Introduction

Myxomycetes (also known as plasmodial slime moulds 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 (Alexopoulos *et al*. 1996). However, since the fruiting bodies produced by some species of myxomycetes can achieve considerable size (those of *Fuligo septica* commonly exceed 10 cm or more in total extent), there is little doubt that myxomycetes have been observed in nature as long as mankind has existed. Evidence from molecular studies indicates that myxomycetes have a long evolutionary history and probably were present on the earth several hundred million years ago. Myxomycetes do not have a particularly attractive name, but many examples produce fruiting bodies that are miniature objects of considerable beauty. However, because of their small size, all but the largest and most conspicuous examples tend to be overlooked in nature.

Since their discovery, myxomycetes have been variously classified as plants, animals or fungi (Martin 1960). Because they produce aerial spore-bearing structures (fruiting bodies) that resemble those of certain fungi and also typically occur in some of the same ecological situations as fungi, myxomycetes traditionally have been studied by mycologists (Martin & Alexopoulos 1969). Indeed, the name most closely associated with the group, first used by Link (1833) more than 185 years ago, is derived from the words '*myxa*' (meaning slime) and '*mycetes*' (referring to fungi). However, myxomycetes are profoundly different from the 'true' fungi and actually belong to another kingdom, the Protista (sometimes called Protoctista).

Classification of the Myxomycetes

Approximately 1000 species of myxomycetes have been described to date (Lado 2005–2019), and the traditional classification used for the group placed these in six different taxonomic orders—the Ceratiomyxales, Echinosteliales, Liceales, Physarales, Stemonitales and Trichiales. Although this system of classification, which was based upon spore colour and easily discernible morphological features, has been used in all previous monographs of the myxomycetes, it does not properly reflect evolutionary relationships within the group. For example, the traditional order Ceratiomyxales (which consists of the single genus *Ceratiomyxa* with four species) is distinctly different from the other orders and is now assigned to a totally different taxonomic class, the Ceratiomyxomycetes. Based on a phylogeny constructed from 18S rDNA sequences (e.g. Fiore-Donno *et al*. 2005, 2008, 2010, 2013), myxomycetes in the other orders make up a monophyletic group which splits into two basal clades. The first clade (the subclass Columellomycetidae) consists mostly of members of the traditional

orders Stemonitales and Physarales, which have dark (different tints of brown to black) spores, along with members of the traditional order Echinosteliales. The second clade (the subclass Lucisporomycetidae) includes the traditional orders Liceales and Trichiales with brightly coloured spores (including red, orange, purple, yellow and olive). However, the traditional orders no longer hold together in the manner in which they have been circumscribed in all earlier treatments of the myxomycetes. Instead, a number of superorders are recognized in each of the two subclasses, with each made up of several orders. For example, the subclass Lucisporomycetidae contains four orders, none of which corresponds exactly to any of the traditional orders, while the subclass Columellomycetidae contains five different newly recognized orders. The classification system used herein essentially follows that outlined by Leontyev *et al.* (2019)

The fact that the vast majority of myxomycetes can be assigned to one of two groups on the basis of the spore colour in mass is not a new concept. It was first proposed by Joszef Rostafinski (1874–1876) and then used in Arthur Lister's *A Monograph of the Mycetozoa* (1894), which was the standard reference on the myxomycetes at the end of the nineteenth and during the early part of the twentieth century. This classic monograph first appeared in 1894, but revised and expanded versions were published in 1911 and 1925 by his daughter Gulielma Lister (Lister 1911, 1925). The 1925 edition is noteworthy in the context of the present monograph because it contains references to species of myxomycetes that had been reported from Australia prior to the third decade of the twentieth century.

