2 Excavata: Acrasiomycota; Amoebozoa: Dictyosteliomycota, Myxomycota

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CONTENTS

I. Introduction

One of the deep branches of the eukaryotic tree of life consists of an assemblage of amoeboid protists referred to as the supergroup Amoebozoa (Fiore-Donno et al. 2010). The most diverse members of the Amoebozoa are the eumycetozoans, commonly referred to as slime molds. Since their discovery, members of the Dictyosteliomycota (dictyostelids) and Myxomycota (myxomycetes or myxogastrids) 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 types of ecological situations as fungi, slime molds have been traditionally studied by mycologists (Martin and Alexopoulos 1969). However, abundant molecular data now confirm that they are amoebozoans and not fungi (Bapteste et al. 2002; Yoon et al. 2008; Baudalf 2008).

Both dictyostelids and myxomycetes are widespread and often common in the microhabitats in which they characteristically occur, where they are major predators of bacteria and other microorganisms (Stephenson and Stempen 1994). However, because of their cryptic life cycles and the fact that the number of specialists studying them is relatively small, they are among the least studied groups of terrestrial organisms in nature, although a few species, such as *Dictyostelium discoideum* (for the dictyostelids) and *Physarum polycephalum* (for the myxomycetes), have become model organisms for laboratory studies. Although once classified in the same group as the dictyostelids, the acrasid cellular slime molds (or acrasids) are not closely related to the other organisms commonly referred to as slime molds. In fact, recent studies of acrasids have revealed that as a whole they are not even closely related to one another and are more appropriately referred to as sorocarpic amoebae (Brown et al. 2011). As a group, they are much less familiar organisms than either dictyostelids or myxomycetes, and many biologists are unlikely to be aware that they even exist.

II. Acrasiomycota

Although grouped with the eumycetozoans until detailed observations of morphological features and the availability of molecular data proved otherwise, members of the phylum

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Acrasiomycota (*sensu* Alexopoulos et al. 1996) are better placed in the supergroup Excavata (Page and Blanton 1985; Roger et al. 1996; Adl et al. 2005; Brown et al. 2009, 2011), with a few examples recently reassigned to the supergroups Opisthokonta and Amoebozoa. This small assemblage of microorganisms (usually referred to as acrasid cellular slime molds or acrasids) was recognized as the class Acrasea by Olive (1975). However, because members of the assemblage are now known to produce sorocarps that have different evolutionary origins, this taxon as circumscribed by Olive is no longer valid. As such, these microorganisms are more appropriately considered as sorocarpic amoebae.

At one time or another, the sorocarpic amoebae were thought to encompass six genera: *Acrasis*, *Pocheina*, *Copromyxa*, *Copromyxella*, *Fonticula*, and *Guttulinopsis*. However, the genus *Copromyxa* has been shown to belong to the supergroup Amoebozoa (Brown et al. 2011) and is probably closely related to *Copromyxella* (Raper 1984), whereas the genus *Fonticula* has been reassigned to the supergroup Opisthokonta and is most closely related to the nucleariid amoebae and fungi (Brown et al. 2009).

Of the taxa historically called acrasids, only members of the taxon Acrasidae, which includes the genera *Acrasis* and *Pocheina*, are currently considered valid (Adl et al. 2005). Of the Acrasidae, only *Acrasis* has been studied in any detail. The type species of the genus is *A. granulata*, described in the late nineteenth century (van Tieghem 1880). However, the taxonomic identity of *A. granulata* is somewhat controversial because the original description provided no illustrations and only limited morphological details (Olive and Stoinaovitch 1960; Olive 1975; Raper 1984). A second species (*A. rosea*) was described 80 years later by Olive and Stoinaovitch (1960). A third species (*A. helenhemmesae*) was more recently added to the genus (Brown et al. 2010). *A. rosea* is by far the best known and most widely distributed of the three species (Reinhardt 1975). Cells in all stages of the life cycle of this species have orange-pink pigmented lipid droplets in the cytoplasm. This causes the cells to have a distinctive pinkish color. In the feeding (trophic) phase, the cells are amoeboid and characterized by lobose pseudopodia (Olive 1975). When conditions are appropriate, the amoeboid cells aggregate singly or in small groups to produce an erect, spore-containing fruiting body (or sorocarp). In *A. rosea*, the sorocarp is made up of chains of spores that collectively form an arborescent-like structure (Fig. 2.1). This is borne on a thin column of living cells, one of the major features that distinguish these microorganisms from dictyostelids, in which the stalk is hollow or filled with dead cells. The sorocarps of *A. helenhemmesae* typically consist of a single chain of spores. Although *A. rosea* has been isolated from a number of localities throughout the world, relatively little is known about its ecology.

Pocheina rosea (called *Guttulina rosea* in the older literature) was first described from dead wood in Russia during the latter part of the nineteenth century and later reported from North Carolina and a number of other localities in the eastern USA by Olive (1975). The sorocarp in this species is short-stalked with an apical, rose-colored, globose structure containing the spores. The genus *Guttulinopsis*, created at the very beginning of the twentieth century by Olive (1901) to accommodate what seemed to be several species of dung-inhabiting slime-mold-like organisms that were characterized by stalked or, more rarely, sessile, globose to somewhat elongated sorocarps. Nothing is currently known about how *Guttulinopsis* is related to any of the other sorocarpic amoebae. Because they have been so poorly studied, little is known about the global distribution and ecology of any of the sorocarpic amoebae.

III. Dictyosteliomycota

The dictyostelids (also commonly called cellular slime molds) are a relatively homogeneous group of approximately 150 described species. In the single most comprehensive monograph on the group, Raper (1984) listed approximately 50 species. Hagiwara (1989) added six more in his treatment of Japanese dictyostelids.

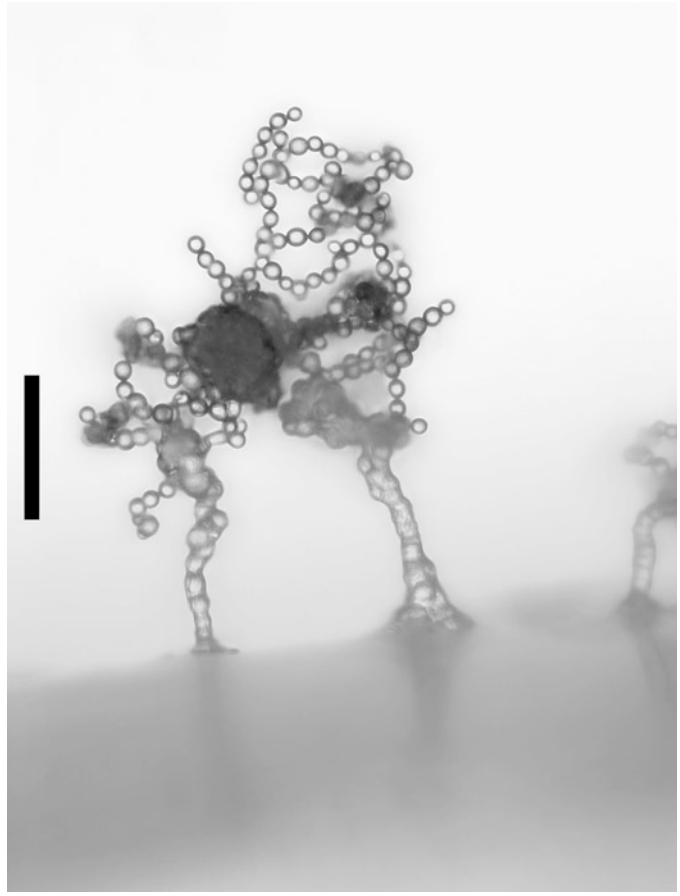

Fig. 2.1 Fruiting body of *Acrasis rosea* (photo by Matt Brown). Scale bar = 0.1 mm

Since then, the number of species has more than doubled. This increase is due to the greater intensity of sampling by a larger number of individuals, sampling in regions of the world (especially the Southern Hemisphere) and habitats not previously investigated (e.g., Landolt et al. 2008; Cavender et al. 2010; Vadell et al. 2011), and evidence that some isolates previously assigned to a single species actually represent separate, distinct taxa (Romeralo et al. 2010). For example, in his treatment, Hagiwara (1989) emphasized stalk tip and base morphology, aggregation patterns, and spore morphology, which helped narrow the species concept for dictyostelids. Since then, there has been greater emphasis on the early developmental stages in delimiting species (Cavender et al. 2013). The utilization of molecular and morphological characters has also contributed to an increased understanding of the variation that exists within this group of organisms.

