Coprophilous myxomycetes: Recent advances and future research directions

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Abstract Species of myxomycetes are adapted to different ecological niches and occupy different microhabitats. The majority of species have a wide ecological amplitude and may be found on various kinds of substrata. Some species have narrower ecological niches and are restricted to or mainly found on one special kind of substratum. Coprophilous species grow on dung or on a substratum in close contact with dung. The vast majority of records stem from moist chamber cultures on dung from herbivorous mammals, but several species have also been recorded on droppings from birds. A limited number of species can be regarded as truly coprophilous in that they have predominantly or in some cases only been recorded on dung. Some of these species are known from very few collections and their dependence on dung may therefore be difficult to judge. No correlation is absolute and species regarded as coprophilous may sometimes, although rarely, turn up on other types of substrata. Dung is rich in bacteria and nutrients and is a favourable substratum for myxomycetes. Many species normally inhabiting other habitats are occasionally found on dung, and up to now about 114 species have been reported from this kind of substratum, a number that will continue to grow. At least three species, *Licea alexopouli*, *Kelleromyxa fimicola* and *Trichia brunnea*, have thick-walled spores, a possible adaptation to passing through the intestinal tract of a herbivore before germination can take place.

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Introduction

Species of true fungi and myxomycetes that predominantly occur on dung or are confined to this substratum are referred to *coprophilous* or *fimicolous* species. Early reports of coprophilous myxomycetes were scattered records included in papers on coprophilous true fungi, for example Marchal (1895), and much information has accumulated as byproducts of studies where ascomycetes and basidiomycetes have been the main objects of the study. One of the first studies restricted to coprophilous myxomycetes is that by Merrill (1969) on species found in California. One of the more comprehensive studies was published by Eliasson and Lundqvist (1979). Although many literature records were summarized in this paper, the bulk of the material originated from Lundqvist's (1972) comprehensive study of coprophilous ascomycetes on a large variety of dung from domestic as well as wild animals representing artiodactyls, hyracoids, rodents, lagomorphs, bats, and birds (for a detailed list of species see Eliasson and Lundqvist 1979). The rich harvest of Lundqvist's cultures was due not only to the large number of cultures and the wide array of different kinds of dung but also to the fact that he let the samples remain in culture for a long time, normally several months. Many species did not fruit until after three months or so. In all, 81 species, literature records included, were listed as having been recorded on dung, of which only a limited number could be regarded as predominantly coprophilous.

A more recent summary of coprophilous myxomycetes was compiled by Eliasson and Keller (1999). Their total list of species comprised 99 species. The number included

scattered records in various papers as well as papers on coprophilous myxomycetes from a certain geographical region, like California (Cox 1981), Uruguay (García-Zorrón 1977) and Taiwan (Chung and Liu 1995, 1996). Another recent review of coprophilous myxomycetes is that of Krug et al. (2004).

Some ecological aspects

Some species of myxomycetes have a clear preference for dung as a substratum whereas for many species with a wider ecological amplitude dung is just one of many possible substrata. Dung is a complex substratum regarding its physical and chemical properties depending on the kind of animal that produced it, remaining vegetable fragments, age, grade of decomposition, and contents of bacteria and fungi. The high microbial content and high nutrient richness together with high moisture level create a favourable substratum and microhabitat for myxomycetes (Hudson 1986; Stephenson 2011). Dung of course contains bacteria of different kinds and the bacterial species composition is likely to differ depending on species of animal and perhaps the kind of food the animal has eaten. It may well be that myxomycetes on dung may be dependent more on certain kinds of bacteria than on the physical properties of the substratum. The pH of the substratum is one of the important factors determining which species grow on a particular substratum and is routinely given today in papers based on moist chamber cultures. Some species like *Arcyria cinerea* (Bull.) Pers. have a wide pH range, whereas other species may be restricted to narrower pH spectra. The composition of the myxomycete community of a given substratum is dependent on or influenced by pH and species may be grouped according to different pH levels (Everhart et al. 2008; Keller and Everhart 2010). Dung normally has a higher pH than has decaying wood and most other myxomycete substrata, and this is probably one of the reasons why certain species may be predominantly coprophilous (Stephenson and Stempen 1994). When it comes to true fungi Lundqvist (1972) found that a fungus growing on several kinds of dung prefers that of related animals, and that seems to hold for myxomycetes as well, the reason being similarities in chemical, physical and microbial properties. He also found that at least some coprophilous ascomycetes may have different ecological requirements in different parts of their distribution areas, being more stenoecious in some regions and more tolerant in others. We don't have enough data to see whether such examples may be found also among myxomycetes.