Historical Background in Australia

The first report of myxomycetes from Australia was by the Reverend Miles Berkeley (1839), who listed two species from Tasmania (but then known as Van Diemen's Land) that had been collected by Robert Lawrence and Ronald Gunn and sent to William Hooker in Britain. The two species—*Aethalium septicum* (now known as *Fuligo septica*) and *Stemonitis fusca*—are both relatively common and form relatively conspicuous fruiting bodies. Later, Berkeley (1845) mentioned eight species (including *Stemonitis fusca*) identified from specimens collected by James Drummond in Western Australia and sent to Hooker. Drummond had arrived at the Swan River Colony in 1829 (May & Pascoe 1996), and the specimens of myxomycetes he sent to Hooker were collected at some point after this date. In another early report, Berkeley (1859) reported 16 species that had been identified from specimens collected by two amateur mycologists (Ronald Gunn and William Archer) in Tasmania during the period 1839-1843. Interestingly, two of these (the first described originally as *Stemonitis echinulata* but renamed *Lamproderma echinulatum* and the second described originally as *Trichia metallica* but now known as *Prototrichia metallica*) were new to science. Some years later, Berkeley (1881) also reported the first records from eastern Australia when he listed nine species from Queensland. Other reports prior to 1900 are those of Mordecai Cooke (1888a, 1888b, 1892) and Daniel McAlpine (1895). In his *Handbook of Australian Fungi*, Cooke (1892) listed approximately 50 species of myxomycetes for Australia. During the period 1900 to 1935, Cheesman & Lister (1915), Cheel (1918), Cleland (1927, 1935) and Fraser (1933) provided additional records, essentially doubling the total number of species known from the country. The best known region of Australia, based on collections made during the first half of the twentieth century, was in and around Sydney in New South Wales, for which Lilian Fraser (1933) listed a

Life Cycle

The life cycle of a myxomycete (**Fig. 1**) encompasses two very different trophic (or feeding) stages, one consisting of uninucleate amoebae, with or without flagella (the term 'amoeboflagellate' applies to both forms), and the other consisting of a distinctive multinucleate structure, the plasmodium (plural: plasmodia). It should be noted that much of what is known about the life cycle in myxomycetes has been derived from intensive studies of just two species (*Physarum polycephalum* and *Didymium iridis*), but it is assumed that all other species follow a similar pattern.

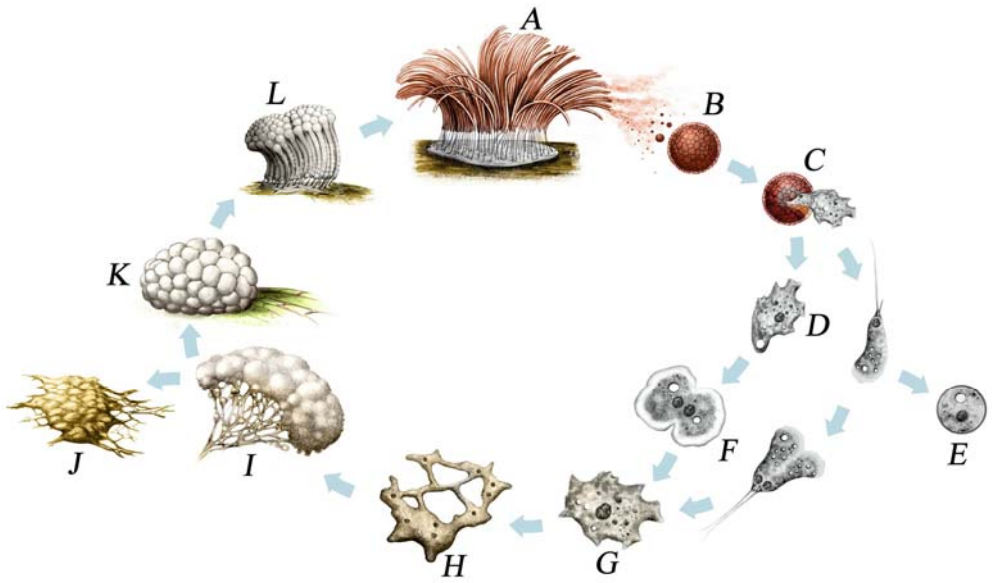

Figure 1. Generalized life cycle in the myxomycetes.