A. Life Cycle

All dictyostelids are characterized by having uninucleate cells with a reticulate, peripheral nucleolus (Olive 1975; Raper 1984; Cavender 1990). Amoeboid trophic cells, with acutely pointed pseudopodia, differentiate into aggregating cells that migrate in streams to an aggregation center (Fig. 2.2). The multicellular aggregation, or pseudoplasmodium, develops into one or more elongated slug-shaped structures that may migrate in some species or transform directly into a mature fruiting body (or sorocarp). The entire process is coordinated by the production of chemoattractants. The

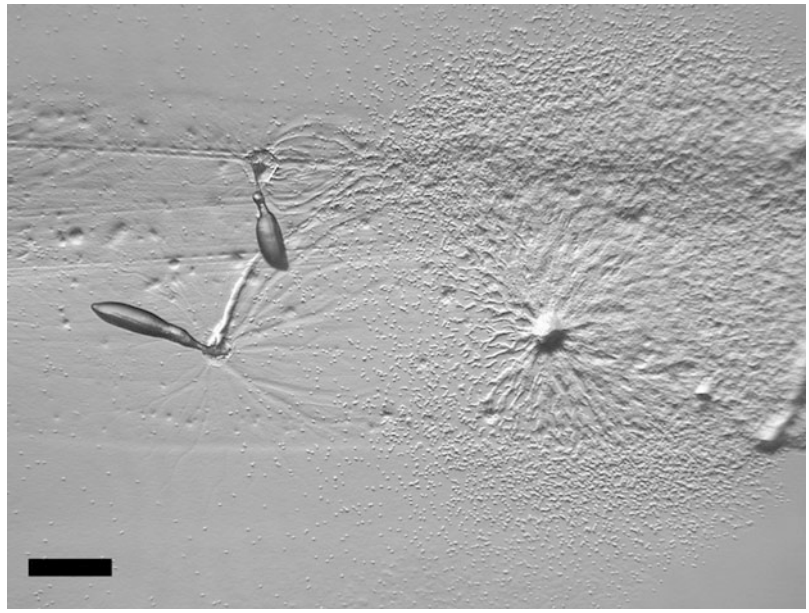

Fig. 2.2 Aggregation center (*right*) and early developing fruiting bodies (*left*) of *Polysphondylium tenuissimum* (photo by Andy Swanson). Scale bar = 0.5 mm

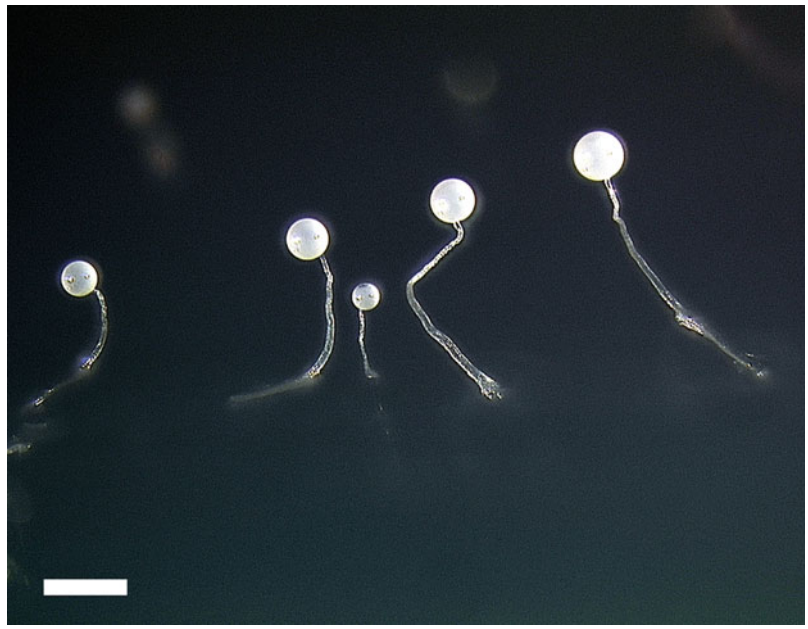

Fig. 2.3 Fruiting body of *Dictyostelium sphaerocephalum* (photo by Andy Swanson). In this species, the fruiting body consists of a stalk with a single sorus at the top. Scale bar = 0.3 mm

fruiting body consists of a stalk that may display branching and one or more sori of spores (Fig. 2.3). Aggregation and fruiting represent an asexual dispersal process, but sex is known for many species (Raper 1984; Cavender 1990; Kessin 2001). The latter involves the formation

of macrocysts. In brief, the process begins with the production of specific chemoattractants that cause some of the amoeboid trophic cells to aggregate. Cells of two mating types fuse under certain well-defined (Lewis and O'Day (1977) showed that a volatile sex hormone was involved) but still not completely understood environmental conditions to form a giant cell, which is essentially a diploid zygote (Chang and Raper 1981; O'Day and Keszei 2012). The giant cell then ingests the surrounding amoeboid trophic cells prior to encysting. Ultimately, meiosis takes place in the resulting macrocyst, and numerous haploid amoeboid trophic cells emerge through a rupture in the multilayered wall of the latter structure. Macrocysts were not recognized as the sexual stage of dictyostelids until the 1960s, and these structures have not yet been observed for many species. Most species of dictyostelids seem to be heterothallic, with mating types required, but homothallic strains have been reported for some species. Macrocysts also serve as a resistant stage in the life cycle, allowing the organism to survive under suboptimal conditions. Individual amoeboid trophic cells also have been observed to encyst (thus forming microcysts) in some species of dictyostelids. Microcysts thus represent yet another way that these organisms can deal with unfavorable environmental conditions (Kessin 2001).

B. Distribution and Occurrence

Dictyostelids are found in the soil microhabitat worldwide, particularly in the surface humus layers (Cavender and Raper 1965b, c; Cavender 1973, 1990; Raper 1984; Feest 1987; Hagiwara 1989; Stephenson and Landolt 1996). They are particularly abundant in the layer of leaf litter found on the forest floor and decrease in number and diversity with increasing depth (Cavender and Raper 1965b; Stephenson and Landolt 1996). Raper (1937) and Singh (1947) showed that dictyostelids can consume a variety of soil bacteria but prefer coliform bacteria if these are available. As such, dictyostelids may play a role in keeping the soil environment free of the pathogenic forms found in this group of bacteria. Dictyostelids are present in pastures and hay fields (Hammer 1984), and certain species are abundant in cultivated garden soil that is amended organically (Kauffman 1986). Moreover, the so-called canopy soil microhabitat (the mantle of soil-like dead organic matter often found at the bases of epiphytes that grow on the larger branches and trunks of trees in moist temperate and tropical forests) is now known to support an assemblage of dictyostelids (Stephenson and Landolt 1998, 2011). Interestingly, a few species were first described from these aerial microhabitats. Dictyostelids seem to be more common in forest soils than in agricultural soils, grassland soils, or deserts (Cavender and Raper 1965c; Raper 1984; Feest 1987; Cavender 1990). More species are found at lower latitudes than at higher latitudes (Cavender 1973), and at a particular latitude, more species are found at lower elevations than at higher elevations (e.g., Hagiwara 1976; Traub et al. 1981; Stephenson et al. 1999). Higher densities of dictyostelids are present in moist soils than in dry soils, although they are rare in saturated soils. Singh (1947) described the relationship that exists for fruiting ability and the level of soil moisture, while Cavender and Raper (1965c) showed that different species vary in abundance along a forest-moisture gradient and also that species abundances can be related to differences in forest composition. Horn (1971) found that there was competitive exclusion between species that depended on the same kind of bacteria.