Most records of coprophilous myxomycetes are from moist chamber cultures on dung from domestic animals like cow and horse. These kinds of substrata are easily available,

but there are probably myxomycetes to be found on almost all kinds of dung. Among non-domestic animals the dung of moose (*Alces*), roe deer (*Capreolus*), hare (*Lepus*) and rabbit (*Oryctolagus*) is among the most productive in the north temperate region, but coprophilous myxomycetes are also known from dung of a large number of artiodactyls and other animals in Africa (Eliasson and Lundqvist 1979; Ing 1994).

Species recorded on dung of herbivores; additions to list in Eliasson and Keller (1999)

The number of species recorded on dung has continued to grow. At least fifteen additional species have been recorded more recently on dung, the majority of species reported from Brazil (Bezerra et al. 2008) and from Russia and Kazakhstan (Novozhilov et al. 2006, 2008). The following list should be added to the summary published by Eliasson and Keller (1999). This makes a total of ca 114 species of myxomycetes recorded on dung. Scattered literature records may have been overlooked, and the list will continue to grow.

Arcyria minuta Buchet (Novozhilov et al. 2006)
Badhamia verrucospora G. Moreno, D. W. Mitch. & Novozh. (Moreno et al. 2011)
Cribraria cancellata (Batsch) Nann.-Bremek. (Bezerra et al. 2008)
Cribraria microcarpa (Schrad.) Pers. (Bezerra et al. 2008)
Didymium inconspicuum Nann.-Bremek. & D. W. Mitch. (Novozhilov et al. 2006)
Didymium melanospermum (Pers.) T. Macbr. (Tóth 1965)
Metatrichia vesparium (Batsch) Nann.-Bremek. (Bezerra et al. 2008)
Oligonema schweinitzii (Berk.) G. W. Martin (Jahn 1916; as *O. nitens*)
Perichaena pachyderma D. W. Mitch., G. Moreno & Lizárraga (Mitchell et al. 2011)
Perichaena polygonospora Novozh. (Novozhilov et al. 2008)
Physarum decipiens M. A. Curtis (Novozhilov et al. 2006)
Physarum notabile T. Macbr. (Krug et al. 2004)
Physarum roseum Berk. & Broome (Bezerra et al. 2008)
Physarum vernum Sommerf. (Novozhilov et al. 2006)
Trichia papillata Adamonyte (Adamonyte 2003)

To the list above should perhaps be added *Trichia crenulata* (Meyl.) Meyl. It was originally first described by Meylan (1924) as a variety of the rather variable *T. contorta* (Ditmar) Rostaf., but later with support of additional uniform material raised to species level (Meylan 1929). Despite

its apparently excellent characteristics, combining sporocarps similar to those of *T. contorta* with spore ornamentation like that of *T. persimilis* (Kowalski 1975), it has commonly been disregarded in taxonomic monographs, although Martin and Alexopoulos (1969) remarked that it was "quite probably worthy of recognition". It was recognized as a distinct species by Lado (2001). Apart from its type locality (Jura Mountains, Switzerland) it has to my knowledge been formally reported only from the Yunnan Province in China. Although the typical substratum is bark and dead wood it has been reported (if the same species) also from dung of lagomorphs.

The vast majority of species recorded on dung typically occurs on other types of substrata and their occurrence on dung is merely accidental. Among such records are many species typically found on decaying wood, for example *Comatricha nigra* (Pers. ex J. F. Gmel.) J. Schröt., *Cribraria cancellata* (Batsch) Nann.-Bremek., *C. microcarpa* (Schrad.) Pers., *Diderma radiatum* (L.) Morgan, *Lycogala epidendrum* (L.) Fr., *Physarum album* (Bull.) Chevall., *Trichia botrytis* (J. F. Gmel.) Pers. and *T. varia* (Pers. ex J. F. Gmel.) Pers., to mention just a few of numerous examples. Typical inhabitants of bark of living trees are *Cribraria violacea* Rex and *Echinostelium minutum* de Bary. Among the rather few predominantly leaf litter inhabiting species that have been found on dung is *Didymium nigripes* (Link) Fr. A most surprising coprophilous record is that of *Physarum roseum* (Bezerra et al. 2008), a species of tropical and warm-temperate regions normally found on wood and leaf litter.