A. Group of fruiting bodies. **B.** Spore. **C.** A protoplast emerges from the spore. **D.** The protoplast can take the form of an amoeba (left) or a flagellated cell (right) during the first trophic stage (the term 'amoeboflagellate' applies to both forms). **E.** Under dry conditions or in the absence of food, an amoeboflagellate can form a microcyst, or resting stage. **F.** Compatible amoeboflagellates fuse to form a zygote. **G.** Zygote. **H.** The nucleus of the zygote divides by mitosis and each subsequent nucleus also divides without being followed by cytokinesis, thus producing a single large cell, the plasmodium. **I.** The plasmodium, which represents the second trophic stage in the life cycle. **J.** Under adverse conditions, the plasmodium can form the second type of resting stage found in myxomycetes, the sclerotium. **K–L.** Fruiting bodies develop from the plasmodium. During fruiting body formation, spores are produced.

Plasmodia are motile, and those of some species can reach a size of a metre or more in total extent. A large example contains many thousands of synchronously dividing nuclei. Under favorable conditions, a plasmodium gives rise to one or more fruiting bodies containing spores. The transformation from plasmodium to fruiting body is a

Figure 3, A–F. Development of fruiting bodies in *Stemonitis axifera*. Photos: © S. Lloyd.

Presumably, the spores produced in the fruiting body of a myxomycete are largely wind-dispersed and complete the life cycle by germinating to produce the uninucleate amoeboflagellate cells (Stephenson *et al*. 2008). 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 rises to the plasmodium. This process can result from gametic fusion between comparable amoeboflagellates or it can be apomictic (Collins 1980, 1981).

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 (plural: sclerotia), which is capable of reforming the plasmodium upon the return of favourable conditions. In addition, amoeboflagellate cells can undergo a

is widely distributed in North America and Europe but apparently uncommon elsewhere in the world (Martin & Alexopoulos 1969).

2. *Cribraria aurantiaca* Schrad., *Nov. Gen. Pl.* 5 (1797).

Cribraria vulgaris var. *aurantiaca* (Schrad.) Pers., *Syn. Meth. Fung.* 1: 194 (1801).

TYPE LOCALITY: Germany.

ILLUSTRATIONS: Martin & Alexopoulos (1969), Martin *et al.* (1983), Nannenga-Bremekamp (1991), Neubert *et al.* (1993), Lado & Pando (1997), Yamamoto (1998), Ing (1999), Poulain *et al.* (2011).

DESCRIPTION: *Fruiting body* a stalked sporangium, gregarious, 1–2 mm tall. *Sporotheca* globose, often nodding, 0.3–0.6 mm in diameter. *Stalk* reddish-brown, often brightly so, tapered upwards. *Hypothallus* inconspicuous. *Peridium* bright yellow fading to ochraceous. *Peridial net* regular, small-meshed, with numerous small, rounded nodes, the threads with few free ends. *Calyculus* well-developed, occupying about a third to a fourth of the sporotheca, the margin with numerous teeth and spines or low triangular projections, dictydine granules up to 1.5 µm in diameter, moderately dark. *Spores* bright yellow in mass at first and then fading to ochraceous, pale yellow to pallid by transmitted light, 6–7 µm in diameter, nearly smooth, with internal refractile oil droplets readily apparent in fresh material. *Plasmodium* bright green.

ECOLOGY AND DISTRIBUTION: Associated with decaying wood, especially that of conifers in forests of the Northern Hemisphere. First reported from Australia by Knight & Brims (2010), based on a specimen from Western Australia.

COMMENTS: *Cribraria aurantiaca* has often been regarded as a variety of (or even combined with) *C. vulgaris*, but the differences between the two are now considered sufficient to recognize them as distinct species. The former is relatively easy to identify from its bright yellow colour and the refractile oil droplets present in the spores if fresh material is available. The vast majority of records of this species are from North America and Europe, with only a few records from the entire Southern Hemisphere. This presumably reflects, at least in part, the association of *C. aurantiaca* with the decaying wood of conifers.

