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CHAPTER 3-2
SLIME MOLDS: BRYOPHYTE ASSOCIATIONS

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Figure 1. Slime mold, probably ***Fuligo septica***, on mosses in New Zealand. Photo by Bernard Spragg, through public domain.

Bryophyte Associations

Slime-mold-bryophyte associations can occur for a number of reasons. These can be accidental associations in which spores find favorable conditions to germinate, *i.e.*, sufficient moisture. Others are facultative, living on logs, but creeping onto mosses as the plasmodium moves about to feed and be able to survive there. Still others may climb up the bryophytes, as indicated in the previous subchapter, to emerge from bark crevices and reach the light for fruiting. Others germinate within the bryophyte mat where moisture conditions are maintained and bryophytes hide the slime mold plasmodium from our searching eyes. It is not until the slime mold is ready to produce sporangia that it climbs out where it is visible on the bryophyte. And finally, there are those slime molds that live only on bryophytes – the **bryophiles**. This latter group is a small one, but of the most interest to a bryologist. This chapter is a gathering of all sources I could find to demonstrate slime molds that ever occur on or with bryophytes.

Bryophiles

Dudka and Romanenko (2006) described a variety of cases in which slime molds interact or co-exist with other organisms. They found 13 species of slime molds on 9 species of mosses and 3 species of liverworts on decaying wood or bark in the Crimean Nature Reserve. These included their relationships with bryophytes and they noted that the slime mold **sporophores** (sporangial stalks) at the surface of mosses and liverworts are rather widespread in nature (Stephenson & Stempen 1994; Härkönen *et al.* 2002; Stojanowska & Panek 2004). But it appears that the best known bryophiles include only ***Barbeyella minutissima*** (Figure 2-Figure 3), ***Colloderma oculatum*** (Figure 4), and ***Lepidoderma tigrinum*** (Figure 5) (Schnittler & Novozhilov 1996; Dudka & Romanenko 2006).

Figure 2. Fruiting bodies of ***Barbeyella minutissima*** on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

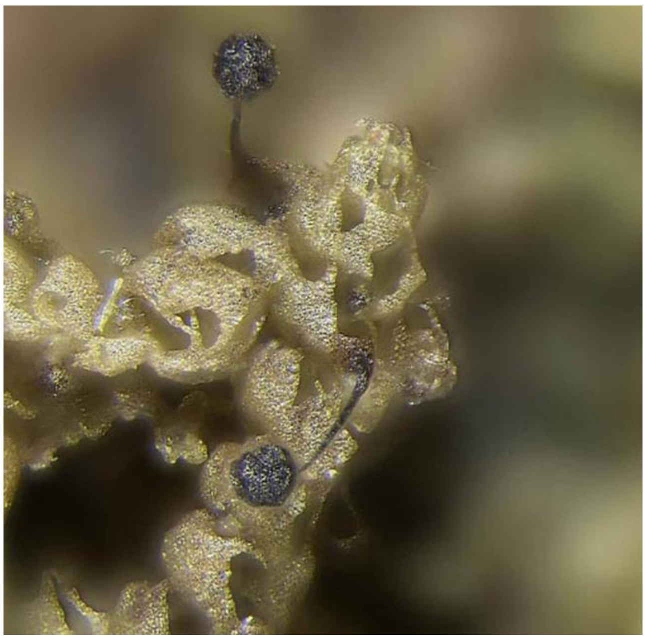

Figure 3. Fruiting bodies of ***Barbeyella minutissima*** on a leafy liverwort. Photo by Steve Stephenson, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 4. ***Colloderma oculatum*** on bryophytes. Photo from the Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 5. Fruiting bodies of ***Lepidoderma tigrinum*** on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Barbeyella minutissima (Figure 2-Figure 3) is a rare slime mold with a disjunct distribution in the northern Alps of Germany and several states in the Appalachian Mountains of the eastern USA (Schnittler *et al*. 2000). The distribution of this species is centered in montane spruce-fir forests, where it commonly associates with ***Colloderma oculatum*** (Figure 4), ***Lamproderma columbinum*** (Figure 6), and ***Lepidoderma tigrinum*** (Figure 5). ***Barbeyella minutissima*** is associated with several leafy liverwort species. In particular, the leafy liverwort ***Nowellia curvifolia*** (Figure 7-Figure 8) serves as an indicator for the presence of ***Barbeyella minutissima***.

