*) remains uncertain.

••••••• *Physarum* Pers., Neues Mag. Bot. 1:88 (1794), incl. *Badhamia* Berk.

Nandipati *et al.* (2012) found three well-separated clades for the genus; two of these contain, in addition to species of *Physarum*, all studied species of *Badhamia*, similar to the tree presented in Fig. 2. Future molecular investigations may split the species-rich *Physarum-Badhamia* complex into several genera.

••••••• *Physarella* Peck., Bull. Torrey Bot. Club 9(5):61 (1882)

The genus is nested within the *Physarum* branch but may represent a natural genus (*Physarum* does not). The deeply umbilicate sporotheca occurs not only in the single described species (*Ph. oblonga*) but also in *Physarum pezizoideum* and *Ph. javanicum*; as such, the genus might have to be enlarged.

••••••• *Physarina* Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl. 118: 431 (1909)

Partial 18S rDNA sequences suggest a position close to *Physarum* (Schnittler, unpubl. data).

••••••• *Kelleromyxa* Eliasson, in Eliasson, Keller & Schoknecht, Mycol. Res. 95(10): 1205 (1991)

A published phylogeny with this monospecific genus, together with our phylogeny, showed the position of *Kelleromyxa* at the base of the Physaraceae clade, which was used as the argument for establishing the separate family Kelleromyxaceae (Erastova *et al.* 2013). However, this decision is not mandatory since the cluster "*Kelleromyxa* + Physaraceae" still remains monophyletic.

[••••••• *Badhamia* Berk., Proc. Linn. Soc. London 2: 199 (1852)]

See comments under *Physarum*.

COLUMELLOMYCETIDAE INCERTAE SEDIS

••••••• *Diachea* Fr., Syst. orb. veg. 143 (1825)

With a capillitium forming a much-branched dendroid-like structure similar to what is found in the Lamprodermataceae but with a stalk and columella filled with lime crystals, this genus seems to be a missing link between the families Lamprodermataceae and Didymiaceae. In the phylogeny of Fiore-Donno *et al.* (2012) it appears as sister to the *Diderma* clade. In our phylogeny it forms one of the weakly supported basal clades of the Physarales.

••••••• *Echinosteliopsis* Reinhardt & L.S. Olive, Mycologia 58(6):967 (1967)

This genus, where flagellated amoebae have never been observed, was considered for a long time as a protosteloid amoeba with uncertain affinities (Spiegel 1990). Kang *et al.* (2017) and Fiore-Donno *et al.* (2018) showed that it is definitely a myxomycete and sister to Echinosteliidia. We follow the conclusion of the latter authors that a wider taxon sampling including more genes is desirable before proposing a higher-rank taxon to accommodate the single known species *E. oligospora*.

••••••• *Leptoderma* G. Lister, J. Bot. 51:1 (1913)

Molecular data are not available, but most likely this genus may occupy a position within the family Didymiaceae.

••••••• *Paradiachea* Hertel, Dusenia 7:349 (1956)

The similarity with both *Lamproderma* s. l. and *Diachea* does not allow us to choose the appropriate family for this genus thus far.

••••••• *Protophysarum* M. Blackw. & Alexop., Mycologia 67(1): 33 (1975)

This genus is certainly isolated but assumes contradicting positions in available phylogenies. It was first shown to be an isolated branch of the order Physarales (Fiore-Donno *et al.* 2008) but later as a member of the family Didymiaceae (see Fig. 3 in Fiore-Donno *et al.* 2012).

••••••• *Trabrooksia* H.W. Keller, Mycologia 72(2): 396 (1980)

Phylogenetic data are not available, but most likely this genus represents a limeless form of a *Didymium*.

••••••• *Willkommlangea* Kuntze, Revis. gen. pl. 2: 875 (1891)

A partial SSU sequence of the single species *W. reticulata* (Schnittler unpubl.) suggests a position within the family Physaraceae but outside of the genus *Physarum*.