Some species of dictyostelids seem to be strictly tropical, others are strictly temperate, and others, although cosmopolitan, are more common in either tropical or temperate regions of the world (Cavender 1973; Raper 1984; Swanson et al. 1999). The highest biodiversity of dictyostelids has been reported from neotropical rain forest soils (Vadell and Cavender 1995), but a few species can be surprisingly abundant even in tundra soils (Cavender 1978; Stephenson et al. 1991). It seems that some dictyostelids display an affinity for marginal or disturbed habitats not often sampled for these organisms previously, whereas others may be confined to a single limited geographical region of the world.

C. Isolation

Dictyostelids are usually isolated from soil (or other soil-like material) using some variation of the so-called Cavender method (Cavender and Raper 1965a; Raper 1984). In brief, this method involves collecting samples from a number of sites in a given habitat, returning these to the laboratory, and then diluting and suspending a measured mass of material from each sample in a known volume of distilled water. A small (but measured) amount of this suspension is spread evenly on a plate of a weak nutrient agar such as hay infusion agar (Raper 1984) or weak malt extract–yeast extract agar (Spiegel et al. 2004) and then overlaid with a turbid suspension of *Escherichia coli* in water. Plates are incubated at ambient temperatures for 3 or 4 days and then examined for colonies of dictyostelid fruiting bodies. Identification to species is made from direct observation of features of the fruiting bodies. When necessary, a particular isolate can be subcultured (often on water agar) to maintain it for further study. A critical consideration is to use a very weak nutrient medium that stimulates spore germination but does not promote the growth of bacteria or fungi. The *E. coli* added to such plates has an amazing ability to inhibit both soil bacteria and fungi.

Samples collected for isolation of dictyostelids should be processed in the laboratory as soon as possible because the species present gradually die off. Many of the rarer species seem to be lost within a few days or weeks (Stephenson and Cavender 1996). The reduction in numbers after 8 weeks is up to 25 % when temperate soils are refrigerated (Cavender and Raper 1965a), and this figure can be even higher when soils are exposed to fluctuating temperatures. Moreover, a number of as yet unidentified factors present in some soils inhibit the growth of dictyostelids, and some temperature-sensitive species (e.g., *Dictyostelium septentrionalis*) may not develop in culture plates even when they are present in a particular sample if the incubation temperature is above 20 °C. However, the Cavender method has yielded a considerable body of qualitative and quantitative data on the occurrence and distribution of dictyostelids throughout much of the world.

D. Taxonomy

In the taxonomic treatment traditionally used for dictyostelids, species have been assigned to three well-known genera (*Dictyostelium*, *Polysphondylium*, and *Acytostelium*) on the basis of the overall morphology and size of the fruiting body. In brief, those taxa having unbranched or laterally branched fruiting bodies have been assigned to *Dictyostelium*, those with repetitive whorls of regularly spaced side branches to *Polysphondylium*, and those characterized by fruiting bodies with acellular stalks to *Acytostelium*. However, Swanson et al. (2002) showed, using rooted cladistic analysis, that the three genera do not represent monophyletic groups. Schaap et al. (2006) developed the first molecular phylogeny of the dictyostelids) with data from the small subunit (SSU) ribosomal RNA and beta-tubulin genes. More than 100 isolates, including the majority of the species in culture at the time the study was carried out, were considered. The phylogenetic tree constructed from these data showed that the dictyostelids consist of four major groups (clades), none of which corresponds to the three traditional genera. Species of *Dictyostelium* are found in all four groups, species of *Polysphondylium* occur in two very well-separated locations in the tree, and species of *Acytostelium* form a mixed group along with species from the two other genera. Only members of the latter genus seemed to show any evidence of being monophyletic.

Romeralo et al. (2011) published an expanded phylogeny of the dictyostelids that was based on SSU ribosomal RNA data from numerous additional isolates of dictyostelids collected in various localities throughout the world. These included at least 50 species new to science. The phylogenetic tree they constructed revealed eight well-supported clades, none of which corresponds to any of the traditional genera, and also showed strong support for the four previously identified major groups (Schaap et al. 2006). In addition, three previously isolated but inconsistently resolved branches were now observed to form major divisions in their own right. These new groups have been referred to as the *polycarpum*, *polycephalum*, and *violaceum* complexes in order to retain the original groups' numbering scheme

until formal names can be assigned. The new species included in the tree also expanded the range of morphological diversity found within the previously established four major groups, which suggests that the dictyostelids as a whole are in need of a major taxonomic revision. An appreciable number of the new species noted previously were characterized by small-sized fruiting bodies (i.e., an average height of no more than 2 cm), and recent data (e.g., Cavender et al. 2005, 2013) indicate that these dictyostelids with small fruiting bodies, particularly those in group 3, as reported by Schaap et al. (2006), are the most common and diverse forms found in nature. As such, most of the species remaining to be discovered are likely to be members of this assemblage.

IV. Myxomycota

Myxomycetes (also called plasmodial slime molds or myxogastrids) have been known from their fruiting bodies since at least the middle of the seventeenth century, when the first recognizable description of a member of the group (the very common species now known as *Lycogala epidendrum*) was provided by the German mycologist Thomas Panckow (Stephenson et al. 2008). Evidence from molecular studies (e.g., Baldauf and Doolittle 1997; Baldauf et al. 2000) suggests that the myxomycetes have a long evolutionary history. However, due to the fragile nature of the fruiting body, fossil records of the group 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, whereas Waggoner and Poinar (1992) reported a rather problematic fossil of a myxomycete plasmodium in amber from Eocene–Oligocene deposits in the Dominican Republic. The maximum age that could be assigned to any of these fossils would not exceed approximately 50 million years, which is greater than that of the few records of fossil spores that seem to be those of myxomycetes, which date only from the Oligocene and Pleistocene (Graham 1971).

Although a number of early workers published recognizable descriptions of various genera and species, the first noteworthy treatment of the myxomycetes was published by de Bary in 1859. Interestingly, de Bary (1859) seems to have been the first to conclude that these organisms were more closely related to the amoeboid protozoa than to fungi. To emphasize his point, he proposed the term Mycetozoa (literally *fungus animals*) for the group. Rostafinski, who was a student of de Bary, is credited with producing the first relatively comprehensive monograph on the myxomycetes (Rostafinski 1873, 1874–1876). Unfortunately, the monograph was written in Polish and thus largely inaccessible to most of the scientific community at the time it appeared. However, much of the information contained in the monograph was made available in publications by Cooke (1877) and Massee (1892), both of which were in English. The single most significant pre-twentieth-century publication on myxomycetes was the first edition of *A Monograph of the Mycetozoa* (Lister 1894). This monograph, revised and expanded versions of which were published in 1911 and 1925 (Lister 1911, 1925), became the standard reference on the group during the early part of the twentieth century. MacBride published the first edition of *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* (MacBride and Martin 1934). Several decades later, Martin collaborated with Alexopoulos to produce their comprehensive world monograph, *The Myxomycetes* (1969). This monograph is now more than 40 years old and out of print. However, it still remains the single most definitive treatment for the myxomycetes, literally representing a bible for those individuals engaged in studies of the group. Other more recent regional monographs include those by Farr (1976), Yamamoto (1998), Nannenga-Bremekamp (1991), Ing (1999), and Stephenson (2003).