Figure 6. ***Lamproderma columbinum*** on mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 7. ***Nowellia curvifolia*** on a decorticated log, an indicator for the slime mold ***Barbeyella minutissima***. Photo from Bioimages, through Creative Commons.

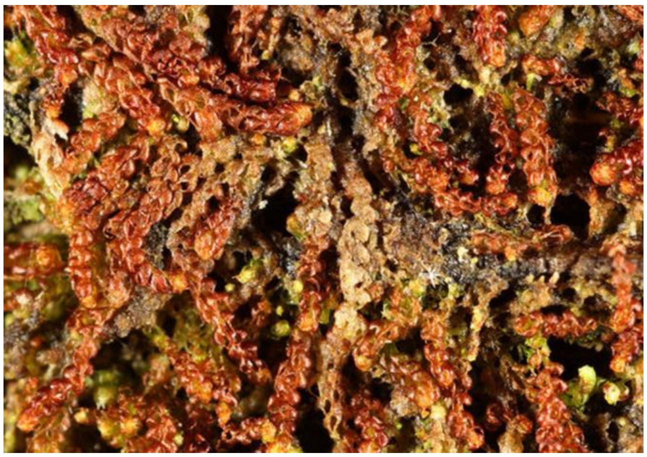

Figure 8. ***Nowellia curvifolia***, a leafy liverwort substrate for the slime mold ***Barbeyella minutissima***. Photo from Bioimages, through Creative Commons.

One very rare slime mold (***Elaeomyxa cerifera*** – Figure 9) is known primarily from the soil-dwelling thallose liverwort ***Pellia epiphylla*** (Figure 10) (Hadden 1921; Ing 1994), a soil-dwelling liverwort that is common on stream banks, but also occurs on decorticated logs, often in association with bryophytes. Similarly, ***E. reticulospora*** (Figure 11) is known only from its type locality on bryophytes in the tropics (Moreno *et al*. 2008).

Figure 9. ***Elaeomyxa cerifera*** with sporangia on bryophytes. Photo by Sarah Lloyd, with permission.

Figure 10. ***Pellia epiphylla*** with capsules. Photo by Li Zhang, with permission.

Figure 11. ***Elaeomyxa*** *cf*. ***reticulospora***, a tropical slime mold known only from bryophytes in its type locality. Photo by Sarah Lloyd, with permission.

Little study of tropical slime molds has occurred, with most of it in the last 20 years. One of these more thorough studies is that of Rojas *et al*. (2010) in Costa Rica. They determined that elevation was a key factor in determining distribution. Lowland substrate preferences include litter, inflorescences, and bryophytes (Schnittler & Stephenson 2000, 2002; Schnittler 2001). Species of these substrates tend to be specialized and have narrow niches. ***Lamproderma columbinum*** (Figure 6) and ***L. scintillans*** (Figure 12) seem to prefer bryophytes. ***Stemonitis fusca*** (Figure 13-Figure 14) and ***Lycogala epidendrum*** (Figure 15), both known from bryophytes, prefer higher elevation forests.

Figure 12. ***Lamproderma scintillans*** sporangia. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 13. ***Stemonitis fusca*** sporangia on moss. Photo by Richard Orr, with permission.