3. *Cribraria bicolor* S.L.Stephenson, Novozh. & P.Wellman, *Novosti Systematiki Nizshikh Rastenii* 52: 381 (2019). **Fig. 7**

TYPE LOCALITY: Northern Territory, Australia.

ILLUSTRATION: Stephenson *et al.* (2019).

DESCRIPTION: *Fruiting body* a stalked sporangium, scattered or in small groups, 400–600 µm tall. *Sporotheca* globose, 100–150 µm in diameter. *Stalk* vivid red or reddish-orange over the lower portion and light orange-yellow over the upper portion, 30–50 µm in diameter at the base and 10–15 µm in diameter at the apex, about two-thirds the total height of the entire sporangium. *Hypothallus* membranous, discoid, yellow or orange-yellow. *Peridium* membranous, glossy vivid violet. *Peridial net* rather open and not well-developed. *Calyculus* shallow but well-developed, representing no more than the lower one-third of the sporotheca, with radial folds, dictydine granules regular, 0.5–1.5 µm in diameter. *Spores* vivid violet in mass, rosy or light pink by transmitted light, 7–8 µm in diameter, verruculose. *Plasmodium* not observed.

ECOLOGY AND DISTRIBUTION: Associated with the bark of living trees (fruiting bodies appearing in moist chamber cultures). First reported from Australia by Stephenson *et al*. (2019), based on a number of specimens from New South Wales and the Northern Territory. All of the specimens appeared on bark samples collected from living *Eucalyptus*.

COMMENTS: The distinguishing features of this species are the glossy vivid violet sporotheca and the red colour of the lower portion of the stalk. The currently known distribution of this species in Australia is rather limited, but it is possible this would be expanded with additional surveys that made use of the moist chamber culture technique.

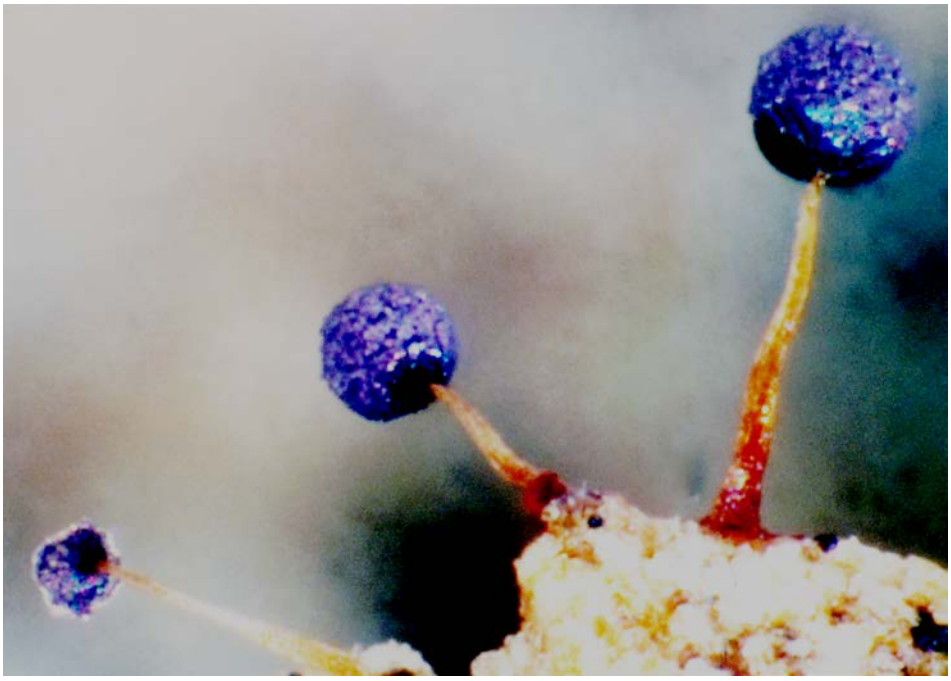

Figure 7. *Cribraria bicolor*. Photo: © Y. Novozhilov.