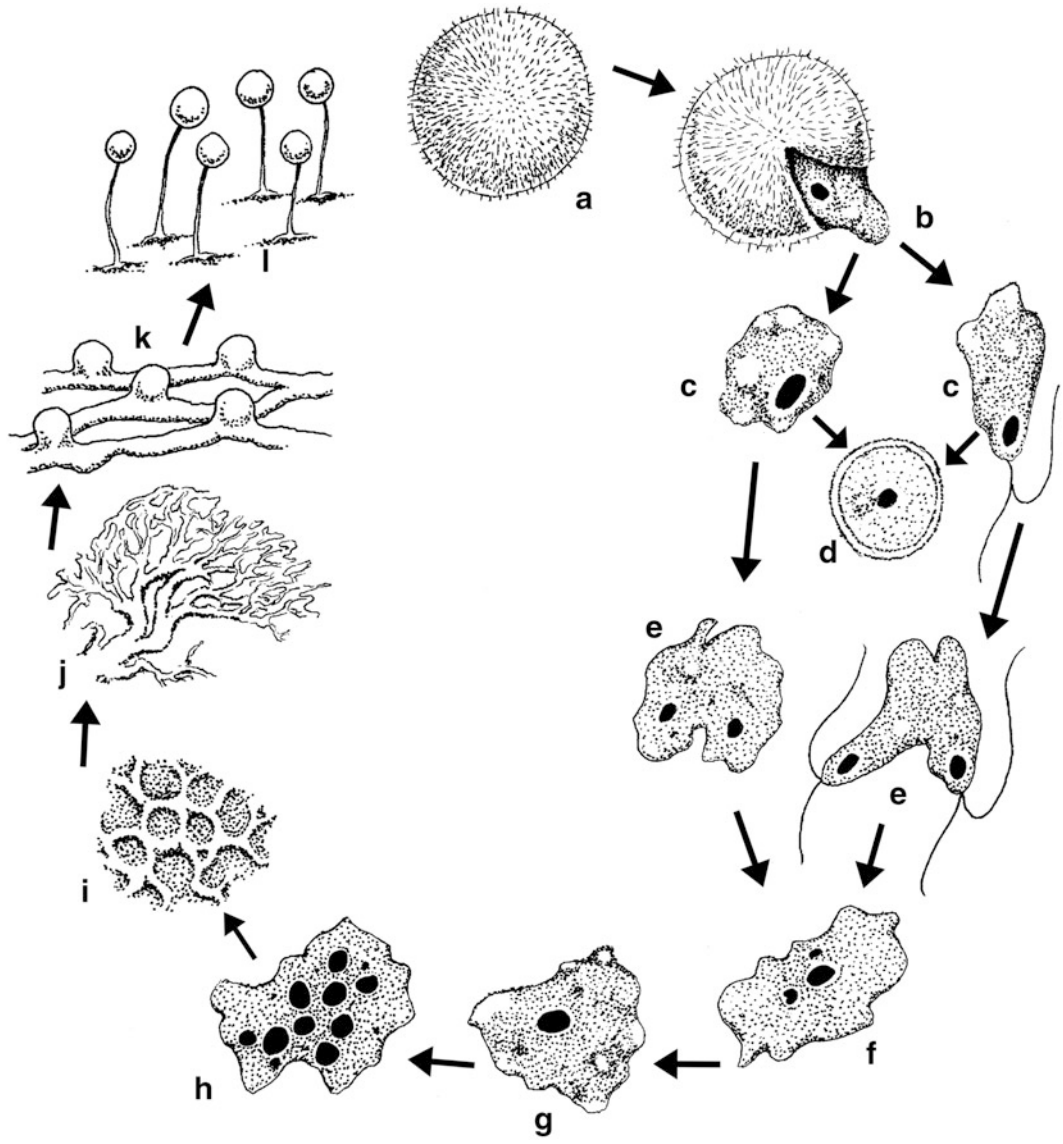

Fig. 2.4 Generalized life cycle in myxomycetes. (**a**, **b**) A protoplast emerges from the spore. (**c**) The protoplast can take the form of an amoeba or a flagellated cell (the term amoeboflagellate refers to both forms) during the first trophic stage. (**d**) Under dry conditions or in the absence of food, an amoeboflagellate forms a microcyst, or resting stage. (**e**–**g**) Compatible amoeboflagellates fuse to form a zygote (**g**). (**h**–**j**) The nucleus of the zygote divides by mitosis (**h**), and each subsequent nucleus also divides without being followed by cytokinesis, thereby producing a single large cell (**j**), the plasmodium, that represents the second trophic stage. Under adverse conditions, the plasmodium can form the second type of resting stage found in myxomycetes, the sclerotium (**i**). (**k**, **l**) Fruiting bodies are formed from the plasmodium. During fruiting body formation, spores are produced. Adapted from Stephenson (2003)

A. Life Cycle

The myxomycete life cycle (Fig. 2.4) encompasses two very different trophic stages, one consisting of uninucleate amoebae, with or without flagella, and the other consisting of a distinctive multinucleate structure, the plasmodium (Martin et al. 1983). Much of what is

Fig. 2.5 Plasmodium of a myxomycete (photo by Randy Darrah). Scale bar = 25 mm

known about the myxomycete life cycle has been derived from studies of *P. polycephalum* and *Didymium iridis*, but the life cycle of a number of other species has been observed in laboratory culture (Clark 2008). Plasmodia are motile, and those of some species can reach a size of several centimeters, with truly extraordinary examples sometimes exceeding 1 m (Fig. 2.5). A large example contains many thousands of synchronously dividing nuclei. Under favorable conditions, the plasmodium gives rise to one or more fruiting bodies (also referred to as sporocarps or sporophores) containing spores (Fig. 2.6). For practical reasons, identification of myxomycetes is based almost exclusively upon features of the fruiting body (Martin and Alexopoulos 1969). The fruiting bodies produced by myxomycetes are somewhat suggestive of those produced by certain macrofungi, although they are considerably smaller (usually no more than 1–2 mm tall). The spores of the vast majority of myxomycetes range in size from 5 to 15 μm in diameter, with most species producing spores 10 ± 2 μm in diameter. The spores are largely wind-dispersed and complete the life cycle by germinating to produce the uninucleate amoeboflagellate cells. These feed and divide by binary fission to build up large populations in the various microhabitats in which these organisms occur. Ultimately, this stage in the life cycle gives rise to the plasmodium. This process can result from gametic fusion between compatible amoeboflagellates or it can be apomictic (Collins 1980, 1981), as is described in more detail in what follows.

Most myxomycetes seem to have a basic one-locus multiple alleleic heterothallic mating system that controls syngamy between haploid amoeboflagellate cells to produce the diploid plasmodium (Clark and Haskins 2010). However, more than a single locus may be involved in some species, and three multiple alleleic loci have been reported for *P. polycephalum* (Kawano et al. 1987). Each of the morphospecies examined to date also contains a number of biological sibling species that are unable to interbreed with each other. It is not unusual for these to occur in different regions of the world. Each morphospecies generally contains numerous nonheterothallic strains that can complete the life cycle from a single isolated spore. Some of these strains are possibly homothallic (i.e., genetically identical amoeboflagellate cells fuse, resulting in a diploid

Fig. 2.6 Fruiting bodies of *Hemitrichia calyculata* (photo by Kim Fleming). In this species, the fruiting body is stalked and the lower part of the peridium persists to form a cuplike structure (or calyculus), above which the capillitium and spores are visible. Scale bar = 1.0 mm

plasmodium), but there is more evidence to suggest that they are characterized by an apomictic system derived from blockage of meiosis during spore formation. As such, these nonheterothallic strains produce diploid amoeboflagellates that can develop directly into plasmodia without the need for syngamy to take place.

In the textbook sexual life cycle outlined previously, two haploid amoeboflagellate cells fuse to form a diploid zygote, and the latter then develops into a multinucleate plasmodium in which all of the cells present are diploid. Under appropriate conditions, a plasmodium gives rise to a fruiting body, within which meiosis occurs when the spores are produced. An amoeboflagellate emerges from the spore to begin the life cycle anew. However, as already noted, some myxomycetes are known to be apomictic and thus do not follow this general pattern. Clark and Haskins (2010) listed 51 different species in which the reproductive system has been examined for one or more isolates. Of these, 14 were found to have both heterothallic and nonheterothallic (presumably apomictic) systems, 8 had only heterothallic systems, and 29 were reported to be nonheterothallic. Rather little is known about the relative proportions of heterothallic versus nonheterothalic reproduction in nature, but the latter may be more common.

The genetic structure in particular populations of myxomycetes is still largely unknown because few studies have been carried out. Fiore-Donno et al. (2011) investigated the genetic variability for three genes (SSU ribosomal, internal transcribed spacer 1, and partial elongation factor 1-alpha) in two species of *Lamproderma* associated with a spatially limited microhabitat (bryophyte-covered boulders in a series of moist ravines in Germany). Identical sequences were found to exist for a number of specimens in each of the two species, which suggests the occurrence of distinct clones that are the result of a nonheterothallic reproductive system.