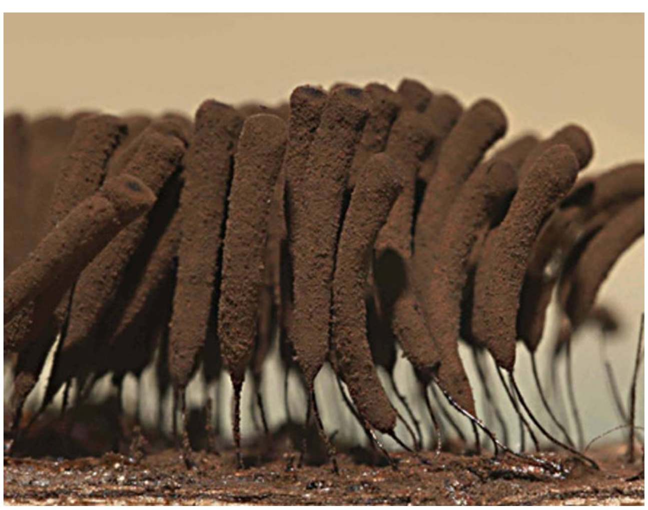

Figure 14. ***Stemonitis fusca*** with mature sporangia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 15. Fruiting bodies of ***Lycogala epidendrum*** (wolf's milk; toothpaste slime) on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Commonly Associated Slime Molds

Despite the apparently limited number of true bryophilous species, other coincidental associations may offer some moisture advantages. ***Arcyria cinerea*** (Figure 16-Figure 17; see also Robbrecht 1974), ***Echinostelium arboreum*** (Figure 18), ***E. minutum*** (Figure 19), ***Macbrideola cornea*** (Figure 20), ***Perichaena vermicularis*** (Figure 21), and ***Physarum cinereum*** (Figure 22-Figure 23) in the montane Crimea are most commonly associated with the mosses ***Hypnum cupressiforme*** (Figure 24) and ***Leucodon sciuroides*** (Figure 25), and leafy liverwort ***Porella platyphylla*** (Figure 26).

Figure 16. ***Arcyria cinerea***. fruiting bodies. Photo by George Barron, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 17. ***Arcyria cinerea*** fruiting on mosses. Photo by Dan Molter, through Creative Commons.

Figure 18. ***Echinostelium arboreum*** fruiting body. Photo from Myxotropic, through Creative Commons.

Figure 19. ***Echinostelium minutum*** fruiting body, a species frequently associated with bryophytes. Myxotropic, through Creative Commons.

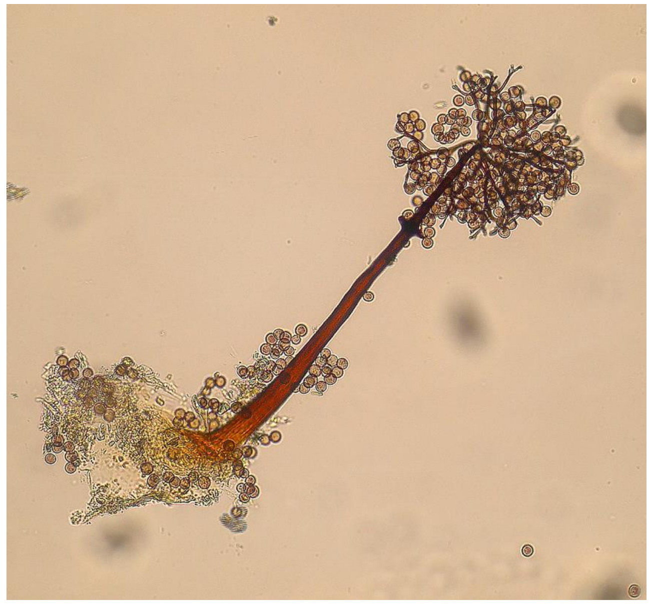

Figure 20. ***Macbrideola cornea***, a species frequently associated with bryophytes. Photo by Shirokikh, through Creative Commons.

Figure 21. ***Perichaena vermicularis***, a species frequently associated with bryophytes. Photo by Sarah Lloyd, with permission.

Figure 22. ***Physarum cinereum*** mature sporangia on log. Photo from Denver Botanical Gardens, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 23. ***Physarum cinereum*** var ***aureonodum*** with dehiscing capsules. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 24. ***Hypnum cupressiforme***, a moss that often provides the substrate for a number of slime mold species. Photo by Janice Glime.