The number of records on various kinds of dung will continue to grow and new species typically restricted to other substrata will occasionally turn up on dung. The causes of this are several. Dung in itself is not a uniform substratum but highly different depending on animal in structure, moisture, contents of bacteria etc. An attempt was made (Eliasson and Lundqvist 1979) to find differences in frequencies of different species between dung from domestic versus forest animals, but differences are difficult to evaluate due to the limited number of samples from different kinds of dung. A plasmodium developing on a leaf or other substratum may expand onto an adjacent piece of dung and develop fructifications there. A film of bacteria or fungal hyphae on which the plasmodium feeds may cover several kinds of substrata, even inorganic substrata like rocks and pieces of glass or metal and make sporocarps develop there. Many species of myxomycetes are opportunistic and may occur in odd places and on odd substrata (Keller et al. 2008). Occasional odd occurrences have a natural cause, and it should not be surprising that species normally regarded as restricted to another substratum may occur on dung. Likewise, species normally found on dung may occasionally expand onto adjacent pieces of other substrata. For example, the normally strictly coprophilous species *Perichaena liceoides*,

may develop sporocarps on fragments of ground litter when these are in contact with dung (Krzemieniewska 1960).

Several species that have a broad ecological spectrum and are mostly associated with other types of substrata are common on dung. Such species are *Arcyria cinerea* (Bull.) Pers., *Didymium difforme* (Pers.) Gray, *D. squamulosum* (Alb. & Schwein.) Fr., *Echinostelium minutum* de Bary and *Stemonitis fusca* Roth.

The occasional occurrence on dung of a species normally strictly associated with a different substratum may be difficult to explain when the two kinds of substrata are not at all in close contact. An example is the normally wood and bark inhabiting species *Lycogala epidendrum* which, although rarely, may occur on cow dung.

Species predominantly occurring on dung of herbivores

There are probably no obligate coprophilous myxomycetes in the strictest sense. However, there is a number of about 16 species that are truly coprophilous in so far as they have predominantly and, in a couple of cases so far only, been found on this kind of substratum. Species so defined could be listed as follows.

Badhamia apiculospora (Härk.) Eliasson & N. Lundq.
B. rhytidosperma H. W. Keller & Schokn.
B. spinispora (Eliasson & N. Lundq.) H. W. Keller & Schokn.
Didymium annulisporum H. W. Keller & Schokn.
D. nullifilum (Kowalski) M. L. Farr
D. rugulosporum Kowalski
Kelleromyxa fimicola (Dearn. & Bisby) Eliasson
Licea alexopouli M. Blackw.
L. pescadorensis Chao H. Chung & C. H. Liu
Macbrideola indica (A. K. Sarbhoy, S. N. Singh & D. K. Agarwal) Nann.-Bremek., T. H. Lakh., K. G. Mukerji & Singh
Perichaena liceoides Rostaf.
P. luteola (Kowalski) Gilert
Trichia brunnea J. J. Cox
T. elaterensis (Mulleavy) Lado
T. fimicola (Marchal) Ing
T. papillata Adamonyte

Among the species most commonly encountered on dung are *Badhamia apiculospora*, *B. spinispora*, *Licea alexopouli*, *Perichaena liceoides* and *P. luteola* (cf Novozhilov et al. 2003).

Some of the species in this list are so far known from a very limited number of collections, perhaps making their assignment to the coprophilous category doubtful. Such species are *Trichia elaterensis* (only from type collection), *Badhamia rhytidosperma*, *Didymium annulisporum*, *D. nullifilum*, *D. rugulosporum*, *Licea pescadorensis*, *Macbrideola indica*, *Trichia brunnea* and *T. papillata*.