Winsett and Stephenson (2010) examined the global distribution and molecular diversity (using the mitochondrial SSU gene) of *Didymium difforme*. Their data seem to support the concept of long-distance dispersal in myxomycetes since similar sequences were found to occur in widely separated regions of the world (e.g., Kenya and the central USA). However, in some instances, collections from a single region showed a very high degree of similarity, which

Fig. 2.7 Fruiting bodies of *Ceratiomyxa fruticulosa* (photo by Kim Fleming). Scale bar = 5 mm

at least suggests that some constraints to gene flow also exist.

Bacteria apparently represent the main food resource for both amoeboflagellates and plasmodia, but the latter are also known to feed upon yeasts, algae (including cyanobacteria), and fungal spores and hyphae (Stephenson and Stempen 1994). Under adverse conditions, such as drying out of the immediate environment or low temperatures, a plasmodium may convert into a hardened, resistant structure called a sclerotium, which is capable of reforming the plasmodium upon the return of favorable conditions. Moreover, amoeboflagellate cells can undergo a reversible transformation to dormant structures called microcysts. Both sclerotia and microcysts can remain viable for long periods of time and are probably very important in the continued survival of myxomycetes in some ecological situations or habitats, such as the bark surface of living trees and deserts.

B. Taxonomy

Approximately 900 species of myxomycetes have been described (Lado 2001), and in all but the most modern treatments of the group, these have been placed in six orders (Ceratiomyxales, Echinosteliales, Liceales, Physarales, Stemonitales, and Trichiales). However, members of the Ceratiomyxales, represented by the single genus *Ceratiomyxa* (Fig. 2.7), are distinctly different (e.g., their spores are produced externally on individual stalklike structures and not within a fruiting body) from any of the organisms assigned to the other orders, and modern workers have removed these organisms from the myxomycetes (Olive 1970, 1975; Olive and Stoianovitch 1979). The exact evolutionary affinities of the Ceratiomyxales are still debated, but they seem to be a sister group to the so-called true myxomycetes (Fiore-Donno et al. 2010). With the removal of the Certiomyxales, the myxomycetes constitute a well-defined and homogenous group. However, evidence from DNA sequence analysis (Baldauf and Doolittle 1997) suggests that even what seem to be closely related taxa on the basis of morphological similarity may have diverged from each other a long time ago (Clark 2000). Fiore-Donno et al. (2005) reported that phylogenetic data based on partial SSU ribosomal RNA and elongation factor-1 alpha sequences suggest a dichotomy between light-spored and dark-spored myxomycetes, with the light-spored clade consisting of the monophyletic Trichiales and the paraphyletic Liceales and the dark-spored clade consisting of the monophylectic Physarales and the paraphyletic Stemonitales.

Members of the genus *Cribraria*, traditionally assigned to the Liceales, seem to represent a sister group to both the Trichiales and Liceales (Fiore-Donno et al. 2010). These data place the genus *Echinostelium* as the sister group to the two major clades. More comprehensive analyses, based on complete SSU ribosomal RNA and elongation factor-1 alpha sequences from a wider range of taxa, indicate that *Echinostelium* branches as the sister group of the dark-spored clade (Fiore-Donno et al. 2008). The concept of this sister group has been expanded by Fiore-Donno et al. (2009), who recently provided evidence that the enigmatic organism *Semimorula liquescens* is a modified echinostelid myxomycete.

Interestingly, it has become increasingly apparent that the myxomycetes include a number of amoeboid forms that apparently do not form fruiting bodies. The latter fact prevented the true phylogenic position of these organisms from being recognized until they were subjected to the appropriate molecular-based studies. For example, Fiore-Donno et al. (2010) reported that sequences they obtained from a number of amoeboid forms previously assigned to the genus *Hyperamoeba* clearly indicated that the organisms involved should be considered as myxomycetes. Moreover, *Hyperamoeba* was found to be polyphyletic, which rendered the genus itself invalid. It seems possible that nonfruiting forms of myxomycetes are widespread in nature, sometimes occurring in certain habitats or microhabitats which would be regarded as rather extraordinary. Dyková et al. (2007) isolated an amoeboid organism from a species of sea urchin (*Sphaerechinus granularis*) that yielded SSU rDNA sequences showing a close relationship with the myxomycete genus *Didymium*. Myxomycetes have been reported from a diverse array of microhabitats, but their presence as apparent endocommensals of a sea urchin clearly indicates that the total range of potential microhabitats is even more extensive than previously realized.

Because of their small size and the limited array of morphological characters upon which their taxonomy is based, determination of what constitutes a natural biological species, in the same sense that the concept is used for many of the more familiar groups of organisms (Mayr 1970), is sometimes rather problematic. As mentioned earlier in this chapter, it is now known that a number of the more common and widespread morphospecies actually consist of complexes of geographically restricted apomictic clonal lines (El Hage et al. 2000; Clark 2000; Clark and Stephenson 2000; Irawan et al. 2000). These genetically isolated lines are capable of independent evolution, which can lead to the accumulation of minor morphological differences that reflect specific adaptations to the particular set of environmental conditions in which they occur. For example, some of the forms found in special microhabitats (e.g., the inflorescences of tropical herbs) differ in some respects (e.g., color and size of the fruiting bodies) from specimens of the same species collected from more typical habitats (Schnittler and Stephenson 2002). These almost certainly represent biotypes that are adapted to the microhabitat in question. Approximately 50 % of all described species of myxomycetes are known only from the type locality, or fewer than five localities worldwide. It seems likely that many of these so-called species are no more than morphologically distinct biotypes present in particular habitats or confined to a certain regions of the world. If so, then the criteria that need to be applied before describing a taxon as new should be reconsidered to account for this phenomenon (Schnittler and Mitchell 2000).

C. Distribution and Occurrence

Myxomycetes have been recorded from all terrestrial ecosystems examined to date. 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 vascular plants providing the resources (various types of detritus) that support the bacteria and other microorganisms upon which the two trophic stages in the myxomycete life cycle feed (Madelin 1984; Stephenson 1989). The pH of the substrates potentially available to myxomycetes in a par-

ticular habitat also represents an important factor influencing the distribution of these organisms (Härkönen 1977; Stephenson 1989; Wrigley de Basanta 2000; Mosquera et al. 2000).

Much of what is known about the distribution and ecology of myxomycetes in terrestrial ecosystems has been derived from studies carried out in temperate forests of the Northern Hemisphere. In such forests, myxomycetes are associated with a number of different microhabitats. These include coarse woody debris on the forest floor, the bark surface of living trees, forest floor litter, the dung of herbivorous animals, 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). Lignicolous myxomycetes associated with coarse woody debris are the best known since the species typically occurring in this microhabitat tend to be among those characteristically producing fruiting bodies of sufficient size to be detected 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. Much less is known about the myxomycetes associated with the microhabitats represented by the bark surface of living trees and forest floor litter. The primary reason for this is that many of the species involved are rather inconspicuous or sporadic in their occurrence and, 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 and often very productive method of supplementing field collections when studying such microhabitats as bark and litter. Since its introduction, the technique has been used with considerable success by many researchers (e.g., Keller and Brooks 1976; Härkönen 1981; Blackwell and Gilbertson 1980; Stephenson 1989). More than 100 species of corticolous myxomycetes have been reported from the bark microhabitat as field or moist chamber collections (Mitchell 1980). The moist chamber culture technique is described in some detail by Stephenson and Stempen (1994).

Studies of the assemblages of myxomycetes associated with tropical forests and other major types of terrestrial ecosystems have been reviewed by Ing (1994) and Stephenson (2011). In some of these ecosystems, myxomycetes are associated with microhabitats poorly represented or absent in temperature forests. Examples include the inflorescences of large tropical herbaceous plants in tropical forests (Schnittler and Stephenson 2002) and succulent plants in deserts (Lado et al. 2007). One ecologically distinct group of myxomycetes is restricted to alpine areas of mountains, where its members are found fruiting along the margins of melting snowbanks in late spring and early summer (Ing 1999; Tamayama 2000; Stephenson and Shadwick 2009). The species that occupy this rather special and very limited habitat are usually referred to as snowbank or nivicolous myxomycetes. Interestingly, the majority of species in some genera tend to belong to this group. For example, this is the case for *Dianema* (Kowalski 1967), *Lamproderma* (Kowalski 1970), and *Lepidoderma* (Kowalski 1971).