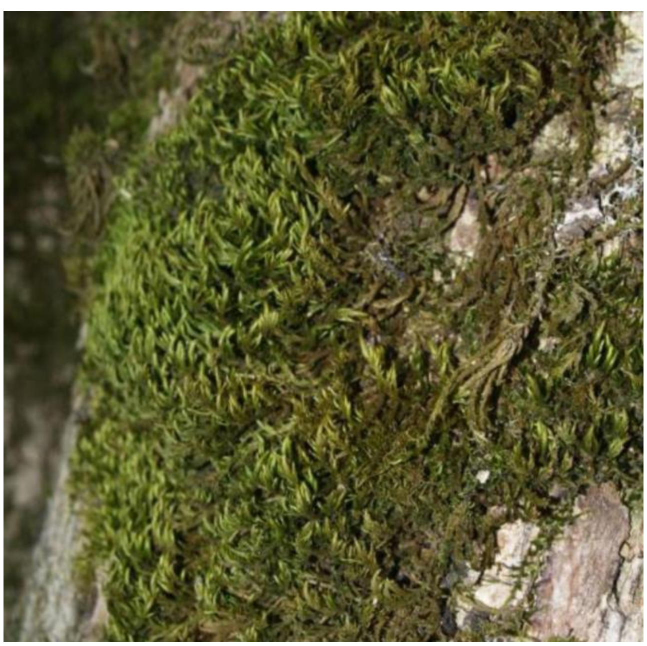

Figure 25. ***Leucodon sciuroides*** dry, a moss that often provides the substrate for a number of slime mold species. Photo by Kai Vellak, through Creative Commons.

Figure 26. ***Porella platyphylla***, a leafy liverwort that often provides the substrate for a number of slime mold species. Photo by Janice Glime.

The following **Myxomycete**-bryophyte associations are also known, but more rarely (Dudka & Romanenko 2006):

Didymium trachysporum (Figure 27) on ***Ctenidium molluscum*** (Figure 28)
Licea minima (Figure 29-Figure 30) on ***Hypnum cupressiforme*** (Figure 24)
Perichaena chrysosperma (Figure 31) on ***Frullania dilatata*** (Figure 32)
Stemonitis fusca (Figure 14) on ***Leucodon sciuroides*** (Figure 25)
Symphytocarpus amaurochaetoides (Figure 33-Figure 34) on ***Pterigynandrum filiforme*** (Figure 35-Figure 36)
Symphytocarpus impexus (Figure 37) on ***Porella platyphylla*** (Figure 26)
Trichia varia (Figure 38-Figure 39) on ***Anomodon viticulosus*** (Figure 40-Figure 41)

In addition to these, ***Physarum cinereum*** (Figure 22-Figure 23) occurs on fallen leaves and decaying wood, but it occurs more frequently on bryophytes.

Figure 27. ***Didymium trachysporum***, a species known from the moss ***Ctenidium molluscum***. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 28. ***Ctenidium molluscum***, a moss occasionally serving as a slime mold substrate. Photo by Michael Lüth, with permission.

Figure 29. ***Licea minima*** fruiting body, a species occasionally using the moss ***Hypnum cupressiforme*** as a substrate. Photo from Myxotropic, through Creative Commons.

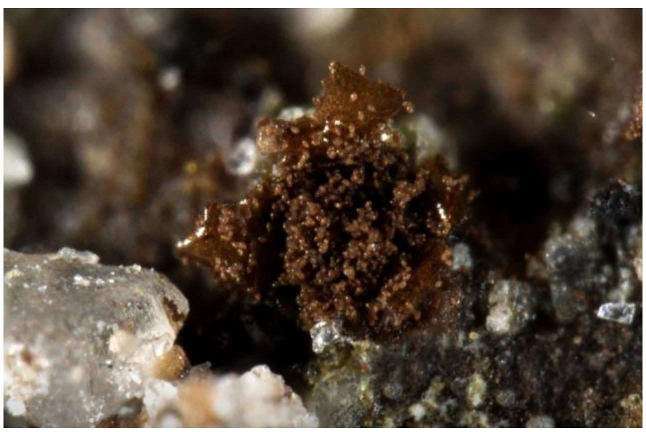

Figure 30. ***Licea minima*** fruiting body showing spores. Photo from Myxotropic, through Creative Commons.

