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Review

Myxomycetes in soil

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ABSTRACT

The myxomycetes are a group of protists that form a monophyletic taxon in the phylum Amoebozoa. Evidence of their evolutionary success is the fact that they account for more species (ca. 900 are currently recognized) than the combined total for the rest of the Amoebozoa. Moreover, myxomycetes are present in every terrestrial environment investigated to date and also, as amoebae or flagellated cells, in aquatic environments where they cannot form fruiting bodies. Even if culture-based methods tend to underestimate their occurrence in soil, myxomycetes probably account for ~50% of soil amoebae. The emergence of molecular-based methods has revolutionized our concepts of biodiversity, but myxomycetes are conspicuously absent from all environmental surveys. Herein we show that this is due to their highly diverging SSU rRNA gene sequences, which contain numerous Group I introns.

Further proof comes from a recent study that used a massive sequencing approach without primer bias to amplify RNAs. The results obtained show that the mycetozoans (myxomycetes along with dictyostelids and protostelids) are indeed a dominant group of soil protozoans.

1. Introduction

The myxomycetes (also referred to as myxogastrids or plasmodial slime molds) have been known from their fruiting bodies since at least the mid-17th century, and their life history has been understood for more than a century (Martin and Alexopoulos, 1969). Approximately 900 species are known (Lado, 2001), with more than 100 of these having been described in the past 25 years. Myxomycete fruiting bodies are predominantly terrestrial and apparently occur anywhere on earth where there are plants (and thus plant detritus). Well known microhabitats are decaying wood, aerial and ground plant litter, or the bark surface of living trees (Stephenson and Stempen, 1994), but myxomycetes also have been found on living leaves (Schnittler, 2001), associated with the inflorescences of large tropical herbs (Schnittler and Stephenson, 2002) or in aquatic habitats (Lindley et al., 2007). Indeed, the amoebae that have been assigned to the now invalid genus "*Hyperamoeba*" (Fiore-Donno et al., 2010b) have been recovered from various aquatic environments, including physiotherapy water baths, drinking water plants, frozen lakes and even the coelomic cavity of sea urchins (Karpov and Mylnikov, 1997; Zaman et al., 1999; Walochnik et al., 2004; Dyková et al., 2007). The currently available data on the distribution of myxomycetes, based on the occurrence of fruiting bodies, are likely to be rather incomplete, as non-fruiting forms might actually be widespread in marine and other habitats where they have been thought to be absent.

Based on the presence of their fruiting bodies, most species of myxomycetes are cosmopolitan, although some appear to be restricted to the tropics and subtropics, whereas others seem to be strictly temperate (Stephenson et al., 2008). The greatest biodiversity of myxomycetes is known from temperate broadleaved forests of the Northern Hemisphere, but they also inhabit a wide spectrum of terrestrial habitats (Alexopoulos, 1963; Martin et al., 1983), including deserts and grasslands (Blackwell and Gilbertson, 1980), mountainous areas (Ronikier and Ronikier, 2009), coniferous forests and tundra at high latitudes (Stephenson and Laursen, 1993; Stephenson et al., 2007), and tropical forests (Farr, 1976; Schnittler and Stephenson, 2000; Stephenson et al., 2004b). The large number of species known from temperate regions undoubtedly reflects, at least in part, the concentration of collector activity, but results from recent studies of Neotropical forests (Stephenson et al., 2004b; Lado and Wrigley de Basanta, 2008) suggest that biodiversity of myxomycetes is lower in tropical forests than in temperate forests. As might be expected, based on what is known for other organisms, overall biodiversity of myxomycetes appears to be lowest in high-latitude regions of the world (Stephenson et al., 2000).

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2. Life cycle

The myxomycete life cycle encompasses two very different trophic (or feeding) stages, one consisting of uninucleate amoebae, with or without flagella (the general term "amoeboflagellate" encompasses both types), and the other consisting of a distinctive multinucleate structure, the plasmodium (Martin et al., 1983). In the sexual life cycle (Fig. 1), this process results from gametic fusion of compatible (thus genetically different) amoeboflagellates. There is also evidence for the occurrence of an asexual life cycle, since some strains derived from single spore (homothallic) cultures have been reported to form plasmodia with or without fusion of genetically identical amoebae (Collins, 1981; Clark, 1997). Under favorable conditions, the plasmodium gives rise to one or more fruiting bodies containing spores. For sexual strains, meiosis is assumed to take place in the maturing spores, which germinate to produce the next generation of uninucleate amoeboflagellate cells. These feed and divide by binary fission to build up large populations that can live indefinitely, even in habitats where the fruiting bodies cannot develop. Bacteria apparently represent the main food resource for both trophic stages, but plasmodia are also known to feed upon yeasts, algae (Lazo, 1961), cyanobacteria, fungal spores and hyphae (Stephenson and Stempen, 1994). Under adverse conditions, such as drying out of the microhabitat, drop of temperature and lack of food organisms, a plasmodium may convert into a hardened, resistant structure called a sclerotium, which can quickly revert to the active stage upon the return of favorable conditions. Moreover, amoeboflagellate cells can undergo a reversible transformation to dormant structures called microcysts, and the spores themselves are capable of resisting relatively harsh conditions. All of these resistant forms can remain viable for long periods of time and are probably very important in the continued survival of myxomycetes in the changing conditions of the habitats in which they occur.