On the whole, myxomycetes would seem to be rather opportunistic or fugitive organisms (sensu Hutchinson 1951) in that they have a high reproductive potential, seem to possess effective dispersal mechanisms, and are characterized by rapid development. These properties allow them to exploit successfully habitat islands occurring both temporally and spatially in nature. Although a particular habitat within which a species of myxomycete has been established may persist for only a short period of time, the species always survives by reestablishing itself in some new habitat (which may indeed be the very same habitat if conditions once again become favorable). Although the spores of myxomycetes would seem to have considerable potential for long-distance dispersal, there is little question that some species are more common in some regions of the world than others, and the nonavailability of certain microhabitats apparently imposes major constraints upon their occurrence even within a particular region. As such, it would seem that myxomycetes do not necessarily conform completely to the "ubiquity of small free-living eukaryotic species" concept as proposed by

Finlay (2002) and Fenchel and Finlay (2004). The very fragmented range of *Barbeyella minutissima*, a species that seems to be confined almost exclusively to a substrate complex (involving leafy liverworts, decorticated wood, and certain species of algae) found only in montane *Picea* or *Abies* forests, provides a good example (Schnittler et al. 2000).

V. Ecological Significance

A major portion of the net annual primary production in forests and other terrestrial ecosystems becomes directly or indirectly available to the decomposers in the detritus food chain. These decomposers (bacteria and fungi) are in turn an important food resource for various phagotrophic invertebrates and protozoa. For example, bacteria are preyed upon by bacterivores (e.g., protozoa and nematodes) as well as some detritivores (e.g., earthworms). Naked amoebae, which can make up 95 % of the protozoan population in some soils (Feest 1987), are the single most important group in terms of bacterial consumption. In addition to their direct influence on the structure of soil microbial communities, these amoebae play a key role in nutrient cycling. Mineralization is stimulated and decomposition enhanced by the amoebae releasing nutrients tied up in the microbial biomass. For example, amoebae are known to release ammonia to plant roots when feeding on bacteria and can produce increases in dry weight and nitrogen content (Clarholm 1981; Rosswall and Paustian 1984). It is not known what percentage of the total population of soil amoebae is made up of the amoeboid stages of dictyostelids and myxomycetes, but judging from the data available from a number of recent studies, it is significant. For example, Feest and Campbell (1986) reported that myxomycete amoebae alone represented more than 50 % of the total amoebae for some agricultural soils. Their study was based upon the use of a culture-based method (Feest and Madelin 1985), but Urich et al. (2008) used an RNA-centered megatranscriptomic approach to generate the largest data set for the entire soil protozoan community available to date. Eumycetozoans were found to represent the single largest component of total soil protozoan biodiversity, which seems to underscore the major ecological role these organisms play in the soil microhabitat.

As noted earlier in this chapter, myxomycetes are commonly associated with the microhabitats represented by the bark surface of living trees and various types of dead plant material. Although their fruiting bodies are often collected from each of these microhabitats, little is known about the exact role that myxomycetes play in each instance, although it might be assumed that it is similar to that already described for soil. For example, amoeboflagellate cells seem to be exceedingly common in decaying wood (A. Feest, unpublished data), and an individual moist chamber culture prepared with a sample of dead plant material often yields several different species, plasmodia several centimeters in total extent, and numerous fruiting bodies. Their sheer number, relative abundance, and biomass suggest that myxomycetes represent an ecologically significant component of the assemblages of organisms associated with such microhabitats.

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References

Adl SM, Simpson AGB, Farmer MA, Andersen RA, Anderson OR, Barta JR, Bonser SS, Brugerolle G, Fensome RA, Fredericq S, James TY, Karpov S, Kugrens P, Krug J, Lane CE, Lewis LA, Lodge J, Lynn LH, Mann DG, McCourt RM, Mendoza L, Moestrup Ø, Mozley-Standridge SE, Nerad TA, Shearer CA, Smirnov AV, Spiegel FW, Taylor MFJR (2005) The new higher level classification of eukaryotes with emphasis on the taxonomy of protists. J Eukaryot Microbiol 52:399–451

Alexopoulos CJ (1963) The myxomycetes II. Bot Rev 29:1–78

Alexopoulos CJ, Mims CW, Blackwell M (1996) Introductory mycology, 4th edn. Wiley, New York, NY

Baldauf SL, Doolittle WF (1997) Origin and evolution of the slime molds (Mycetozoa). Proc Natl Acad Sci 94:12007–12012

Baldauf SL, Roger AJ, Wenk-Siefert J, Doolittle WF (2000) A kingdom-level phylogeny of eukaryotes based on combined protein data. Science 290:972–977

Bapteste E, Brinkmann H, Lee JA, Moore DV, Sensen CW, Gordon P, Duruflé L, Gaasterland T, Lopez P, Müller M, Philippe H (2002) The analysis of 100 genes support the grouping of three highly divergent amoebae: *Dictyostelium*, *Entamoeba*, and *Mastigamoeba*. Proc Natl Acad Sci U S A 99:1414–1419

Baudalf SL (2008) An overview of the phylogeny and diversity of eukaryotes. J Syst Evol 46:263–273

Blackwell M, Gilbertson RL (1980) Sonoran desert myxomycetes. Mycotaxon 11:139–149

Brown MW, Spiegel FW, Silberman JD (2009) Phylogeny of the "forgotten" cellular slime mold, *Fonticula alba*, reveals a key evolutionary branch within Opisthokonta. Mol Biol Evol 26:2699–2709

Brown MW, Silberman JD, Spiegel FW (2010) A morphologically simple species of *Acrasis* (Heterolobosea, Excavata), *Acrasis helenhemmesae* n. sp. J Eukaryot Microbiol 57:346–353

Brown MW, Silberman JD, Spiegel FW (2011) "Slime molds" among the Tubulinea (Amoebozoa): molecular systematics and taxonomy of *Copromyxa*. Protist 162:277–287

Cavender JC (1973) Geographical distribution of Acrasiae. Mycologia 65:1044–1054

Cavender JC (1978) Cellular slime molds in tundra and forest soils of Alaska including a new species, *Dictyostelium septentrionalis*. Can J Bot 56:1326–1332

Cavender JC (1990) Phylum dictyostelida. In: Margulis L, Corliss CO, Melkonian M, Chapman DJ (eds) Handbook of proctotista. Jones and Bartlett, Boston, MA, pp 88–101

Cavender JC, Raper KB (1965a) The Acrasieae in nature. I. Isolation. Am J Bot 52:294–296

Cavender JC, Raper KB (1965b) The Acrasieae in nature. II. Forest soil as a primary habitat. Am J Bot 52:297–302

Cavender JC, Raper KB (1965c) The Acrasieae in nature. III. Occurrence and distribution in forests of eastern North America. Am J Bot 52:302–308

Cavender JC, Vadell EM, Landolt JC, Stephenson SL (2005) New species of small dictyostelids from the Great Smoky Mountains National Park. Mycologia 97:493–512

Cavender JC, Landolt JC, Ndiritu GG, Stephenson SL (2010) Dictyostelid cellular slime molds of Africa. Mycosphere 1:147–152

Cavender JC, Vadell EM, Landolt JC, Winsett KE, Stephenson SL, Rollins AW, Romeralo M (2013) Ten new small dictyostelids from seasonal rain forests of Central America. Mycologia 105(3):610–635

Chang MT, Raper KB (1981) Mating types and macrocyst formation in *Dictyostelium rosarium*. J Bacteriol 147:1049–1053

Clarholm M (1981) Protozoan grazing of bacteria in soil—impact and importance. Microb Ecol 7:343–350

Clark J (2000) The species problem in the myxomycetes. Stapfia 73:39–53

Clark J (2008) Reproductive systems and taxonomy in the myxomycetes. Syst Geogr Pt 74:209–216

Clark J, Haskins E (2010) Reproductive systems in the myxomycetes: a review. Mycosphere 1:337–353