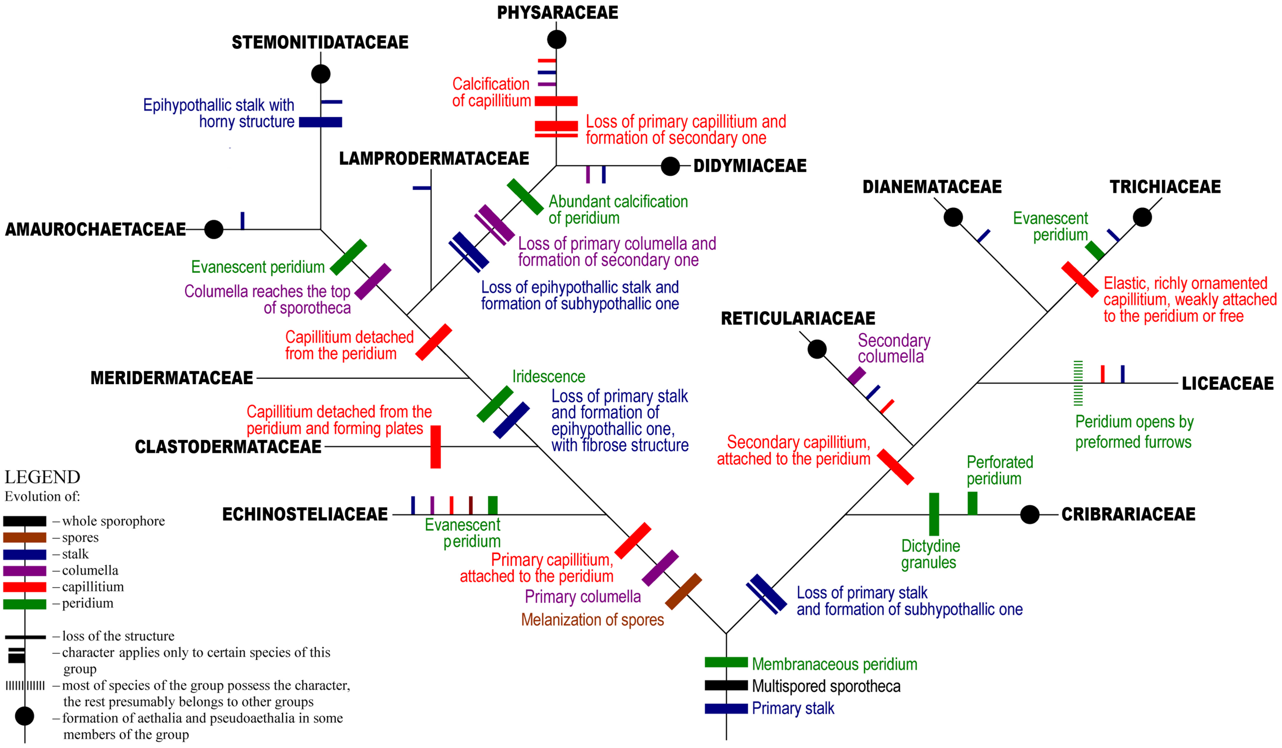


FIGURE 3. Evolution of morphological characters in Myxomycetes. The simplified tree (see Fig. 2 for an exact topology) presents a scheme for evolution of myxomycetes to the level of families. Changes in major morphological traits (see Fig. 1 for explanation) of the fructifications are shown in different colors.

Discussion

Position of the Myxomycetes within Amoebozoa.—The available phylogenies of Amoebozoa (Shadwick *et al.* 2009, Tice *et al.* 2016, Kang *et al.* 2017) support Myxomycetes as a monophyletic clade within the subgroup Evosea (Table 1). Within this group myxomycetes branch together with dictyostelids and three genera of fruiting amoebae (*Ceratiomyxa*, *Clastostelium* and *Protosporangium*), which comprise the group Protosporangiida, considered here as the class Ceratiomyxomycetes (Spiegel 1990, Shadwick *et al.* 2009, Fiore-Donno *et al.* 2010, Adl *et al.* 2012, 2018, Tice *et al.* 2016, Kang *et al.* 2017). The other members of the former class Protostelida branch together with other amoebozoan lineages (Shadwick *et al.* 2009) and are more distantly related to myxomycetes (Kang *et al.* 2017). These organisms, forming stalked fructifications with one to a few spores, are now called protosteloid amoebae (Spiegel 1990, Shadwick *et al.* 2009).

