# Myxomycetes

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**Abstract**

The myxomycetes (class Myxogastria), also commonly known as plasmodial slime molds or acellular slime molds, are the most species-rich group within the Amoebozoa, with approximately 1,000 morphologically recognizable species having been described. These organisms are free-living predators of bacteria and other eukaryotic protists. Myxomycetes have been recorded from every terrestrial habitat investigated to date. The two trophic stages (amoeboflagellates and plasmodia) in the life cycle are usually cryptic, but the fruiting bodies are often large enough to be observed directly in nature. Fruiting bodies release airborne spores that are dispersed by air or, more rarely, animal vectors. Myxomycetes are associated with a wide variety of different microhabitats, the most important of which are coarse woody debris, ground litter, aerial litter, and the bark surface of living trees. Specimens can be obtained as fruiting bodies that have developed in the field under natural conditions or cultured in the laboratory. A substantial body of data on the worldwide biodiversity and distribution of myxomycetes has been assembled over the past 200 years, but there is a relative lack of molecular data, since myxomycetes are neither pathogenic nor of

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economic importance. However, recent studies have produced the first, albeit still incomplete, molecular phylogenies of the group. Moreover, there appears to be a much higher level of diversity on the molecular level than reflected in the number of morphospecies, with the latter often consisting of reproductively isolated populations which can be considered as biospecies.

**Keywords**

Amoebozoa • Biodiversity • Biospecies • Ecology • Introns • Plasmodial slime molds • Soil microbiology • Molecular phylogeny

## Contents



## Summary Classification

●**Myxogastria**
●●**Collumellidia**
●●●**Echinosteliales** (e.g., *Echinostelium*)
●●●**Physarales** (e.g., *Badhamia*, *Didymium*, and *Physarum*)
●●●**Stemonitales*** (e.g., *Meriderma* and *Stemonitis*)
●●**Lucisporidia**
●●●**Liceales*** (e.g., *Licea* and *Lycogala*)
●●●**Trichiales** (e.g., *Trichia* and *Hemitrichia*)

* Paraphyletic, based on molecular phylogenetic evidence; see Table 1 for comparison of traditional classification and groupings based on molecular phylogenetics.

## Introduction

### General Characteristics

One of the major branches of the eukaryotic tree of life consists of an assemblage of amoeboid protists referred to as the supergroup Amoebozoa, which are close relatives to the Opisthokonta (Holozoa and Holomycota) as indicated by Baldauf (2008) and Bapteste et al. (2002). Dictyostelid (cellular) and true (acellular) slime molds are part of the Amoebozoa (Pawlowski and Burki 2009) the myxomycetes (class Myxogastria) are one of the most diverse groups in the Amoebozoa. Myxomycetes (also known as plasmodial slime molds or myxogastrids) are a group of free-living terrestrial heterotrophs with complex life cycles. The unicellular forms are amoebae and flagellates (collectively, the "amoeboflagellate" stage). These develop, usually via sexual fusion, into a multinucleate "plasmodium" stage, which is also trophic. The plasmodium stage can produce fruiting bodies, which release airborne spores that are dispersed by air or, more rarely, animal vectors. The amoeboflagellates and plasmodia are usually cryptic, but the fruiting bodies are often large enough to be observed directly in nature. Myxomycetes have been recorded from every terrestrial habitat investigated to date. They are associated with a wide variety of different microhabitats, the most important of which are coarse woody debris, ground litter, aerial litter, and the bark surface of living trees. Specimens can be obtained as fruiting bodies that have developed in the field under natural conditions or cultured in the laboratory. A substantial body of data on the worldwide biodiversity and distribution of myxomycetes has been assembled over the past 200 years, but there is a relative lack of molecular data, since myxomycetes are neither pathogenic nor of economic importance.

Since their discovery, the myxomycetes have been variously classified as plants, animals, or fungi. Because they produce aerial spore-bearing structures that resemble those of certain fungi and typically occur in some of the same ecological situations as fungi, myxomycetes have traditionally been studied by mycologists (Martin and Alexopoulos 1969). Indeed, the name most closely associated with the group, first used by Link (1833) more than 175 years ago, is derived from the Greek words *myxa* (which means slime) and *mycetes* (referring to fungi). However, abundant molecular evidence now confirms that they are amoebozoans and not fungi (Yoon et al. 2008). Interestingly, the fact that myxomycetes are protists was first pointed out by de Bary (1864) more than a century and a half ago, and he proposed the name Mycetozoa (literally meaning "fungus animal") for the group. However, myxomycetes continued to be considered as fungi by most mycologists until the latter half of the twentieth century and are still governed by the Botanical Code of Nomenclature.

### Other Similar Microorganisms

The myxomycetes are the most prominent representatives of a guild of sometimes unrelated nonpathogenic microorganisms that share a number of ecological features

(Schnittler et al. 2006). For this reason, some of these non-related forms can be confused with myxomycetes (see below). All of these organisms have a free-living, predatory lifestyle and a life cycle that begins with solitary amoeboid cells. The latter increase their biomass by aggregation of cells or by undergoing nuclear divisions without cell division (e.g., the plasmodia of myxomycetes) and convert this biomass into typically stalked fruiting bodies that can develop within hours or days. These fruiting bodies are produced not as a true growth process but by rearrangement of the available biomass, ultimately to release propagules for (potentially, at least) long-distance dispersal. The production of airborne propagules is the key innovation that enables these microorganisms to colonize terrestrial habitat islands with a locally higher density of microbes serving as prey (Schnittler and Tesmer 2008).

Myxomycetes are neither pathogenic nor of economic importance. Only a few model species, especially *Physarum polycephalum* and *Didymium iridis*, have been used to investigate cell division and developmental biology in myxomycetes (Hüttermann 1973) or the importance of mating type genes (Collins 1979) and the distribution of group I introns in these organisms (Wikmark et al. 2007; Feng and Schnittler 2015).