As already mentioned most, perhaps all, species found on dung may occasionally occur on other substrata. Thick-walled spores have been demonstrated in *Licea alexopouli* (Blackwell 1974), *Kelleromyxa fimicola* (Eliasson et al. 1991) and *Trichia brunnea* (Eliasson and Keller 1999) (Fig. 2). The wall thickness might be an adaptation to passage through the intestinal tract of herbivores, requiring the action of digestive juices on the spore wall before germination can take place. To my knowledge all three species so far seem to have been found only on dung. Thick-walled spores may occur in other species as well.

Several of the species regarded as truly coprophilous are known from very few collections in the world, but the records may be from geographically widely separate regions, even different continents, indicating that the species are of world-wide distribution. One such example is *Trichia papillata* which was described from Lithuania on moist chamber cultures on dung from hare and roe deer (Adamonyte 2003) but a few years later reported from Taiwan on plant litter (Liu et al. 2007).

Myxomycetes on bird droppings

Myxomycetes are known from dung of birds which feed on seeds, buds or other plant parts, for example, in the case of Capercaillie, pine needles. Among such birds are Capercaillie (*Tetrao urogallus*) (*Arcyria cinerea, Physarum confertum, Didymium difforme*); grouse (*Lagopus?*) (*Physarum* cf. *bitectum, Didymium difforme*); Black Grouse (*Lyrurus tetrix*) (*Didymium difforme*); goose (*Anser?*) (*Perichaena corticalis*); and Rock Dove (*Columba livia*) (*Physarum compressum*). (For references see Eliasson and Lundqvist 1979.)

Of great interest is the inventory of myxomycetes made by Adamonyte and collaborators (Adamonyte et al. 2011) in a Great Cormorant (*Phalacrocorax carbo*) colony in Lithuania. Among species obtained in moist chamber cultures on various kinds of substrata from the colony are *Arcyria leiocarpa, Badhamia apiculospora* and *Comatricha mirabilis,* all species regarded as rare.

Some species of true fungi seem to be specialized on dung of reptiles (Lundqvist 1972) but data on myxomycetes are lacking.

Comments on selected species

Licea alexopouli has been recorded from several states in the USA (Blackwell 1974; Eliasson and Lundqvist 1979), from Kenya and Tanzania in Africa (Eliasson and Lundqvist 1979) but may be overlooked elsewhere due to its inconspicuous sporocarps.

Kelleromyxa fimicola was originally described (as *Licea fimicola*) from the state of Manitoba in southern Canada

Fig. 1 *Trichia brunnea* (holotype, *Cox 570*, UC), a coprophilous species known from very few collections. Individual sporocarps are about 1.5 mm in total height

(Bisby et al. 1929). Other records are from USA (Angel and Wicklow 1975; Keller and Anderson 1978), Kenya (Eliasson and Lundqvist 1979), Russia (Novozhilov et al. 2006), China (Schnittler et al. 2012), Mongolia (Eliasson and Lundqvist 1979). All records are from moist chamber cultures of herbivore dung.

Trichia brunnea (Figs. 1, 2) was described from moist chamber cultures on cow dung in California (Cox 1981) and is also known from Norway and Montenegro (Eliasson and Keller 1999). Records are from moist chamber cultures of dung from cow, reindeer and horse, respectively. Records from Russia are from dung and from bark of living trees (Novozhilov et al. 2006).

Perichaena liceoides tends to be regarded today by most authors as a distinct species with a strong preference for dung of herbivorous animals. When found on other substrata it is usually in close association with dung. In its most
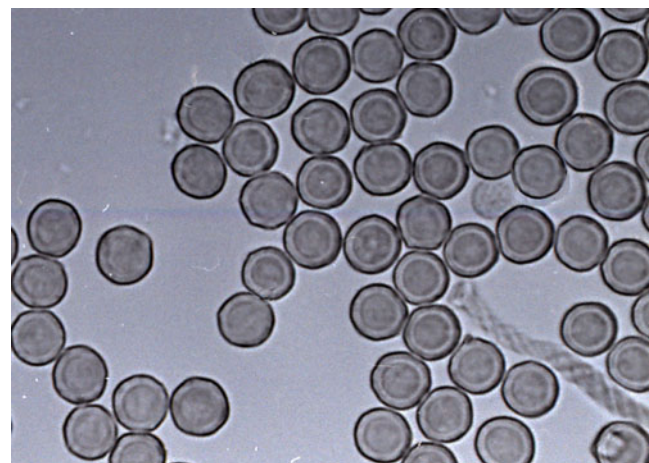