4. *Cribraria cancellata* (Batsch) Nann.-Bremek., *Nederlandse Myxomyceten* 92 (1975). **Figs. 8, 9**

Mucor cancellatus Batsch, *Elench. Fung. Continuatio Secunda* 135 (1789).

Dictydium cancellatum (Batsch) T.Macbr., *N. Amer. Slime-Moulds*, ed. 1, 172 (1899).

Cribraria cancellata var. *fusca* (Lister) Nann.-Bremek., *Nederlandse Myxomyceten* 93 (1975).

TYPE LOCALITY: Germany.

ILLUSTRATIONS: Martin & Alexopoulos (1969), Martin *et al*. (1983), Nannenga-Bremekamp (1991), Neubert *et al*. (1993), Stephenson & Stempen (1994), Lado &

TYPE LOCALITY: Sweden.

ILLUSTRATIONS: Martin & Alexopoulos (1969), Martin *et al*. (1983), Nannenga-Bremekamp (1991), Neubert *et al*. (1993), Lado & Pando (1997), Yamamoto (1998), Ing (1999), Poulain *et al*. (2011), Lloyd (2014, 2018).

DESCRIPTION: *Fruiting body* a stalked sporangium, crowded and sometimes more or less tangled, 2.0–3.5 mm tall. *Sporotheca* subglobose to subcylindrical, 0.5–1.0 mm in diameter. *Stalk* cylindrical, up to 1.0 mm long. *Hypothallus* thin, membranous, colourless. *Peridium* wine-red to dark red but becoming red-brown, persisting in mature fruiting bodies only as a rather deep and asymmetrical (or rarely shallow and symmetrical) calyculus. *Capillitium* consisting of a network of threads 3.5–8.0 µm in diameter and marked with warts, spines, cogs, half-rings and rings, also with a number of ridges that may unite locally to form a reticulum. *Spores* reddish-brown in mass, almost colourless by transmitted light, 7–8 µm in diameter, with a few scattered small warts and sometimes a few groups of larger warts. *Plasmodium* white.

Figure 33. *Arcyria affinis*. Photo: © S.Lloyd.

ECOLOGY AND DISTRIBUTION: Associated with decaying wood. First reported from Australia (as *Arcyria incarnata* var. *fulgens*) by Cheesman & Lister (1915), based on specimens from New South Wales and Victoria, and more recently recorded from Tasmania and Western Australia (Knight & Brims 2010; Lloyd 2014, 2018).

COMMENTS: This species has been considered as doubtfully distinct from *Arcyria incarnata* by some authors, and the two species are certainly very close. The major distinguishing features are differences in the calyculus (deep, funnel-shaped in *A. affinis* and shallow dish-shaped in *A. incarnata*) and capillitium (expanding longitudinally to form a long procumbent plume in *A. affinis* and usually expanding

evenly and remaining more or less erect in *A. incarnata*). *Arcyria affinis* appears to be most common in Europe and is known from scattered records elsewhere in the world. However, the fact that the species hasn't always been recognised as distinct makes any determination of its distribution somewhat problematic.

2. *Arcyria afroalpina* Rammeloo, *Bull. Jard. Bot. Belg.* 51(1/2): 229 (1981).

TYPE LOCALITY: Rwanda.

ILLUSTRATIONS: Yamamoto (1998), Schnittler *et al.* (2002).

DESCRIPTION: *Fruiting body* a stalked sporangium, solitary or scattered, 0.6–1.2 mm tall. *Sporotheca* subglobose to ovoid, 0.1–0.4 mm in diameter. *Stalk* cylindrical, very slender, 0.5–1.0 mm long, striate, pale yellow or light grey, the base darker. *Hypothallus* inconspicuous. *Peridium* pale yellow to almost white, persisting in mature fruiting bodies only as a shallow saucer-shaped calyculus, the inner surface either smooth or faintly punctate. *Capillitium* consisting of a network of threads, 2–3 µm in diameter, these slightly elastic, hyaline by transmitted light, firmly attached to the calyculus, decorated with faint warts, spines and cogs. *Spores* pale yellow in mass, very pale yellow to hyaline by transmitted light, 9–11 µm in diameter, warted. *Plasmodium* not observed.