For the group including Myxomycetes, Dictyosteliomycetes and Ceratiomyxomycetes, Fiore-Donno *et al.* (2010) proposed the name Macromycetozoa, whereas Kang *et al.* (2017) restricted the traditional name Eumycetozoa to this group. This may cause confusion, because Eumycetozoa, as originally proposed by Olive and Stoianovitch (1975), included all of the protosteloid taxa (Table 1). However, if all the protosteloid amoebae with all their non-fruiting relatives are included, the group Eumycetozoa becomes nearly synonymous with the Amoebozoa and is therefore superfluous (Shadwick *et al.* 2009). To save this widely used name, we support its emendation by Kang *et al.* (2017).

Position of the genus Ceratiomyxa *within Amoebozoa.*—The genus *Ceratiomyxa* is definitely a member of the Eumycetozoa. However, should it also be considered as a member of the class Myxomycetes? Traditional classifications did so: *Ceratiomyxa* was the sole member of a separate subclass Exosporeae (=Ceratiomyxomycetidae) within the Myxomycetes, while the rest of myxomycetes were considered as a second subclass Endosporeae (=Myxogastromycetidae) (Rostafiński 1875, Lister 1925). An alternative view was proposed by Olive and Stoianovitch (1975), who transferred *Ceratiomyxa* to the newly created class Protostelia (=Protosteliomycetes Alexop. & Mims 1979). As explained above, this class was shown to be a polyphyletic group of spore-forming amoebozoans (Shadwick *et al.* 2009), and, compared with its other members, *Ceratiomyxa* assumes a position close to the endosporous Myxomycetes. This caused the revival of the traditional subclass Exosporeae and returned *Ceratiomyxa* back to the Myxomycetes (Cavalier-Smith 2013, Ruggiero *et al.* 2015, Kretzschmar *et al.* 2016). However, available phylogenies (Tice *et al.* 2016, Kang *et al.* 2017) group *Ceratiomyxa* with two other protosteloid genera, *Clastostelium* and *Protosporangium*. Kang *et al.* (2017), based on a broad sampling of transcriptomic data for 86 Amoebozoan taxa, found it as sister to only the Myxomycetes. Therefore, all phylogenies support the recognition of three classes within the Eumycetozoa: Dictyosteliomycetes, Ceratiomyxomycetes and Myxomycetes, as proposed in our classification.

Advantages and limitations of the proposed classification.—In contrast to data relating to the Amoebozoa in general, phylogenetic information within the Myxomycetes is largely limited to 18S rDNA and a few other genes, since most species cannot be cultured easily (Clark and Haskins 2010). Usually only dormant stages (spores) are readily available, which makes transcriptomes difficult to obtain. Although 18S rDNA is the marker of choice for barcoding protists in general (Adl *et al.* 2014) and myxomycetes in particular (Schnittler *et al.* 2017), it is a single gene with some disadvantages (see above).

In contrast to the previously published phylogenies based on manual alignments (Fiore-Donno *et al.* 2012, 2013, 2018), the phylogeny presented herein (Fig. 2) employs a fully reproducible approach, including automated alignment and automated selection of well-aligned conservative blocks. Due to the high within-group divergence (28.7% of all positions) we can retain less informative positions than for alignments with narrower taxonomic focus. Therefore, we based our proposal wherever possible on phylogenies of certain subgroups (Supplementary file 4).

The exact phylogenetic position of many species, often described from only a few records of fructifications (Schnittler and Mitchell 2000), is still unknown. Increased taxon sampling and multigene studies are needed to consolidate several of the branches recovered in 18S rDNA phylogenies (Figs. 2). In addition, 18S rDNA sequences seem to produce long branches in a few myxomycete taxa (e.g., *Stemonitopsis*), and due to long-branch attraction this may result in an incorrect position of these taxa in phylogenies.

Of the five hitherto recognized orders of endosporous myxomycetes, only Trichiales and Physarales seem to be monophyletic. However, taking into account the transfer of the Lamprodermataceae to the Physarales and of several genera, such as *Dictydiaethalium*, to the Trichiales, none of the nine orders proposed herein is identical in species content to one of the five traditional orders.

Morphological traits in the light of molecular data.—The comparatively rich display of morphological characters in myxomycete fructifications (Keller *et al.* 2017) allows us to compare phylogenies with morphological data to elucidate the evolution of major traits concerning sporocarp structures (Fig. 3).