Clark J, Stephenson SL (2000) Biosystematics of the myxomycete *Physarum melleum*. Nova Hedwigia 71:161–164

Collins OR (1980) Apomictic-heterothallic conversion in a myxomycete, *Didymium iridis*. Mycologia 72:1109–1116

Collins OR (1981) Myxomycete genetics, 1960–1981. J Elisha Mitch Sci Soc 97:101–125

Cooke MC (1877) The Myxomycetes of Great Britain arranged according to the method of Rostafinski: the characters of all the orders, families and genera, with descriptions of the British species, and original analytical tables, translated from the Polish. Williams and Norgate, London

de Bary A (1859) Die Mycetozoen. Ein Beitrag zur Kenntnis der niedersten Thiere. Z Wiss Zool 10:88–175

Domke W (1952) Der erste sichere Fund eines Myxomyceten im Baltischen Bernstein (*Stemonitis splendens* Rost. Fa. Succini fa. Nov. Foss.). Mitteilungen aus dem Gologischen Staatsinstitut in Hamburg 21:154–161

Dörfelt H, Schmidt AR, Ullmann P, Wunderlich J (2003) The oldest fossil myxogastroid slime mold. Mycol Res 107:123–126

Dyková I, Lom J, Dvořáková H, Pecková H, Fiala I (2007) *Didymium*-like myxogastrids (class Mycetozoa) as endocommensals of sea urchins (*Sphaerechinus granularis*). Folia Parasitol 54:1–12

El Hage N, Little C, Clark J, Stephenson SL (2000) Biosystematics of *Didymium squamulosum*. Mycologia 92:54–64

Farr ML (1976) Myxomycetes. Flora Neotropica, Monograph No. 16. The New York Botanical Garden, New York

Feest A (1987) The quantitative ecology of soil Mycetozoa. Prog Protistol 2:331–361

Feest A, Campbell R (1986) The microbiology of soils under successive wheat crops in relation to take-all disease. FEMS Microbiol Lett 38:99–111

Feest A, Madelin MF (1985) A method for the enumeration of myxomycetes in soils and its application to a wide range of soils. FEMS Microbiol Ecol 31:103–109

Fenchel T, Finlay BJ (2004) The ubiquity of small species: patterns of local and global diversity. BioSci 54:777–784

Finlay BJ (2002) Global dispersal of free-living microbial eukaryotic species. Science 296:1061–1063

Fiore-Donno AM, Berney C, Pawlowski J, Baldauf SL (2005) Higher-order phylogeny of plasmodial slime molds (Myxogastria) based on elongation factor 1-α and small subunit rRNA gene sequences. J Eukaryot Microbiol 52:1–10

Fiore-Donno AM, Meyer M, Baldauf SL, Pawlowski J (2008) Evolution of dark-spored Myxomycetes (slime-molds): molecules versus morphology. Mol Phylogenet Evol 46:878–889

Fiore-Donno AM, Haskins EF, Pawlowski J, Cavalier-Smith T (2009) *Semimorula liquescens* is a modified echinostelid myxomycete (Mycetozoa). Mycologia 101:773–776

Fiore-Donno AM, Nikolaev SI, Nelson M, Pawlowski J, Cavalier-Smith T, Baldauf SL (2010) Deep phylogeny and evolution of slime moulds (Mycetozoa). Protist 161:55–70

Fiore-Donno AM, Novozhilov YK, Meyer M, Schnittler M (2011) Genetic structure of two protist species (Myxogastria, Amoebozoa) suggests asexual reproduction in sexual amoebae. PLoS One. doi:10.1371/journal.pone.0022872

Gilbert HC, Martin GW (1933) Myxomycetes found on the bark of living trees. Univ Iowa Stud Nat His 15:3–8, 31

Graham A (1971) The role of Myxomyceta spores in palynology (with a brief note on the morphology of certain algal zygospores). Rev Palaeobot Palynol 11:89–99

Hagiwara H (1976) Distribution of the Dictyosteliaceae (cellular slime molds) in Mt. Ishizuchi, Shikoku. Trans Mycol Soc Jpn 17:226–237

Hagiwara H (1989) The taxonomic study of Japanese dictyostelid cellular slime molds. National Science Museum, Tokyo

Hammer CH (1984) Dictyostelids in agricultural soils. MS Thesis, Ohio University, Athens

Härkönen M (1977) Corticolous myxomycetes in three different habitats in southern Finland. Karstenia 17:19–32

Härkönen M (1981) Myxomycetes developed on litter of common Finnish trees in moist chamber cultures. Nord J Bot 1:791–794

Horn EG (1971) Food competition among the cellular slime molds. Ecology 52:475–484

Hutchinson GE (1951) Copepodology for the ornithologist. Ecology 32:571–577

Ing B (1994) The phytosociology of myxomycetes. New Phytol 126:175–201

Ing B (1999) The myxomycetes of Britain and Ireland: an identification handbook. Richmond Publishing, Slough

Irawan B, Clark JD, Stephenson SL (2000) Biosystematics of the *Physarum compressum* morphospecies. Mycologia 92:884–893

Kauffman G (1986) Effects of organic matter and moisture content on dictyostelids in agricultural soils. MS Thesis, Ohio University, Athens

Kawano S, Kuroiwa T, Anderson RW (1987) A third multialletic mating-type locus in *Physarum polycephalum*. J Gen Microbiol 133:2539–2546

Keller HW, Brooks TE (1976) Corticolous myxomycetes V: observations on the genus *Echinostelium*. Mycologia 68:1204–1220

Kessin RH (2001) *Dictyostelium*: evolution, cell biology, and the development of multicellularity. Cambridge University Press, Cambridge

Kowalski DT (1967) Observations on the Dianemaceae. Mycologia 59:1075–1084

Kowalski DT (1970) The species of *Lamproderma*. Mycologia 62:621–672

Kowalski DT (1971) The genus *Lepidoderma*. Mycologia 63:490–516

Lado C (2001) Nomenmyx. A nomenclatural taxabase of Myxomycetes. Cuadernos de Trabajo Flora Micológica Ibérica 16:1–221

Lado C, Mosquera J, Estrada-Torres A, Beltrán-Tejera E, Wrigley de Basanta D (2007) Description and culture of a new succulenticolous *Didymium* (Myxomycetes). Mycologia 99:602–611

Landolt JC, Cavender JC, Stephenson SL, Vadell EM (2008) New species of dictyostelid cellular slime moulds from Australia. Aust Syst Bot 21:50–66

Lewis KE, O'Day DH (1977) The sex hormone of *Dictyostelium discoideum* is volatile. Nature 268:730–731

Lister A (1894) A monograph of the Mycetozoa. Printed by order of the trustees, London

Lister A (1911) A monograph of the Mycetozoa. British Museum of Natural History, London (revised by G. Lister)

Lister A (1925) A monograph of the Mycetozoa. British Museum of Natural History, London (revised by G. Lister)

Macbride TH (1899) North American slime-moulds. Macmillan, New York, NY

Macbride TH (1922) North American slime-moulds, 2nd edn. Macmillan, New York, NY

Macbride TH, Martin GW (1934) The Myxomycetes. Macmillan, New York, NY

Madelin MF (1984) Myxomycetes, microorganisms and animals: a model of diversity in animal-microbial interactions. In: Anderson JN, Rayner DA, Walton DWH (eds) Invertebrate-microbial interactions. Cambridge University Press, New York, NY, pp 1–33

Martin GW, Alexopoulos CJ (1969) The myxomycetes. University of Iowa Press, Iowa City, IA

Martin GW, Alexopoulos CJ, Farr ML (1983) The genera of myxomycetes. University of Iowa Press, Iowa City, IA

Massee G (1892) A monography of the Myxogastres. Methuen, London

Mayr E (1970) Population, species, and evolution. Belknap Press, Harvard University Press, Cambridge