Other non-related members of this guild include the prokaryotic myxobacteria (a group consisting of perhaps 40–60 species), which produce fruiting bodies that in some species can reach a height of as much as 1 mm (Reichenbach 1993). Their spores are distinctly smaller than the smallest myxomycete spores, which usually fall within the range of (4–)7–12(–22) μm. Eukaryotic microorganisms with a similar lifestyle are the sorocarpic amoebae formerly known as the acrasid cellular slime molds or Acrasea (Olive 1975; Stephenson 2014). This is a group of approximately 20 species now known to be polyphyletic, containing aggregating, fruiting body-forming amoebae of different supergroups, with most not belonging to the Amoebozoa (Brown et al. 2009, 2010, 2012). Examples include the genera *Acrasis*, *Copromyxa*, *Guttulinopsis*, and *Fonticula* (Dykstra and Keller 2000; Brown et al. 2012). All these genera form fructifications by the aggregation of amoebae; *Acrasis* possesses a cellular stalk, whereas the others form sessile fruiting bodies. The ciliate genus *Sorogena* (Colpodea) produces stalked fruiting bodies strikingly similar to those found in myxomycetes, but the spores contain both a micro- and a macro-nucleolus (Bardele et al. 1991; Sugimoto and Endoh 2008).

## Other Eumycetozoan Slime Molds

The eumycetozoans as defined by Olive (1975) include the Myxogastria (true or acellular slime molds, myxomycetes), the paraphyletic protosteloid amoebae (protostelids; see ▶ Protosteloid Amoebae (Protosteliida, Protosporangiida, Cavosteliida, Schizoplasmodiida, Fractoviteliida, and Sporocarpic Members of Vannellida, Centramoebida, and Pellitida)), and the Dictyostelia (dictyostelid cellular slime molds or dictyostelids; see ▶ Dictyostelia). There are approximately 160 species known for the Dictyostelia (Romeralo et al. 2011) and about 35–40 species for the protosteloid amoebae (Spiegel et al. 2004), whereas at least 1,000 morphologically recognizable species of myxomycetes have been described (Lado 2005–2016).

**Fig. 1** Fruiting bodies of *Ceratiomyxa fruticulosa*, the most commonly encountered species *Ceratiomyxa*. What is recognized as *C. fruticulosa* is most likely a species complex, with one of the morphotypes producing exclusively cylindrical fruiting bodies as it can be observed in this image. These consist, in contrast to all other myxomycetes, of a slimy matrix and solitary spores which develop on tiny stalks, giving the surface of the fruiting body a fur-like appearance (Photograph by M. Schnittler)

As recognized by Olive (1975), both the Myxogastria and protosteloid amoebae are sporocarpic, with fruiting bodies ultimately derived from a single amoeboid cell. In contrast, the fruiting bodies in the Dictyostelia are derived from an aggregation of amoebae. Both the Myxogastria and Dictyostelia appear to represent monophyletic groups (Fiore-Donno et al. 2010a; Schaap et al. 2006), whereas the protosteloid amoebae are found in several lineages throughout the Amoebozoa, although apparently restricted to the Conosa (Shadwick et al. 2009; Adl et al. 2012).

In all but the most recent treatments of the myxomycetes, the four described species of the genus *Ceratiomyxa* were considered as part of the Myxogastria as the sole members of its own order, Ceratiomyxales (Fig. 1). However, these organisms differ by exogenous spore development (solitary spores are formed individually on stalks emerging from a joint matrix) from all other myxomycetes (in which spores develop inside a fruiting body surrounded, at least in the early stages, by a peridium). It has been suggested that they should be regarded as a sister group to the Myxogastria (Fiore-Donno et al. 2008, 2010a), and there are as well treatments which consider them with the protostelids (Olive 1970, 1975; Olive and Stoianovitch 1979; Adl et al. 2012), a group better referred to as the protosteloid amoebae (Shadwick et al. 2009). Chapter 36, ▶ Protosteloid Amoebae (Protosteliida, Protosporangiida, Cavosteliida, Schizoplasmodiida, Fractoviteliida, and Sporocarpic Members of Vannellida, Centramoebida, and Pellitida) assigns *Ceratiomyxa* to the taxon Protosporangiida (and does not employ the taxon Ceratiomyxales). Nevertheless, they are mentioned in this chapter because of their long history of study as myxomycetes. Other than *Ceratiomyxa*, all of the organisms assigned to the myxomycetes constitute a well-defined monophyletic group traditionally placed into five different taxonomic orders (Echinosteliales, Liceales, Trichiales, Stemonitales, and Physarales; Martin and Alexopoulos 1969).

## Occurrence and Distribution

Myxomycetes can be detected directly in the field by fruiting bodies (about 60% of all known species). Over the past 200 years, a substantial body of data on their worldwide diversity and distribution has been assembled (Stephenson et al. 2008). More recent studies have incorporated the use of moist chamber cultures (Stephenson and Stempen 1994), and about 40% of all species of myxomycetes are known primarily or even exclusively from specimens appearing in moist chamber (or sometimes, agar) cultures (Schnittler et al. 2015). Checklists are available for a number of regions of the world, such as arctic and boreal zones (Stephenson et al. 2000), Africa (Ndiritu et al. 2009), and the Neotropics (Lado and Wrigley de Basanta 2008). This is quite unlike the situation that exists for most other protists, for which distributional data are often very limited. Based on recordable occurrence of fruiting bodies, methods of community ecology can be applied to study these organisms (e.g., Stephenson 1988; Stephenson et al. 1993; Schnittler 2001b; Rojas and Stephenson 2011) and have shown surprisingly narrow ecological niches for some species.

It seems certain that the trophic stages of myxomycetes, especially the amoebae, have a much wider distribution in nature than reflected by the occurrence of fruiting bodies. In fact, some species may have lost the ability to fruit altogether. For example, molecular phylogeny shows the free-living amoebae formerly treated as *Hyperamoeba* are instead several different lineages of myxomycetes (Fiore-Donno et al. 2010b). These have been recovered from artificial as well as natural aquatic environments, including the coelomic cavity of sea urchins (Karpov and Mylnikov 1997; Zaman et al. 1999). An RNA-based study (Urich et al. 2008) identified the amoebae of eumycetozoans as a key group of soil microbes. Studies that have used environmental PCR to investigate the presence of myxomycetes in alpine soils (Kamono et al. 2012; Clissmann et al. 2015; Fiore-Donno et al. 2016) recovered numerous sequences hitherto not known from fruiting bodies.