TABLE 1. The names of higher-rank taxa, which include myxomycetes.
Groups including myxomycetes are shown in grey.

<table>
<tr><th>Taxa traditionally recognized as “slime molds”</th><th colspan="4">Traditional meaning of names</th><th colspan="5">Meaning of names used in this paper</th></tr>
<tr><td><i>Endostelium</i>
<i>Protosteliopsis</i>
<i>Luapelamoeba</i></td><td rowspan="11">Mycetozoa
= Slime molds</td><td rowspan="7">Eumycetozoa s.l.
= Myxomycota
= True slime molds</td><td colspan="2" rowspan="4">Protosteliomycetes
= Protostelida</td><td rowspan="8">Amoebozoa</td><td colspan="4">members of Discosea</td></tr>
<tr><td>Protosteliids s.str.
Schizoplasmodiids
Soliformoviids
Cavosteliids</td><td rowspan="7">Tevosa</td><td rowspan="6">Evosea</td><td colspan="2">members of Variosea</td></tr>
<tr><td><i>Clastostelium</i></td><td rowspan="5">Eumycetozoa s.str.
= Macromycetozoa</td><td rowspan="3">Ceratiomyxomycetes
= Ceratiomyxea
= Protosporangiida</td></tr>
<tr><td><i>Protosporangium</i></td></tr>
<tr><td><i>Ceratiomyxa</i></td><td rowspan="2">Myxomycetes s.l.</td><td>Exosporeae</td></tr>
<tr><td>Myxomycetes</td><td>Myxogastrea
= Endosporeae</td><td>Myxomycetes s. str.
= Myxogastrea</td></tr>
<tr><td>Dictyostelids</td><td colspan="2">Dictyosteliomycetes
= Dictyostelida</td><td>Dictyosteliomycetes
= Dictyostelea</td></tr>
<tr><td>Copromyxids</td><td colspan="3" rowspan="3">Acrasiomycota (sometimes included dictyostelids)</td><td colspan="3">members of Tubulinea</td></tr>
<tr><td>Fonticulids</td><td colspan="5">members of Opisthokonta</td></tr>
<tr><td>Acrasids</td><td colspan="5">members of Excavata</td></tr>
<tr><td>Plasmodiophorids</td><td colspan="3">Plasmodiophoromycota</td><td colspan="5">members of Rhizaria</td></tr>
</table>

Spore color. The last common ancestor of myxomycetes is likely to possess hyaline spores, as present in all Ceratiomyxomycetes (Spiegel *et al.* 2007, Kang *et al.* 2017). Spores become clearly melanized only within the Columellomycetidae. This character may have been secondarily lost in the genus *Echinostelium* (Fiore-Donno *et al.* 2012), or not yet developed, since a faint melanization has never been ruled out for this genus. Members of the Lucisporomycetidae never possess highly melanized spores (with melanin giving visible color); instead, the evolution of various other spore pigments occurred independently within this subclass (Wang *et al.* 2017).

Stalk formation. For fruiting members of the Amoebozoa, stalk formation is most likely an ancestral character (Kang *et al.* 2017). Protosteloid amoebae have a stalk excreted from a single cell, which may cleave into several spores (Spiegel *et al.* 2018). The Echinosteliaceae (Haskins 1968) may have inherited this type of the stalk from Ceratiomyxomycetidae (Clark and Haskins 2014), but in their multispored fructifications the stalk is usually reinforced by granular deposits, and its upper part may become connected with the true columella (see below). This, perhaps extraprotoplasmic, secretion of an originally hollow (Mims 1973) stalk in Echinosteliales was previously named the third (beside epi- and subhypothallic) type of stalk development (Clark and Haskins 2014), but seems to be ancestral to the epi- and subhypothallic type. Here, this type is referred to as the primary stalk.

The intraprotoplasmic secretion of amorphous matter into vacuoles (Mims 1973) allowed the formation of more flexible and longer stalks, called epihypothallic (Clark and Haskins 2014). This stalk is connected to the columella and capillitium, both formed within an anastomosing system of tubular vacuoles, and may represent a continuation of the capillitium beyond the sporotheca. The transition between the primary and the epihypothallic stalk is probably visible in the genus *Clastoderma*, where the basal part of the stalk is hollow and stuffed with granular matter, as it may happen in a primary stalk, while the upper part, smoothly passing into the capillitium, may represent a rudiment of the epihypothallic stalk. In Meridermatales, Stemonitidales and part of Physarales (Lamprodermataceae) the primary stalk is completely replaced by the epihypothallic one (Fiore-Donno *et al.* 2008).