Figure 31. ***Perichaena chrysosperma*** fruiting bodies, a species occasionally using a bryophyte substrate. Photo from Myxotropic, through Creative Commons.

Figure 32. ***Frullania dilatata***, a known leafy liverwort substrate for ***Perichaena chrysosperma***. Photo by Barry Stewart, with permission.

Figure 33. ***Symphytocarpus amaurochaetoides*** on moss, a species also known from the moss ***Pterigynandrum filiforme***. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 34. ***Symphytocarpus amaurochaetoides*** and snails eating the fruiting bodies of slime molds on a decorticated log. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 35. ***Pterigynandrum filiforme*** on tree, a known but uncommon moss substrate for ***Symphytocarpus amaurochaetoides***. Photo by Dick Haaksma, with permission.

Figure 36. ***Pterigynandrum filiforme*** a known but uncommon substrate for ***Symphytocarpus amaurochaetoides***. Photo by Michael Lüth, with permission.

Figure 37. ***Symphytocarpus impexus*** on log, a species that can sometimes occur on the leafy liverwort ***Porella platyphylla***. Photo by Thomas Laxton, through Creative Commons.

Figure 38. ***Trichia varia*** fruiting bodies, a species known to occur on the moss ***Anomodon viticulosus***. Photo by Harley Barnhard, The Eumycetozoan Project, DiscoverLife.org, with online permission.

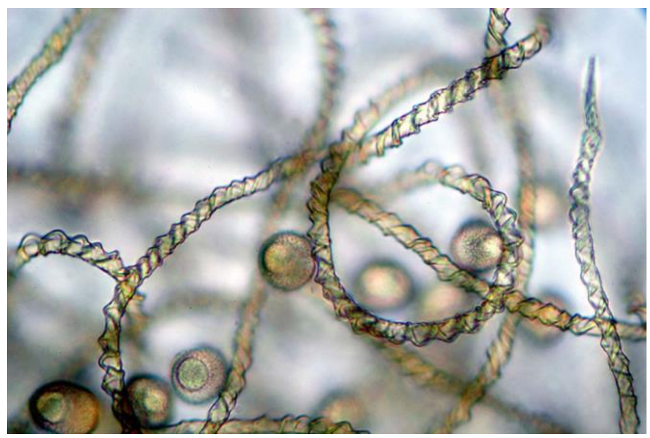

Figure 39. ***Trichia varia*** capillitia and spores. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 40. ***Anomodon viticulosus*** on bark, one of the mosses known to serve as a substrate for ***Trichia varia***. Photo by Michael Lüth, with permission.

Figure 41. ***Anomodon viticulosus***, a suitable substrate for ***Trichia varia***. Photo by Janice Glime.

While some slime molds prefer bryophyte substrates, lichens are rarely preferred (Ing 1999; Leontyev 2010). Among these bryophyte inhabitants in the Ukraine are ***Metatrichia vesparia*** (Figure 42; probably should be ***Trichia***) and ***Tubifera ferruginosa*** (Figure 43-Figure 44), two slime molds typically found on decaying wood that is covered with mosses (Leontyev 2010).

Figure 42. ***Metatrichia vesparia*** fruiting on mosses. Photo by Alexey Zakharinskij, through Creative Commons.

Figure 43. ***Tubifera ferruginosa*** with mosses and liverworts. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 44. ***Tubifera ferruginosa*** with mature sporangia on mosses and wood. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Novozhilov *et al*. (2006) reported slime mold diversity and ecology from arid regions in Russia. They noted that ***Physarum bivalve*** (Figure 45), ***Physarum leucophaeum*** (Figure 46), and ***Didymium melanospermum*** (Figure 47-Figure 48) occurred on living mosses. It is likely that the mosses lengthened the period of available moisture in these dry habitats.