Due to their dormant stages (spores can survive for decades, microcysts and sclerotia for months to years), myxomycetes are capable of surviving under rather severe environmental conditions, even the extremely xeric conditions found in the Atacama Desert (Lado et al. 2007; Wrigley de Basanta et al. 2012), parts of the Arabian Peninsula (Schnittler et al. 2015), and Mongolia (Novozhilov and Schnittler 2008). In theory, long-distance dispersal by means of spores (Kamono et al. 2009) would seem to provide myxomycetes with the potential to occur anywhere on the earth, but the actual distribution of most species is usually determined by the availability of suitable microhabitats for their establishment, growth, and development (Schnittler et al. 2000). However, global patterns of distribution do appear to exist as well, since some species are predominantly subtropical to tropical, whereas others are restricted to temperate regions of the world (Stephenson et al. 2008). Temperature certainly limits the formation of fruiting bodies in tropical species, which sometimes appear in Europe in greenhouses. However, habitat preferences are currently known only from fruiting bodies. Future studies that make use of environmental PCR (as noted above) may provide a very different picture of myxomycete distribution.

## History of Knowledge

Since Linnaeus provided the first descriptions of a few organisms now known to be myxomycetes (e.g., *Lycoperdon epidendrum*, the original name for the common species *Lycogala epidendrum*), the nomenclatural starting point for the taxonomy of the group is the publication of *Species Plantarum* in 1753. The first noteworthy taxonomic treatment of the myxomycetes was published by de Bary (1859), who was the first to conclude that these organisms are protists and not fungi. Rostafinski, a student of de Bary, is credited with producing the first relatively comprehensive monograph (Rostafinski 1873, 1874–1876), albeit in Polish. However, much of the information in the monograph was made available in English publications by Cooke (1877) and Massee (1892).

The single most significant pre-twentieth century publication on the myxomycetes was the first edition of Arthur Lister's *A Monograph of the Mycetozoa* (Lister 1894). This monograph, revised and expanded versions were published by his daughter Gulielma Lister (1911, 1925), became the standard reference to the myxomycetes during the early part of the twentieth century. Thomas Macbride published the first edition of his book *The North American Slime-Moulds* in 1899 and followed this with a greatly expanded second edition in 1922. These two works (Macbride 1899, 1922) are of particular importance because they were the basis of yet another work, *The Myxomycetes*, which Macbride coauthored with George Martin (Macbride and Martin 1934). Several decades later, Martin collaborated with Constantine Alexopoulos to produce their comprehensive world monograph, *The Myxomycetes* (1969). The Martin and Alexopoulos monograph, published by the University of Iowa Press, still remains the single most definitive treatment for the myxomycetes.

Until recently, identification of myxomycetes was based almost exclusively upon morphological characters of the fruiting body (Martin and Alexopoulos 1969), and keys and descriptions to the various morphospecies have been provided in a number of monographs over a period of almost a century and a half (e.g., Rostafinsky 1874–1876; Lister 1894, 1911, 1925; Martin and Alexopoulos 1969; Nannenga-Bremekamp 1991; Neubert et al. 1993, 1995, 2000; Ing 1999; Stephenson 2003; Poulain et al. 2011). However, recent molecular phylogenies (Fiore-Donno et al. 2012, 2013) show that the classical system of classification used for myxomycetes is in need of revision (see Table 1).

## Practical Importance

Myxomycetes are neither pathogenic nor of economic importance. Only a few model species, especially *Physarum polycephalum* and *Didymium iridis*, have been used to investigate cell division and developmental biology in myxomycetes (Hüttermann 1973) or the importance of mating type genes (Collins 1979) and the distribution of group I introns in these organisms (Wikmark et al. 2007; Feng and Schnittler 2015).

**Table 1** Comparison between the traditional classification of myxomycetes followed in most monographs and groupings emerging from molecular phylogenetics. Only important genera (e.g., isolated position or species-rich) are listed

| Groups supported by molecular phylogenies | Traditional classification |
|---|---|
| Myxogastria[a] | Class Myxogastria (myxomycetes) |
| Dark-spored basal clade/Collumellidia[b] | |
| Echinosteliid superclade (*Echinostelium*) | Order Echinosteliales |
| Fuscisporoid superclade | |
| Meridermid clade (*Meriderma*) | Order Stemonitales *pro parte (p.p.)*[d] |
| Stemonitid clade (*Stemonitis*, *Comatricha*) | Order Stemonitales *p.p.*[e] |
| Lamprodermid clade (*Badhamia*, *Physarum*, *Didymium*, *Lamproderma*) | Orders Physarales, Stemonitales *p.p.*[f] |
| Bright-spored basal clade/Lucisporidia[c] | |
| Cribrarioid superclade (*Cribraria*) | Order Liceales *p.p.*[g] |
| Trichioid superclade | |
| Reticularioid clade (*Lycogala*, *Reticularia*, *Tubifera*) | Order Liceales *p.p.*[h] |
| Liceoid clade (*Licea*) | Order Liceales *p.p.*[i] |
| Trichoid clade (*Arcyria*, *Hemitrichia*, *Trichia*) | Order Trichiales[j] |

[a]The genus *Ceratiomyxa*, highly distinct from all other members of the group, is probably best excluded from the Myxogastria, which is supported by current molecular investigations (Kretzschmar et al. 2016). This would make endogenic spore formation a uniting character for all Myxogastria. *Ceratiomyxa* shows affinities to some of the protostelids, which are not a monophyletic group (Shadwick et al. 2009, ▶ Protosteloid Amoebae (Protosteliida, Protosporangiida, Cavosteliida, Schizoplasmodiida, Fractoviteliida, and Sporocarpic Members of Vannellida, Centramoebida, and Pellitida))