Mitchell DW (1980) A key to the corticolous myxomycetes. The British Mycological Society, Cambridge
Mosquera J, Lado C, Beltrán-Tejera E (2000) Morphology and ecology of *Didymium subreticulosporum*. Mycologia 92:978–983
Nannenga-Bremekamp NE (1991) A guide to temperate myxomycetes. Biopress, Bristol
O'Day DH, Keszei A (2012) Signalling and sex in the social amoebozoans. Biol Rev Camb Philos Soc 87:313–329. doi:10.1111/j.1469-185X.2011.00200.x
Olive EW (1901) A preliminary enumeration of the Sorophoreae. Proc Am Acad Arts Sci 37:333–344
Olive LS (1970) The Mycetozoa: a revised classification. Bot Rev 36:59–87
Olive LS (1975) The Mycetozoans. Academic, New York, NY
Olive LS, Stoianovitch C (1979) Observations of the mycetozoan genus *Ceratiomyxa*: description of a new species. Mycologia 71:546–555
Olive LS, Stoinaovitch C (1960) Two new members of the Acrasiales. Bull Torrey Bot Club 87:1–20
Page FC, Blanton RL (1985) The Heterolobosea (Sarcodina: Rhizopoda), a new class uniting the Schizopyrenida and the Acrasidae (Acrasida). Protistologica 21:121–132
Raper KB (1937) Growth and development of *Dictyostelium discoideum* with different bacterial associates. J Agr Res 55:289–316
Raper KB (1984) The Dictyostelids. Princeton University Press, Princeton, NJ
Reinhardt DJ (1975) Natural variants of the cellular slime mold *Acrasis rosea*. J Protozol 22:309–317
Roger AJ, Smith MW, Doolittle RF, Doolittle WF (1996) Evidence for the Heterolobosea from phylogenetic analysis of genes encoding glyceraldehyde-3-phosphate dehydrogenase. J Eukaryot Microbiol 43:475–485
Romeralo M, Spiegel FW, Baldauf SL (2010) A fully resolved phylogeny of the social amoebas (Dictyostelia) based on combined SSU and ITS rDNA sequences. Protist 161:539–548
Romeralo M, Cavender JC, Landolt JC, Stephenson SL, Baldauf S (2011) The expanding phylogeny of social amoebae defines new major lineages and emerging patterns in morphological evolution. BMC Evol Biol. doi:10.1186/1471-2148-11-84
Rosswall T, Paustian K (1984) Cycling of nitrogen in modern agricultural systems. Plant and Soil 76:3–21
Rostafinski JT (1873) Versuch eines Systems der Mycetozoen. Inaugural dissertation, University of Strassberg, Germany
Rostafinski JT (1874–1876) Sluzowce (Mycetozoa) monografia. Towarz Nauk Scis Paryzu 5:1–215 (1874); 217–432 (1875); Dodatek [appendix] 8:1–43 (1876)
Schaap P, Winckler T, Nelson M, Alvarez-Curto E, Elgie B, Hagiwara H, Cavender JC, Milano-Curto A, Rozen DE, Dingermann T, Mutzel R, Baldauf SL (2006) Molecular phylogeny and evolution of morphology in the social amoebas. Science 314:661–663
Schnittler M, Mitchell D (2000) Species diversity in myxomycetes based on the morphological species concept—a critical examination. Stapfia 73:55–62
Schnittler M, Stephenson SL (2002) Inflorescences of Neotropical herbs as a newly discovered microhabitat for myxomycetes. Mycologia 94:6–20
Schnittler M, Stephenson SL, Novozhilov YK (2000) Ecology and world distribution of *Barbeyella minutissima* (Myxomycetes). Mycol Res 104:1518–1523
Singh BN (1947) Studies of soil Acrasieae. 1. Distribution of species of *Dictyostelium* in soils of Great Britain and the effect of bacteria on their development. J Gen Microbiol 1:11–21
Spiegel FW, Stephenson SL, Keller HW, Moore DL, Cavender JC (2004) Mycetozoans. In: Mueller GM, Bills GF, Foster MS (eds) Biodiversity of fungi: inventory and monitoring methods. Academic, Amsterdam, pp 547–576
Stephenson SL (1988) Distribution and ecology of myxomycetes in temperate forests. I. Patterns of occurrence in the upland forests of southwestern Virginia. Can J Bot 66:2187–2207
Stephenson SL (1989) Distribution and ecology of myxomycetes in temperate forests. II. Patterns of occurrence on bark surface of living trees, leaf litter, and dung. Mycologia 81:608–621
Stephenson SL (2003) Myxomycetes of New Zealand. Fungal Diversity, Hong Kong
Stephenson SL (2011) From morphological to molecular: studies of myxomycetes since the publication of the Martin and Alexopoulos (1969) monograph. Fungal Divers 50:21–34
Stephenson SL, Cavender JC (1996) Dictyostelids and myxomycetes. In: Hall GS (ed) Methods for the examination of organismal diversity in soils and sediments. CAB International, Oxon, pp 91–101
Stephenson SL, Landolt JC (1996) The vertical distribution of dictyostelids and myxomycetes in the soil/litter microhabitat. Nova Hedwigia 62:105–117
Stephenson SL, Landolt JC (1998) Dictyostelid cellular slime molds in canopy soils of tropical forests. Biotropica 30:657–661
Stephenson SL, Landolt JC (2011) Dictyostelids from aerial "canopy soil" microhabitats. Fungal Ecol 4:191–195
Stephenson SL, Shadwick JD (2009) Nivicolous myxomycetes from alpine areas of south-eastern Australia. Aust J Bot 57:116–122
Stephenson SL, Stempen H (1994) Myxomycetes: a handbook of slime molds. Timber, Portland, OR
Stephenson SL, Landolt JC, Laursen GA (1991) Cellular slime molds in soils of Alaskan tundra. Arctic Alpine Res 23:104–107
Stephenson SL, Landolt JC, Moore DL (1999) Protostelids, dictyostelids, and myxomycetes in the litter

microhabitat of the Luquillo Experimental Forest, Puerto Rico. Mycol Res 103:209–214
Stephenson SL, Schnittler M, Novozhilov YK (2008) Myxomycete diversity and distribution from the fossil record to the present. Biodivers Conserv 17:285–301
Swanson AR, Vadell EM, Cavender JC (1999) Global distribution of forest soil dictyostelids. J Biogeogr 26:133–148
Swanson AR, Spiegel FW, Cavender JC (2002) Taxonomy, slime molds, and the questions we ask. Mycologia 94:968–979
Tamayama M (2000) Nivicolous taxa of the myxomycetes in Japan. Stapfia 73:121–129
Traub F, Hohl HR, Cavender JC (1981) Cellular slime molds of Switzerland. II. Distribution in forest soils. Am J Bot 68:172–182
Urich T, Lanzén A, Qi J, Huson DH, Schleper C, Schuster SC (2008) Simultaneous assessment of soil microbial community structure and function through analysis of the meta-transcriptome. PLoS One. doi:10.1371/journal.pone.0002527
Vadell EM, Cavender JC (1995) Dictyostelid cellular slime molds from forest soils of the Iguazú Falls and the Jesuitic Missions Ruins of Argentina. In: Lado C, Hernández JC (eds) Abstracts volume of the second international congress on the systematics and ecology of myxomycetes (ICSEM 2), vol 1, p 110
Vadell EM, Cavender JC, Romeralo M, Edwards SM, Stephenson SL (2011) New species of dictyostelids from Patagonia and Tierra del Fuego, Argentina. Mycologia 103:101–117
van Tieghem MP (1880) Sur quelques myxomycetes a plasmode agrege. Bull Soc Fr 27:317–322
Waggoner BM, Poinar GO (1992) A fossil myxomycete plasmodium from Eocene-Oligocene amber of the Dominican Republic. J Protozool 39:639–642
Winsett KE, Stephenson SL (2010) Global distribution and molecular diversity of *Didymium difforme*. Mycosphere 2:135–146
Wrigley de Basanta D (2000) Acid deposition in Madrid and corticolous myxomycetes. Stapfia 73:113–120
Yamamoto Y (1998) The myxomycete biota of Japan. Toyo Shorin, Tokyo
Yoon HS, Grant J, Tekle YI, Wu M, Chaon BC, Cole JC, Logsdon JM Jr, Patterson DJ, Bhattacharya D, Katz LA (2008) Broadly sampled multigene trees of eukaryotes. BMC Evol Biol 8:14. doi:10.1186/1471-2148-8-14

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