In the subclass Lucisporomycetidae the primary stalk may have been completely lost (although the slender stalks of small species of *Cribraria* may still represent primary stalks reinforced with granular matter, Clark and Haskins 2014). In other members of the subclass it was secondarily replaced by subhypothallic stalk, formed by a constriction of the peridium (which may, similar to the primary stalk, be reinforced by granular matter, or spore-like cells). In the subclass Columellomycetidae, in a similar way the epihypothallic stalk has been lost in Didymiaceae and Physaraceae, and was also replaced by a subhypothallic one. Therefore, subhypothallic stalks evolved at least two times independently (Clark and Haskins 2014).

Columella. A primary columella, connected with the capillitium, appears early in the evolution of the subclass Columellomycetidae, in *Echinostelium arboreum* (Haskins and McGuiness 1989) or *Barbeyella minutissima* (Schnittler *et al.* 2000), and first coexists with a primary, later with an epihypothallic stalk. In the Clastodermatales, the columella extends to form the upper portion of the stalk which may be epihypothallic in nature. The Meridermatales, Stemonitidales and Lamprodermataceae develop a fully epihypothallic stalk connected with a columella.

Together with the epihypothallic stalk, the columella apparently became lost in the families Didymiaceae and Physaraceae, although in some species of these families the tip of the subhypothallic stalk may form a columella-like extension protruding into the sporotheca, e.g., *Didymium* (Clark *et al.* 2001, Clark and Haskins 2014). This structure may be considered as the secondary columella. In some species of *Physarum*, lime nodes may condense at the bottom of the sporotheca, forming a structure called a pseudocolumella (Fig. 1).

In the Lucisporomycetidae the primary columella is completely absent, since the primary stalk is lost (*Cribraria* may be an exception, Clark and Haskins 2014). However, the tubular structures found in *Tubifera casparyi* (Leontyev 2016), which probably originate from the peridium of adjacent sporocarps, may be termed a secondary columella.

Capillitium. In the multispored myxomycetes, this structure prevents the spore mass against detaching from the stalk and allows spores to disperse separately as they dry out. The primary capillitium appeared early in the evolution of the Columellomycetidae and was most likely connected to the peridium. This trait is preserved in *B. minutissima*, *E. arboretum* (Schnittler *et al.* 2000) and species of *Meriderma* (Poulain *et al.* 2011), all taxa found within deep branches in the Columellomycetidae. In most other dark-spored myxomycetes the connection between capillitium and peridium is absent. Although the epihypothallic stalk was lost, a primary capillitium seems to be preserved in the family Didymiaceae. In the family Physaraceae the tubular capillitium can accumulate lime granules; therefore, we suppose that in this group the primary capillitium may have been replaced by a secondary one (Fig. 3).

In all of the Lucisporomycetidae a primary capillitium was lost together with the primary stalk and columella, or these structures never evolved. Capillitia in this group show mostly tubular structure and originate from the peridium, not from a primary columella (McHugh and Reid 2008, Leontyev *et al.* 2014c). The similarity between some members of Lucisporomycetidae (*Alwisia*, and *Dianema*) and Columellomycetidae (*Barbeyella* and *Meriderma*), both of which possess funnel-like junctions between the capillitium and peridium, is probably an example of convergent evolution.

Peridium. This structure is known for all multispored myxomycetes and may be considered as an apomorphic character for the class Myxomycetes. It is evanescent in the genus *Echinostelium*, in most members of the order Stemonitidales and in numerous Trichiales. In the genus *Cribraria* the perforated peridium seems to take over the function of the missing capillitium, regulating spore dispersal by preventing the spores to fall out all at once. In *Licea*, *Perichaena*, *Arcyria* and other bright-spored genera, the peridium usually opens by preformed furrows, being divided into the lid and a cup-like structure or separated into polygonal plates. In the families Didymiaceae and Physaraceae the peridium is usually reinforced with crystalline or granular lime. Incomplete calcification is also observed in some members of the Lamprodermataceae. In the Lucisporomycetidae the peridium is mineralized as is also the case for some members of the Trichiaceae (*Perichaena*) and Cribrariaceae (*Cribraria* and *Lindbladia*); in the latter family calcium compounds occur as dictydine granules (Schoknecht and Keller 1989, Lado and Eliasson 2017, Keller *et al.* 2017).