[b]Dark-spored myxomycetes sensu Cavalier-Smith (2013): spores with melanin (except for *Echinostelium*), therefore usually violaceous brown in color

[c]Bright-spored myxomycetes sensu Cavalier-Smith (2013): spores with various other pigments (yellowish or reddish colors)

[d]*Meriderma* was split off from *Lamproderma* and forms a distinct clade within the dark-spored myxomycetes; the peridium, which fragments into tiny pieces, distinguishes the genus from *Lamproderma*

[e]The classical Stemonitales include all dark-spored myxomycetes with non-calcareous fruiting bodies. However, molecular phylogenies (Fiore-Donno et al. 2012) show the classical Physarales nested within the Stemonitales

[f]*Lamproderma* shows closer affinities to the classical Physarales, defined by calcareous fruiting bodies, even if calcareous structures are absent or reduced to little splinters on the peridium

[g]The order Liceales, with only the absence of a capillitium as the unifying character, were long thought not to be monophyletic (Eliasson 1977, 2015), but *Cribraria* forms a highly distinct clade in molecular phylogenies (Fiore-Donno et al. 2013)

[h]The genera *Lycogala*, *Reticularia*, and *Tubifera* form a monophyletic clade, but the latter does not include *Dictydiaethalium*, which shows a closer relationship to the traditional Trichiales (Leontyev et al. 2014)

[i]*Licea*, as the largest genus of the traditional Liceales, is not monophyletic, since at least some species show closer affinities to the traditional Trichiales

[j]This order, defined by free elaters as capillitial structures, is best maintained in the light of molecular investigations, although the traditional boundaries between genera do not seem to reflect natural relationships

## Habitats and Ecology

Myxomycetes have been recorded from every major type of terrestrial ecosystem examined to date (Stephenson et al. 2008), and at least a few species have been recovered from aquatic habitats (Lindley et al. 2007). Temperature and moisture are thought to be the main factors limiting the occurrence of myxomycetes in nature (Alexopoulos 1963), and species richness tends to increase with increasing diversity and biomass of the associated vegetation giving rise to the plant detritus that supports the bacteria and other microorganisms upon which both trophic stages feed (Madelin 1984; Stephenson 1989). Some species of myxomycetes (e.g., *Badhamia utricularis* and *Fuligo septica*) are known to excrete exoenzymes, thus enabling them to literally consume the fruiting bodies of fungi. The pH of the substrates potentially available to myxomycetes in a particular habitat also represents an important factor influencing their distribution (Harkönen 1977; Stephenson 1989; Wrigley de Basanta 2000; Mosquera et al. 2000; Rojas et al. 2010). Although many myxomycetes appear to have a relatively wide pH tolerance, this is not the case for all species. For example, some species of *Paradiacheopsis* are found almost exclusively on bark that is quite acidic (Schnittler et al. 2016), whereas numerous species in the Physarales are restricted largely to substrates with a pH >5.0 (Schnittler and Stephenson 2002).

### Microhabitats

Virtually all knowledge we have about myxomycete ecology and distribution is based only upon the occurrence of fruiting bodies. A few studies employing environmental PCR to detect myxomycete sequences in various types of substrates (Clissmann et al. 2015: bright-spored myxomycetes in wood; Fiore-Donno et al. 2016: dark-spored myxomycetes in soil) indicated that amoebal populations seem to be more widely distributed than data on fruiting body occurrence would suggest. In temperate regions of the world, where the fruiting bodies of myxomycetes appear to be most abundant, these organisms are associated with a number of different microhabitats. These include coarse woody debris, the bark surface of living trees, ground litter, and aerial portions of dead but still standing herbaceous plants. Each of these microhabitats tends to be characterized by a distinct assemblage of species (Stephenson 1988, 1989; Stephenson and Stempen 1994). The myxomycetes associated with coarse woody debris are the best known, since the lignicolous (wood-inhabiting) species typically occurring in this microhabitat tend to be among those characteristically producing fruiting bodies of sufficient size to be detected with the naked eye in the field (Martin and Alexopoulos 1969). Many of the more common and widely known myxomycete taxa, including various species of *Arcyria*, *Lycogala*, *Stemonitis*, and *Trichia*, are predominantly lignicolous. The assemblage of myxomycetes present on coarse woody debris changes with the stage of decomposition (Takahashi and Hada 2009). For example, some taxa (e.g., *Badhamia*) are restricted largely to the early stages when bark is still present. Several hundred species of myxomycetes are predominantly or completely lignicolous,

including most of the species with large compound fruiting bodies. As such, it is one of the most diverse microhabitats for myxomycetes.

## Moist Chamber Cultures

The myxomycetes associated with the bark surface of living trees and with ground litter tend to be much less conspicuous and more sporadic in their occurrence and are thus difficult to detect in the field. However, the moist chamber culture technique as it applies to myxomycetes (Gilbert and Martin 1933) provides a convenient method of supplementing field collections (see, e.g., Novozhilov et al. 2017) when studying such microhabitats as bark and litter. It essentially involves blind collection of substrates with populations of amoebae, microcysts, and/or spores present and incubating these with at first abundant and then decreasing moisture conditions. The technique has been used with considerable success by many researchers (e.g., Keller and Brooks 1976; Blackwell and Gilbertson 1980; Harkönen 1981; Stephenson 1989) and works best in arid habitats (Schnittler et al. 2015). More than 200 species of "corticolous" (bark-associated) myxomycetes have been reported from bark in the field and/or in moist chamber culture (Mitchell 1980; Snell and Keller 2003). Many of these species are also known to occur in other microhabitats, but at least some species appear to be restricted to the bark of living trees. Prominent examples include various species of *Echinostelium*, *Licea*, and *Macbrideola* (Alexopoulos 1964; Mitchell 1980) with small fruiting bodies.