Figure 45. ***Physarum bivalve*** on wood, a slime mold known to inhabit mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 46. ***Physarum leucophaeum***, a slime mold known to grow on mosses. Photo by Jerry Cooper, through Creative Commons.

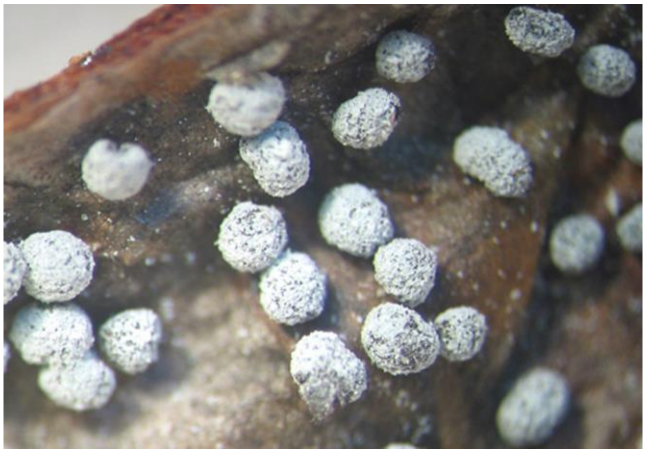

Figure 47. ***Didymium melanospermum*** fruiting bodies. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 48. ***Didymium melanospermum*** fruiting bodies. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Although I have found few Asian records, Ukkola *et al*. (2001) reported ***Physarum album*** (Figure 49) on moss-covered rotting logs and ***P. pusillum*** (Figure 50-Figure 51) on moss-covered bark of a living tree in China. In Nainital, India, ***Fuligo intermedia*** (Figure 52) occurs on mosses (Pant & Tewari 1982).

Figure 49. ***Physarum album***, a species known from moss-covered rotting logs. Photo by George Shepherd, through Creative Commons.

Figure 50. ***Physarum pusillum*** fruiting bodies on leaf litter. Photo by Gustavo F. Morejón J., through Creative Commons.

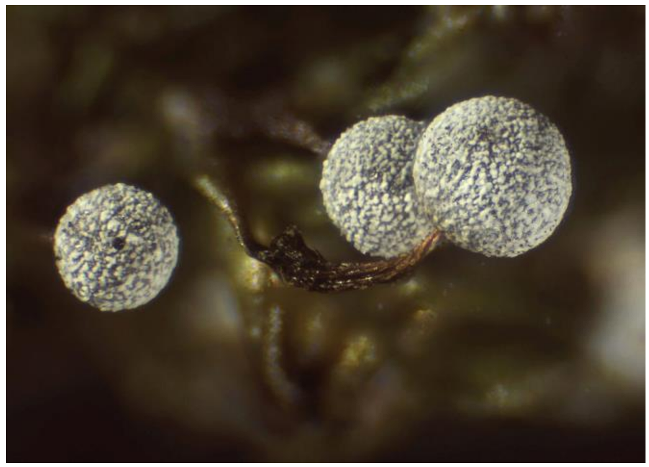

Figure 51. ***Physarum pusillum*** sporangium on mosses. Photo by TAO92, through Creative Commons.

Figure 52. ***Fuligo intermedia*** on ***Polytrichum***. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

It is clear that slime molds are often associated with bryophytes (Sean Edwards, pers. comm. 7 December 2013). But these associations may simply be two organisms with similar environmental requirements, particularly for moisture. Among these, Edwards was able to list several of these moss-slime mold associations from England:

Fuligo septica (Figure 53, Figure 62) pulsing plasmodium with ***Hypnum andoi*** (Figure 54)
Physarum leucophaeum (Figure 46) encrusted sporangia, dehiscing on ***Leptodictyum riparium*** (Figure 55)
Diderma deplanatum (Figure 56-Figure 58) on ***Mnium hornum*** (Figure 59).

Figure 53. ***Fuligo septica*** on ***Hypnum andoi***. Photo by Sean Edwards, with permission.