*Reductive evolution.—*The loss of entire structures, often connected with miniature sporocarps, occurs throughout the tree of myxomycetes (Fig. 3). This is most prominent for the loss of a stalk, which occurred in all families except for the Clastodermataceae and Meridermataceae. The stalk elevates spores above a film of water covering the substrate, thus allowing them to dry out and then become airborne (Schnittler *et al.* 2012). For species inhabiting substrates that dry out rapidly, the resources required for producing a stalk can be saved. But for substrates that stay permanently wet, a stalk is necessary, and indeed it has been found that fructifications of widely distributed morphospecies possess longer stalks in moist tropical regions compared to periodically dry temperate regions (Stephenson *et al.* 2004, 2008). Although the presence/absence of a stalk was often used to delimit genera (e.g., *Echinostelium*/*Semimorula* and *Lamproderma*/*Diacheopsis*), clades defined by molecular data often unite sessile and stalked forms. The two largest genera of the order Physarales (*Didymium* and *Physarum*) include both species with stalked and sessile sporocarps.

Similarly common is the loss of a primary capillitium parallel to the miniaturization of fructifications. This can be observed in the Echinosteliales (*Echinostelium colliculosum*) and in some members of the Physarales (*Didymium eremophilum*, *Kelleromyxa fimicola*). The same applies to the secondary capillitium found in bright-spored myxomycetes in the Liceaceae (all except for *Listerella*) and the Trichiaceae (e.g., *Perichaena liceoides*). Reductive evolution is usually accompanied in myxomycetes by a shortening of the life cycle (Schnittler 2001). Prominent examples are the bark-inhabiting (corticolous) myxomycetes in which the full lifecycle may take several days (Mitchell 1978, Ing 1994).

In general, the lack of morphological structures is not a good predictor for monophyly, as shown by the breakdown of the classical order Liceales and the genus *Licea* (Eliasson 1977, 2017, Lado and Eliasson 2017).

*Compound fructifications.—*Whereas small plasmodia usually form a single fructification (Spiegel *et al.* 2018), large ones may segregate into smaller units shortly before fructification, and each independently forms a sporocarp. Plasmodial segregation may be an ancient character, as it occurs in other Evosean lineages (Fractovitelliida *sensu* Kang *et al.* (2017), the genera *Schizoplasmodium*, *Nematostelium* and *Ceratiomyxella*; the Cavosteliid *Schisoplasmodiopsis pseudoendospora*) and in most species of myxomycetes, including such with sessile sporocarps. However, in some myxomycete lineages this segregation was secondarily reverted. In these taxa the single sporocarps are merged into compound fructifications, formed by discernible (pseudoaethalia) or completely fused (aethalia) sporocarps (Fig. 1). Some compound fructifications of myxomycetes resemble puffballs and indeed have been confused with those (*Schenella*, see Estrada-Torres *et al.* 2005). These changes were accompanied by the ultimate loss of the stalk, a tremendous increase in size of the fructification, and often by different spore dispersal strategies (dispersal by insects or raindrops). Some ethaliate and pseudoaethaliate taxa eveloved reticulate, highly hydrophobic spores, adapted for dispersal by rain (Eliasson 1977).

The formation of compound fructifications occurred independently in nearly all major branches of the myxomycetes (Fig. 3). Several families comprise species with solitary sporocarps (+), fascicled sporocarps, sharing a common stalk (++), pseudoaethalia (+++), and aethalia (++++):

Cribraria + → *Lindbladia* +++ → *Licaethalium* ++++ (Cribrariaceae);
Alwisia +, ++ → *Tubifera* +++ → *Reticularia* ++++ (Reticulariaceae);
Arcyria cinerea + → *A. cinerea* var. *digitata* ++ → *Arcyriatella* +++ (Trichiaceae);
Stemonitis + → *Symphytocarpus* +++ (Stemonitidaceae);
Comatricha + → *Stemonaria* +, ++ → *Amaurochaete* ++++ (Amaurochaetaceae);
Didymium + → *Didymium crustaceum* ++ → *Mucilago* +++ (Didymiaceae).