Ground litter supports an exceedingly diverse assemblage of myxomycetes, with approximately 400 species having been reported from this microhabitat, including many members of the Physarales that can be cultured. It seems likely that many myxomycetes fruiting on the upper litter layers actually inhabit the soil-litter interface as amoebae (Stephenson et al. 2011). A number of special microhabitats support rare assemblages of myxomycetes with seemingly specialized species present. In tropical regions, myxomycetes have been reported from epiphyllous liverworts growing on living leaves (Schnittler 2001a) and on decaying portions of the inflorescences of large tropical herbaceous plants, especially members of the order Zingiberales, which provide a highly basic pH (Schnittler and Stephenson 2002). An additional microhabitat in temperate regions supports about two dozen species of bryophilous (bryophyte-inhabiting) myxomycetes, which are found associated with mosses covering the surface of rocks, usually sandstone, in moist cool gorges (Schnittler et al. 2010). Likewise, about 25 species, some with specially adapted thick-walled spores, are known from dung (coprophilous myxomycetes, Eliasson and Keller 1999). In deserts, decaying portions of succulent plants represent another special microhabitat, from which about 50 species of "succulenticulous" myxomycetes have been reported (Lado et al. 1999). The amoebae of these myxomycetes probably prey on yeasts, and their spores are likely to be dispersed by fruit flies (*Drosophila* spp., Stephenson 2010).

The amoebae of myxomycetes are exceedingly abundant in most arable soils (Madelin 1984). Environmental PCR approaches that target the 18S rRNA (gene)

are problematic because so-called universal primers are poorly suited to detecting myxomycetes (Stephenson et al. 2011; Schnittler et al. 2017). However, in a large molecular data set for the soil microbial community obtained using a metatranscriptomic approach, Urich et al. (2008) found that myxomycetes indeed represent a major component of total protozoan soil biodiversity. The occurrence of myxomycetes in soil was discussed in detail by Stephenson et al. (2011) and Stephenson and Feest (2012).

## Characterization and Recognition

### General Life Cycle

The myxomycete life cycle (Fig. 2) includes two very different trophic stages, one consisting of uninucleate haploid amoebae, with or without flagella (the term "amoeboflagellate" encompasses both types of cells), and a distinctive multinucleate

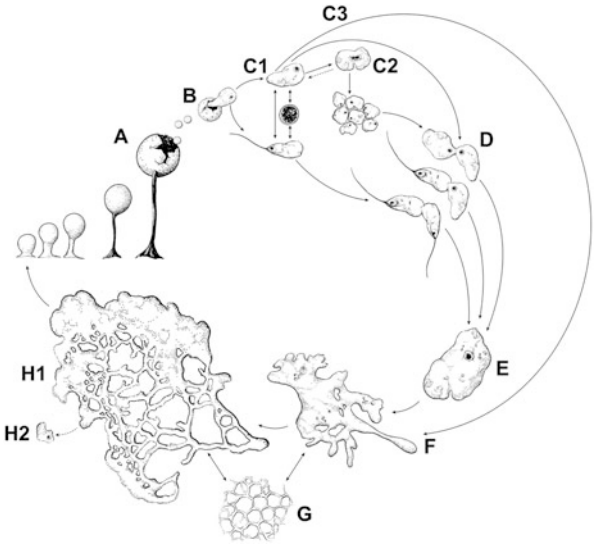


**Fig. 2** Life cycle of a myxomycete. A fruiting body (*A*) releases spores (*B*) that germinate to produce uninucleate amoebae (*C1*), which can convert into resistant microcysts (middle structure) or flagellated forms (lower structure). The uninucleate cells divide (*C2*) to build up often large populations. The sexual cycle involves syngamy of two compatible uninucleate cells (*D*) to produce a zygote (*E*). [An additional hypothetical life cycle involves a uninucleate cell developing directly into a plasmodium.] The zygote gives rise to a plasmodium (*F*). The latter increases in size by phagocytosis and subsequent nuclear divisions to develop into a larger structure (*H1*). It has been reported that small portions of the plasmodia can separate as amoebae (*H2*). Under adverse conditions a plasmodium can transform into a resistant sclerotium (*G*). The segregation of a plasmodium into fruiting bodies (left side of the figure) completes the life cycle (Drawing by A. Mele)

**Fig. 3** Phaneroplasmodium of a myxomycete. This is one of three different types of plasmodia produced by these organisms. The phaneroplasmodia of some species of myxomycetes can reach more than a meter in total extent (Photograph by R. Darrah)

**Fig. 4** Group of solitary fruiting bodies of *Didymium bahiense* var. *microsporum* (Physarales). Such fruiting bodies usually develop by segregation of a larger plasmodium into smaller portions (Photograph by M. Poulain)

structure, the plasmodium (Martin et al. 1983). Plasmodia (Fig. 3) are motile and in some species can reach a size of more than a meter across. Large plasmodia contain many thousands of synchronously dividing diploid nuclei. Under suitable conditions, the plasmodium gives rise to one or (in most species) many fruiting bodies (also referred to as sporocarps for the Myxogastria or sporophores in *Ceratiomyxa*) containing haploid spores (Figs. 4 and 5). The spores represent the most durable of the three dormant stages in the life cycle, with the others being microcysts (derived from amoebae) and sclerotia (derived from plasmodia).

The fruiting bodies produced by myxomycetes are somewhat suggestive of those produced by certain dicaryan fungi (Eumycota), but they are considerably smaller (usually no more than 1–3 mm tall) and totally different in structure, since all visible components, except for the spores, are composed of extracellular material and thus do not show a cellular structure. Presumably, the spores are wind dispersed and

**Fig. 5** Fruiting bodies of *Leocarpus fragilis* (Physarales). This is one of the most distinctive of all myxomycetes (Photograph by M. Schnittler)

complete their life cycle by germinating to produce uninucleate amoebae or flagellate cells (both forms are convertible; Stephenson et al. 2008). These feed and divide by binary fission to build up large clonal populations in the various microhabitats in which these organisms occur. Ultimately, this stage in the life cycle gives rise to the plasmodium, usually following gametic fusion between mating-type compatible amoeboid cells. Presumed apomictic strains occur in culture (Collins 1980, 1981; Clark and Haskins 2013); to what extent these occur in nature is unknown (Feng et al. 2016). Bacteria apparently represent the main food resource for both trophic stages, but plasmodia are also known to feed upon yeasts, eukaryotic microalgae, and fungal spores and hyphae (Stephenson and Stempen 1994; Smith and Stephenson 2007).