Fig. 2 *Trichia brunnea*, spores (holotype of *Hemitrichia stipata* var. *fusca* Z. Moravec; *Moravec s. num.* PRM). Spores are about 8 μm in diam. and thick-walled, a possible adaptation to passing through the intestinal tract of a herbivore before germination can take place

typical appearance it has a single (?) membranous peridium, a scantily developed or entirely missing capillitium and spiny spores (Gilert 1990). Although easily overlooked because of its small size it has been recorded from many countries in Europe, from Mongolia, Africa and the USA.

Perichaena luteola is morphologically close to and perhaps doubtfully distinct from *P. liceoides* with which it seems to be connected through intergrading forms and the two taxa seem to differ mainly in the degree of development of the capillitium. Typical specimens of *P. luteola* have a well developed capillitium forming a reticulum (Gilert 1995). *Perichaena luteola*, originally described from California (as *Calonema luteolum*), has been recorded in scattered localities in Europe from Great Britain in the west to Russia in the east and probably has a world-wide distribution.

Hemitrichia leiocarpa (Cooke) Lister [= *Arcyria leiocarpa* (Cooke) Massee] is a widespread but rare species that has occasionally been recorded on dung, but records are too few to evaluate the degree of possible preference for this substratum. Of great interest is the report of numerous collections of this species obtained on various substrata in a Great Cormorant colony in Lithuania (Adamonyte et al. 2011), where it was found together with two other rare myxomycetes, *Badhamia apiculospora* (Härk.) Eliasson & N. Lundq. and *Comatricha mirabilis* R. K. Benj. & Poitras. *Hemitrichia leiocarpa* is a species on the borderline between the genera *Hemitrichia* and *Arcyria* and, as far as morphology is concerned, could equally well be placed in either genus. The sporocarps are *Arcyria*-like in general habit and may closely resemble sporocarps of *Arcyria cinerea* (Bull.) Pers. The predominantly sinistrorse spiral ornamentation on the capillitial threads has been regarded as a character of taxonomic importance (Martin and Alexopoulos 1969; Eliasson and Keller 1999) but its taxonomic value has, perhaps rightly, been questioned. Dextrorse versus sinistrorse helical orientation remains an interesting conundrum in biology that requires further study.

Future research

As already mentioned, dung of herbivorous animals is a suitable substratum for myxomycetes because of the combination of a high microbial content, high moisture level, high nutrient richness and an alkaline or near neutral pH value. A piece of dung is a miniature ecosystem with an intense microbial activity influenced by the outer environment and with new organisms colonizing from the environment. This ecosystem is continuously changing during the process of decomposition of the substratum. Species that do not occur until during the latest stages of the decomposition develop on a very different substratum and it is questionable whether they should be regarded as coprophilous in the

strictest sense. Dung may be a more important substratum for myxomycetes in high-latitude and desert ecosystems than in warmer regions due to the much slower decomposition process in a colder and drier climate (Stephenson 2011). Nevertheless, the African plains with large herds of animals could be expected to harbour an interesting myxomycete community, so far largely unexplored.

Among the species mentioned in this paper only a restricted number are truly coprophilous in that they are predominantly known from dung. No correlation is absolute and there are probably no strictly obligate coprophilous species of myxomycetes. Even species with thick-walled spores may occasionally occur on other substrata as shown by the record of *Trichia brunnea* on bark of living trees or shrubs (Novozhilov et al. 2006). The majority of myxomycete species are opportunistic and the number of species found on dung will continue to grow. Many species typically found on other substrata will occasionally occur on dung and species thought to be restricted to dung will sooner or later be found on other substrata.

More studies are needed on possible adaptations to coprophily. We already know a small number of species with thick-walled spores but closer TEM-studies of the spore-wall are needed. Also, it would be interesting to study the germination process more closely. How important is the passing through the intestinal system of a herbivore for stimulating the germination process of the spores?

The majority of studies on coprophilous myxomycetes have been based on dung from domestic animals like horse, cow and goat. We know that these substrata produce many myxomycetes but it is difficult to compare these data with those from wild animals because the latter are so few in comparison.

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