ECOLOGY AND DISTRIBUTION: Associated with ground litter, aerial litter and lianas (fruiting bodies appearing in moist chamber cultures). First reported from Australia by Wrigley de Basanta *et al*. (2008), based on a series of specimens from Queensland, and more recently reported from Christmas Island (Stephenson & Stephenson 2019).

COMMENTS: The single most distinguishing feature of *Arcyria afroalpina* is the very long, usually curved stalk. This is not a common species, but there are scattered records throughout tropical regions of the world, with very few records outside the tropics.

3. *Arcyria cinerea* (Bull.) Pers., *Syn. Meth. Fung.* 1: 184 (1801). **Figs. 34, 35**

Trichia cinerea Bull., *Herb. France* 10(109-120): pl. 47 (1790).

TYPE LOCALITY: France.

ILLUSTRATIONS: Martin & Alexopoulos (1969), Martin *et al.* (1983), Nannenga-Bremekamp (1991), Neubert *et al.* (1993), Stephenson & Stempen (1994), Lado & Pando (1997), Yamamoto (1998), Ing (1999), Poulain *et al*. (2011), Lloyd (2014, 2018).

DESCRIPTION: *Fruiting body* a stalked sporangium, scattered, gregarious or sometimes united by their fused stalks and occurring in digitate clusters of 2–20 or more fruiting bodies, 0.3–4.0 mm tall. *Sporotheca* ovate to cylindrical, usually tapering towards the tip, 0.1–0.8 mm in diameter. *Stalk* slender, pallid to black, up to 2 mm in length. *Hypothallus* discoid or contiguous for a group of fruiting bodies, transparent and often not evident. *Peridium* pale grey to light brown, ochraceous or less commonly yellowish-brown, persisting in mature fruiting bodies only at the base of the sporotheca, where it forms a rather small, shallow calyculus with a smooth, delicately stippled, finely reticulate inner surface. *Capillitium* consisting of a network of threads, 2–6 µm in diameter, these firmly attached to the calyculus, colourless or nearly so by transmitted light, densely covered with small blunt spines (occasionally also with cogs,

bands or reticulations). *Spores* pale grey or light yellow in mass, colourless by transmitted light, 6–7 µm in diameter, with a few scattered warts. *Plasmodium* white, less commonly grey or pale yellow.

Figure 34. *Arcyria cinerea*. Drawing: © A. Mele.

Figure 35. *Arcyria cinerea*. Photo: © P. Vallier.

cylindrical, longitudinally wrinkled, lacking lime, translucent, expanded at the base. *Hypothallus* membranous, more or less transparent. *Peridium* membranous, scarlet or bright purplish red, almost smooth, with included clusters of purplish red lime globules. *Columella* absent. *Capillitium* open; nodes few, large, bright red, angular or irregularly branched, connected by pale pink tubules. *Spores* purplish black in mass, pale pinkish brown by transmitted light, 7–10 µm in diameter, minutely spinulose with scattered clusters of darker warts. *Plasmodium* maroon or bright red.

ECOLOGY AND DISTRIBUTION: Associated with ground litter and various other types of plant debris; specimens have been collected in the field and from moist chamber cultures. First reported from Australia by Cribb & Cribb (1992), based on a specimen from Queensland, and recorded again from the same state in 2002. The species is also known from New South Wales and Norfolk Island.

COMMENTS: The combination of a long stalk and the bright red to maroon peridium of the sporotheca make this a very easy species to recognize. *Physarum roseum* is known from numerous localities throughout temperate and tropical regions of the world but appears to be most common in the tropics and subtropics (Martin & Alexopoulos 1969).

Figure 128. *Physarum roseum.* Photo: © T. & J. Van der Heul.