## Plasmodium

Plasmodia are characterized by often colorful pigments (including white, yellow, or orange to red tints), but possess only a few characters useful in distinguishing among species of myxomycetes. It is possible to recognize three fundamentally different types (Alexopoulos 1960). These are protoplasmodia, aphaneroplasmodia, and phaneroplasmodia. Protoplasmodia are microscopic structures with only a few nuclei present, whereas aphaneroplasmodia and phaneroplasmodia are larger, multinucleate structures that are essentially giant cells. Aphanoplasmodia, characteristic of those myxomycetes assigned to the Stemonitales, are thin, transparent, and difficult to observe in nature; they generally become evident only when emerging from a particular substrate (e.g., a decaying log) just prior to the formation of fruiting bodies. Phaneroplasmodia are more robust and often highly pigmented and represent the type of plasmodium usually observed in nature. Plasmodia are extremely flexible structures and are capable of penetrating even very solid wood, most likely through the pits present in the dead cells making up the wood (Feest et al. 2015). Both aphanoplasmodia and phaneroplasmodia go through a stage that resembles a

protoplasmodium in the earliest stages of development. As a result of active cytoplasmic streaming, portions of a plasmodium are able to reach relatively distant food sources (Nakagaki et al. 2007).

## Fruiting Body

Myxomycete fruiting bodies are morphologically very diverse (see Stephenson and Stempen 1994 or Schnittler et al. 2012 for a summary of morphological terms and characters; Neubert et al. 1993–2000, Poulain et al. 2011, www.slimemold.uark.edu for images showing their diversity). In *Ceratiomyxa*, fruiting bodies produce external spores on separate stalks, which is one of the characters that distinguishes the four members of this genus from all of the "true" myxomycetes. In spite of the fact that "slime mold" is the most widely used common name applied to the myxomycetes, *Ceratiomyxa* is the only genus in which the fruiting body actually has a slimy appearance at maturity. All of the true myxomycetes possess stalked or sessile fruiting bodies with internally formed spores (Fig. 6). Large aphaneroplasmodia and phaneroplasmodia primarily segregate into subportions by plasmotomy, with each subportion developing into a fruiting body (usually referred to as a sporocarp), often with a hypothallus at the base. Although possession of a stalk seems to be an

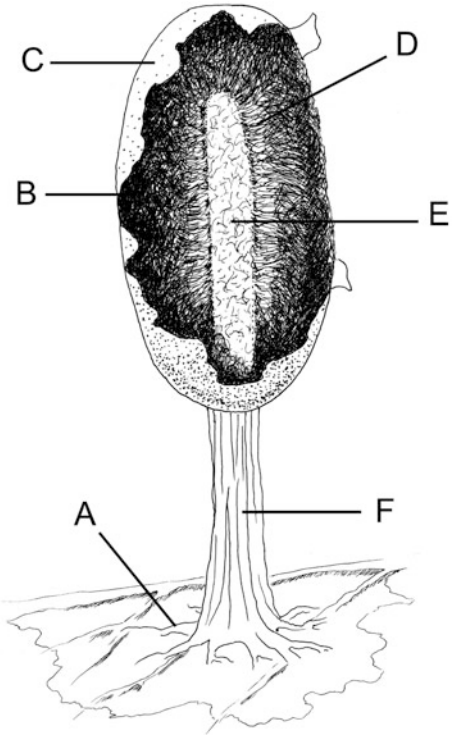


**Fig. 6** Morphological features of the fruiting body of a myxomycete. (**a**) Hypothallus, (**b**) spores, (**c**) peridium, (**d**) capillitium, (**e**) columella, and (**f**) stalk (Adapted from Stephenson (2003))

**Fig. 7** Compound fruiting body of *Tubifera montana* (Liceales), with evidence of the individual fruiting bodies still apparent. This type of compound fruiting body evolved, most likely independently, in several different groups of myxomycetes (Photograph by M. Schnittler)

ancient character (Fiore-Donno et al. 2012), in the majority of genera, sessile species exist beside stalked ones. In some species several fruiting bodies may share a common stalk, which seems to be the first step in the evolution of compound fruiting bodies. Large compound fruiting bodies, which are most often sessile, have evolved independently within several different lineages (Fig. 7). In some of these, single fruiting bodies are still recognizable (pseudoaethalia), but in other instances (aethalia) they are not.

The stalk, if present, is always acellular (although it can be filled with spore-like cells in some members of the Trichiales) and is secreted externally (Spiegel and Feldman 1989). In the dark-spored orders Echinosteliales and Stemonitales, the stalk forms as an invagination into the developing fruiting body, and the fruiting body rises upwards on it. Stalks formed in such a fashion usually extend into the spore mass as a central continuation, called a columella, which often diverges into many fine branches. In the other myxomycetes, the visible stalk emerges by constriction of the external surface of the plasmodial mass from which the fruiting body is derived. All structures holding the spore mass and allowing it to dry out slowly are referred to as a capillitium (Figs. 8 and 9). In the case of internal stalks, these are the branches of the columella, which is connected with the peridium in some taxa (Echinosteliales, genus *Meriderma*) but is not in others (most other Stemonitales). Capillitial structures are thus either extensions of the stalk (Echinosteliales and Stemonitales), tubular threads that are often stuffed with lime (Physarales), or free, threadlike structures called "elaters" that are often ornamented with spiral bands (Trichiales). In compound fruiting bodies, peridial remnants from the individual fruiting bodies may form a pseudocapillitium (found in some members of the Liceales).