The fruiting bodies produced by myxomycetes are somewhat suggestive of those produced by small fungi, 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 (Schnittler and Tesmer, 2008), and they are presumably wind-dispersed (Stephenson et al., 2008; Kamono et al., 2009a).

3. Phylogenetic position and classification

Myxomycetes belong to the phylum Amoebozoa (Cavalier-Smith, 1998), which includes all testate and naked lobose amoebae that were traditionally classified in the class Lobosea Carpenter 1861 (Page, 1987) along with the pelobionts, entamoebids, and other mycetozoans (Bolivar et al., 2001; Fahrni et al., 2003; Cavalier-Smith et al., 2004; Nikolaev et al., 2006; Pawlowski and Burki, 2009). All of these organisms share the characteristic of possessing lobose or pointed pseudopodia (neither filopodial nor

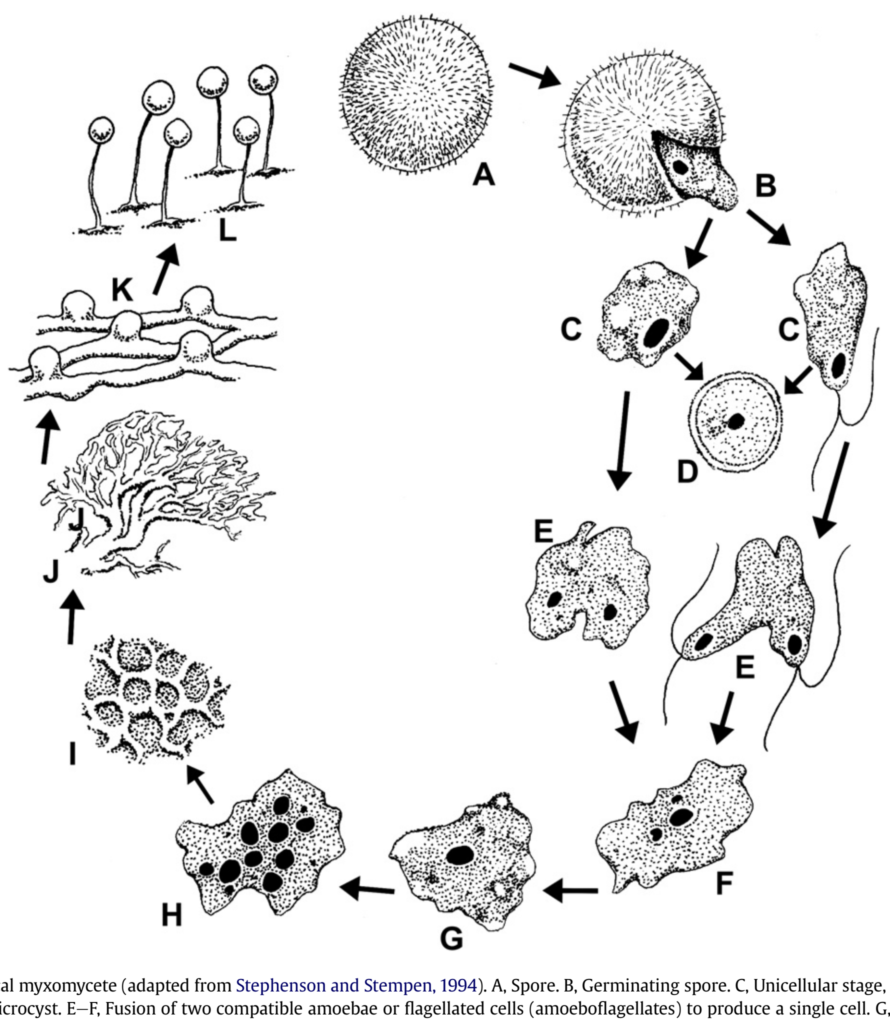

Fig. 1. Sexual life cycle of a typical myxomycete (adapted from Stephenson and Stempen, 1994). A, Spore. B, Germinating spore. C, Unicellular stage, which is either an amoeba (left) or a flagellated cell (right). D, Microcyst. E–F, Fusion of two compatible amoebae or flagellated cells (amoeboflagellates) to produce a single cell. G, Zygote. H, Early plasmodium. I, Sclerotium. J, Portion of a mature plasmodium. K, Beginning of sporulation. L, Mature fruiting bodies with spores still enclosed.