Species with compound fructifications are highly conspicuous, and separate genera have been erected for most of them. However, in molecular phylogenies they often branch within clades composed of species developing individual sporocarps (e.g., *Lindbladia tubulina*). This raises concern about the justification of separate genera for compound-fruiting species.

New diagnostic characters.—In contrast to the traditionally recognized conspicuous traits, we expect that more inconspicuous, even not yet discovered, characters will support much better a system based on molecular data. An example is the structure of the peridium and its connection with the capillitium, which substantiates the separation of the genus *Meriderma* from *Lamproderma* (Poulain *et al.* 2011). Hollow stalks filled with spore-like cells represent another, hitherto overlooked, character that may support the inclusion of the species *Trichia decipiens* into a modified genus *Hemitrichia* (Fiore-Donno *et al.* 2013). Such inconspicuous characters may escape selective pressure, thus becoming somewhat independent from variation in ecological conditions and therefore remaining in nearly all members of the lineage. In contrast, characters of the fructification that affect dispersal abilities of spores depend strongly upon the environment. Some of the most conspicuous characters (fructification type, degree of stalk and capillitium reduction) may have evolved several times independently, as it was predicted by L.S. Olive (Olive and Stoianovitch 1975).

Competing species concepts for myxomycetes.—Several recent studies discovered multiple biological species nested within morphologically described species in myxomycetes (Feng and Schnittler 2015, Feng *et al.* 2016, see discussion in Walker and Stephenson 2016). This will significantly increase species numbers (Feng and Schnittler 2017) but hardly shatters the foundations of a natural classification of the group as outlined in this study. Reproductive isolation within morphospecies, which often leads to the formation of cryptic biospecies, is a consequence of the ancestral sexuality of amoebae (Lahr *et al.* 2011, Spiegel 2011, Tekle *et al.* 2017). At the species level, the challenge is to bring the traditional morphospecies concept in accordance with the biospecies concept, which was originally developed for a few taxa which could be cultured (Clark and Haskins 2014).

Myxomycete taxonomy now seems to have reached a point at which research in other groups of organisms arrived three decades ago. Molecular data have shattered the traditional system which had been accepted for a long time but are not yet sufficient to construct a fully comprehensive natural system down to the species level. Of the approximately 1000 currently accepted species (Lado 2005–2018), virtually all of which were described on the basis of a morphospecies concept, about 150 dark-spored and 70 bright-spored are represented by ca. 1000 partial 18S rDNA sequences (see supplementary files in Borg Dahl *et al.* 2018), while complete 18S rDNA sequences are known for a much smaller number of species (Supplementary files 2–4). For this reason, new combinations for species names should be postponed until the respective genus or family has been treated in a monographic manner by a combination of morphological and molecular methods. The suggestions presented herein may provide a starting point for such efforts.

Acknowledgements

This research was partially supported by a grant from the Deutsche Forschungsgemeinschaft to MS and DL (RTG 2010 "RESPONSE") and a Fulbright Scholarship to DL (grant 68130017). Additional support was provided by the Slime Mold Project at the University of Arkansas (SLS), by the Russian Foundation of Basic Research (18-04-01232A, YN and OS) and the Program "Biodiversity, ecology, structural and functional features of fungi and fungus-like protists" (AAAA-A19-119020890079-6, YN and OS). In addition, YN and OS acknowledge the use of equipment of the Core Facility Center "Cell and Molecular Technologies in Plant Science" at the Komarov Botanical Institute RAS (St. Petersburg). We are especially grateful to Dr. Scott A. Redhead (Ottawa, Canada) for his helpful comments on questions relating to botanical nomenclature, to Carlos Lado (Madrid, Spain) for his input relating to the taxonomic status of many of the names included herein, to Dr. Fred W. Spiegel and Dr. Lora Shadwick (Fayetteville, Arkansas) for fruitful discussions, especially regarding the evaluation of phylogenetic data, to anonymous reviewers whose comments and suggestions helped to make this paper much more accurate and neat.

This publication is dedicated to the memory of the late Prof. Dr. Irina O. Dudka (1934–2017), who inspired DL to begin the work on this paper.

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