Fruiting bodies are usually surrounded by an extracellular layer (peridium), although it may often be evanescent. In the latter situation, the peridium is simple and membranous, but it can as well be multilayered and covered with organic material or lime which shows different degrees of crystallization (Physarales). Spores are usually dispersed by air in nearly all species with solitary, stalked sporocarps, but dispersal may also occur by means of insects, especially in taxa

**Fig. 8** Capillitial structures in *Lamproderma echinosporum* (Stemonitales), showing the stalk extending into the spore mass as a columella, where the capillitium branches off. Scale bar = 100 µm (Photograph by Y. K. Novozhilov)

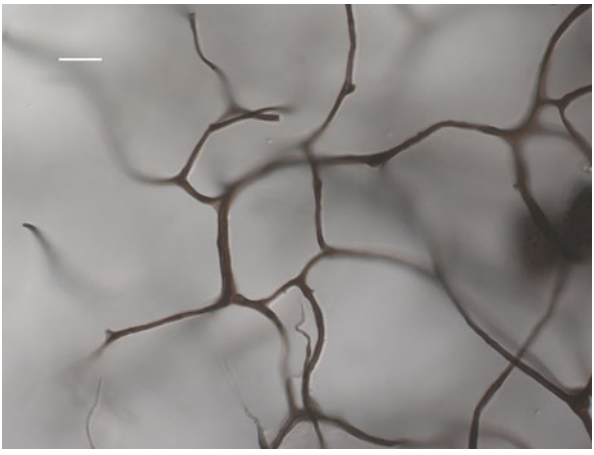

**Fig. 9** Expanded view of the outer capillitial structures in *Lamproderma echinosporum*. Scale bar = 10 µm (Photograph by Y. K Novozhilov)

with compound fructifications (e.g., *Fuligo*, *Tubifera*, or *Reticularia*), or from the impact of falling raindrops (*Lycogala* or *Reticularia*). The latter are an example of convergent evolution with some of the gasteromycetes (e.g., puffballs) in Basidiomycetes (Estrada-Torres et al. 2005). Similar to many gasteromycetes, these

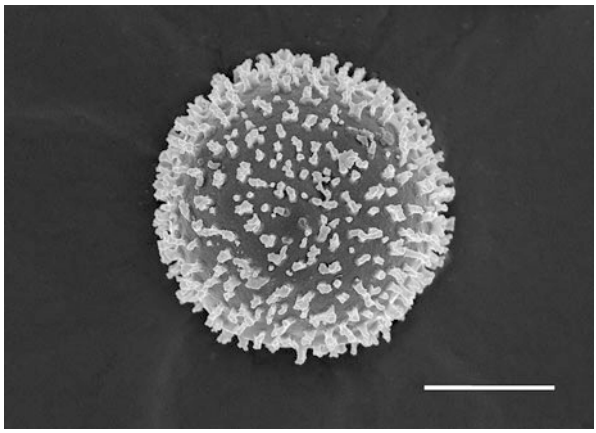

**Fig. 10** A single spore of *Meriderma spinulisporum* (Stemonitales) as observed by scanning electron microscopy. Typically, myxomycete spores are nearly completely spherical, lack a hilum, and are ornamented with warts, spines, or ridges which sometimes form a more or less complete reticulum. Scale bar = 5 μm (SEM micrograph by A. Ronikier)

myxomycete species possess spores with an extremely hydrophobic ornamentation composed of a reticulum of ridges (Hoppe and Schwippert 2014).

Spore number per fruiting body ranges from just two in *Echinostelium bisporum* to $10^4$–$10^6$ (but up to $10^{11}$) in large compound fruiting bodies (Schnittler and Tesmer 2008). The spores of the vast majority of myxomycetes are spherical and range from 4 to 22 μm in diameter, with most species producing spores $10 \pm 2$ μm in diameter. Except for *Ceratiomyxa*, these spores lack a microscopic indentation (hilum) due to their internal development and are rarely smooth but more often ornamented with hydrophobic warts, spines, or elevated ridges (Fig. 10). Spores with yellow, reddish, or brown pigments (Trichiales: naphthoquinones; Iwata et al. 2003) occur in the bright-spored myxomycetes (Blackwell and Busard 1978; Rebhahn et al. 1999), whereas the dark-spored Stemonitales and Physarales have more uniform brown to nearly black spores pigmented by melanin (Loganathan et al. 1989; Dembitsky et al. 2005). Except for peridia with thick outer layers of organic material or lime, spore color determines the color of the fruiting body as a whole. In addition, false silvery to blue colors may also occur, as is the case for *Diachea leucopodia* or many species of *Lamproderma*. These false colors derive from interference of light reflected on the outer and inner surface of extremely thin peridia.

## Sexual and Asexual Reproduction

Myxomycetes should be expected to be primarily sexual (Lahr et al. 2011; Spiegel 2011), as sex is a general attribute of eukaryotic life (Speijer et al. 2015). However, experiments on monosporic cultures suggest that they include a mixture of heterothallic (sexual) strains, where fusion of amoebae leads to the formation of a diploid plasmodium, and non-heterothallic presumably asexual strains, where single amoeboflagellates can mature into haploid plasmodia (Clark and Haskins 2010). Heterothallic isolates reproduce sexually, and fusion of compatible amoebae is controlled by mating type genes. As such, monosporic cultures, grown from a single

spore, usually do not form plasmodia. In contrast, non-heterothallic isolates can form plasmodia in monosporic cultures; most likely the life cycle can be completed by means of automixis (a degenerated meiosis or coalescence of meiotic products leading to diploid spores). In this case, the life cycle should be completed in the diploid stage (Clark and Haskins 2013). In addition, in the model organism *Physarum polycephalum*, the (temperature-dependent) diploidization of a haploid plasmodium has been identified as a possible initial event (Schaap et al. 2016). Conversion from heterothallic (sexual) to non-heterothallic (presumably automictic) forms within a species was reported by Collins (1980). Figure 1 in Feng et al. (2016) presents and discusses possible reproductive options.

Apart from cultivated stains, which are mostly limited to members of the Physarales, our knowledge about the occurrence of these reproductive modes in natural populations is very limited. A molecular investigation of bryophilous (bryophyte-associated) species of *Lamproderma* did not exclude the possibility of asexual reproduction (Fiore-Donno et al. 2011). Feng and Schnittler (2015) found that the distribution of introns in the 18S rRNA gene of the morphospecies *Trichia varia* was consistent with the existence of three sexual but reproductively isolated cryptic species. A third case study in *Meriderma* spp. (Feng et al. 2016) suggested predominant sexual reproduction. As such, we must assume that natural populations of myxomycetes consist mostly of clonal strains of amoebae, but the development of fruiting bodies is predominantly coupled with a sexual event.

The chromosomes of myxomycetes are small and difficult to count (Hoppe and Kutschera 2013). Ribosomal RNA genes that are most important for barcoding in this group of organisms are located in a few to several hundred copies on extrachromosomal plasmids (Torres-Machorro et al. 2010) and do not show Mendelian inheritance (Ferris et al. 1983). The only relatively complete myxogastrid genome sequence to date is that of an axenic culture of *Physarum polycephalum*, which shows extremely long stretches of single-sequence repeats together with large homopolymeric tracts, hampering assembly (Schaap et al. 2016).

## Systematics

Recent molecular phylogenies have found a monophyletic clade (referred to as the "macromycetozoa"; Fiore-Donno et al. (2010a)) composed of the Dictyostelia, Myxogastria, and *Ceratiomyxa* (Pawlowski and Burki 2009). The Myxogastria is monophyletic but deeply divided into two groups (Fiore-Donno et al. 2010b), the bright-spored myxomycetes and the dark-spored myxomycetes; this division corresponds largely to the occurrence of melanin in spore walls. Cavalier-Smith (2013) recently proposed the formal names Lucidisporidia and Columellidia, respectively. Detailed phylogenetic relationships within the two groups have yet to be resolved; therefore, current knowledge does not allow the arrangement of all myxomycete genera into a natural system. Most of the traditional orders seem not to be

monophyletic, as shown by the contrasting traditional and informal classifications provided in Table 1.

Particularly problematic is the circumscription and sometimes the systematic position of a number of genera in several of the orders (Erastova et al. 2013). This suggests that morphological characters that are easy to observe tend to be overweighed (Schnittler and Mitchell 2000). These include traits like spore arrangement (single versus clustered). There are several rare cluster-spored species which essentially differ only in this character from more common single-spored species. The same is true for solitary versus compound fruiting bodies and the presence or absence of fruiting bodies with stalks (i.e., stalked versus sessile). In contrast, molecular data suggest that characters such as the structure of the peridium and the type of connection it has with the capillitium are evolutionarily conservative and appear to be seriously underweighted.

## Maintenance and Cultivation

Only a small percentage (about 70 species, Clark and Haskins 2010, 2011) of the approximately 1,000 morphologically described species of myxomycetes can currently be induced to complete their life cycle in cultures with an appropriate bacterium present as a food source. Even fewer have been cultured under axenic conditions. The vast majority of these are litter-inhabiting members of the order Physarales. Media typically used to culture myxomycetes include weak nutrient agar to which various substrate decoctions have been added (Haskins and Wrigley de Basanta 2008). Fruiting can often be induced by adding sterile oatmeal flakes to a particular culture. Groups with specialized growth requirements, such as the nivicolous myxomycetes, are often difficult or impossible to culture (Shchepin et al. 2014). From these experiments, an independent biological species concept was developed (Clark 2000), which is not necessarily consistent with the prevailing morphological species concept (see discussion in Feng et al. 2016; Walker and Stephenson 2016).

For diversity studies, the moist chamber culture technique (Stephenson and Stempen 1994) is often used. For this simple technique, which is very convenient as well for demonstrations and school experiments (Keller and Braun 1999), samples of various types of dead plant material are placed on filter or toilet paper in sterile Petri dishes and allowed to soak with water. During the slow desiccation of the cultures, myxomycetes (particularly corticolous species) are regularly induced to fruit.

Spiegel et al. (2004) provided a synopsis of the eumycetozoans, with special regard to the methods used for carrying out inventories, various culturing techniques, and the preservation of specimens. A relatively nontechnical description of all of the techniques involved in collecting and studying myxomycetes is given in Stephenson and Stempen (1994).

## Evolutionary History

A complete molecular phylogeny of the myxomycetes is gradually being developed (Fiore-Donno et al. 2008, 2010a, b, 2012, 2013). Many genes (Schaap et al. 2016) and especially rRNA sequences are rich in introns and extremely divergent, which makes it difficult if not impossible to develop universal primers. As is the case for other groups of protists (Adl et al. 2014), the most promising sequence for barcoding seems to be the first part of the 18S rRNA gene (SSU, Feng and Schnittler 2017; Schnittler et al. 2017). In contrast to the fungi, the ITS region is extremely variable even among closely related species of myxomycetes. The 18S region contains several insertion sites for group I introns (ten are currently known), which makes the myxomycetes an interesting model system for studying these structures (Johansen et al. 1993, 1997; Haugen et al. 2003). Introns may be independently acquired even within closely related biospecies (Feng and Schnittler 2015) and can contain homing endonuclease genes, seemingly following the Goddard-Burt cycle of intron acquisition and loss (Goddard and Burt 1999).

Due to the fragile nature of the fruiting body, fossil records of myxomycetes are exceedingly rare. Domke (1952) described a species of *Stemonitis* and Dörfelt et al. (2003) a species of *Arcyria* from Baltic amber dating from the Eocene. The maximum age that could be assigned to either of these fossils is about 50 million years, which is older than that of the few records of fossil spores that appear to be those of myxomycetes, which date only from the Oligocene and Pleistocene (Graham 1971). Molecular dating analyses that have considered eumycetozoans seem to indicate that the sorocarpic ancestors of myxomycetes may have existed even before the colonization of land by plants (Fiz-Palacios et al. 2013), but the highly divergent 18S rRNA gene sequences point as well to recent speciation events (Aguilar et al. 2013; Feng and Schnittler 2017).

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