Figure 54. ***Hypnum andoi***, a moss known to form a substrate for ***Fuligo septica***. Photo by Michael Lüth, with permission.

Figure 55. ***Leptodictyum riparium***, a moss known to form a substrate for ***Physarum leucophaeum***. Photo by Michael Lüth, with permission.

Figure 56. ***Diderma deplanatum*** fruiting bodies on moss. David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 57. ***Diderma deplanatum*** fruiting bodies on moss. David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 58. ***Diderma deplanatum*** fruiting on moss. David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 59. ***Mnium hornum***, a moss known to provide a substrate for ***Diderma deplanatum***. Photo by Tim Waters, through Creative Commons.

Elsewhere in Europe, Eliasson and Adamonyte (2009) reported ***Licea operculata*** on mosses in Sweden.

Figure 60. ***Licea operculata*** sporophytes, a species also known from mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Stephenson and Studlar (1985) found that a number of species of slime molds are associated with bryophytes in temperate North America (Table 1). Although their study was targetted and extensive, revealing a number of bryophytes that have slime mold associates, the data were insufficient to determine any preferences.

Table 1. Slime molds occurring among the 17 most frequent species of bryophytes with sporulating slime molds (120 collections) from 20 localities in Tennessee, Kentucky, West Virginia, Virginia, Pennsylvania, Colorado, and Montana, USA, and one from British Columbia, Canada. Number of collections indicates the number of times the slime mold species was collected among the 120 collections. Based on table in Stephenson & Studlar 1985.

	Numb. Bryo. Host Taxa	Numb. Collections	Fig. Numb.
Stemonitis axifera	8	19	Figure 61
Fuligo septica	6	13	Figure 62
Stemonitis fusca	8	11	Figure 14
Trichia favoginea	3	9	Figure 63
Lepidoderma tigrinum	4	8	Figure 5
Lycogala epidendrum	10	8	Figure 15
Tubifera ferruginosa	5	7	Figure 64-Figure 65
Barbeyella minutissima	2	6	Figure 2
Didymium melanospermum	4	6	Figure 47-Figure 48
Arcyria cinerea	3	5	Figure 16-Figure 17
Physarum viride	4	5	Figure 66
Didymium iridis	0	4	Figure 67
Physarum album	3	4	Figure 49
Trichia decipiens	2	4	Figure 68
Diderma effusum	2	3	Figure 69
Lamproderma columbinum	4	3	Figure 6
Physarum cinereum	3	3	Figure 22
Physarum globuliferum	3	3	Figure 70
Physarum leucophaeum	3	3	Figure 46
Trichia subfusca	2	3	Figure 71
Ceratiomyxa fruticulosa	2	2	Figure 72
Stemonitopsis typhina	1	2	Figure 74
Cribraria spp.	2	2	Figure 75
Cribraria cancellata	2	2	Figure 76
Hemitrichia calyculata	1	2	Figure 77-Figure 79
Leocarpus fragilis	2	2	Figure 81
Physarum braunianum	2	2	Figure 82
Physarum rubiginosum	2	2	Figure 83-Figure 84
Trichia varia	2	2	Figure 39
Others	11		

Figure 61. ***Stemonitis axifera*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 62. ***Fuligo septica***, a species that can live on bryophytes. Photo by Kim Fleming, through Creative Commons.

Figure 63. ***Trichia favoginea***, a slime mold with three known bryophyte host taxa in North America. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 64. Young ***Tubifera ferruginosa*** sporangia on moss. Photos by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 65. Old sporangia of ***Tubifera ferruginosa*** on moss. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 66. ***Physarum viride*** dehiscing fruiting bodies. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 67. ***Didymium iridis***, a species here on decaying wood, but that may coincide with bryophytes. Photo by Willa Schrlau, through Creative Commons.

Figure 68. ***Trichia decipiens*** with sporangia, on moss. Photo by Anneli Salo, through Creative Commons.

Figure 69. ***Diderma effusum***. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 70. ***Physarum globuliferum*** on decaying wood. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

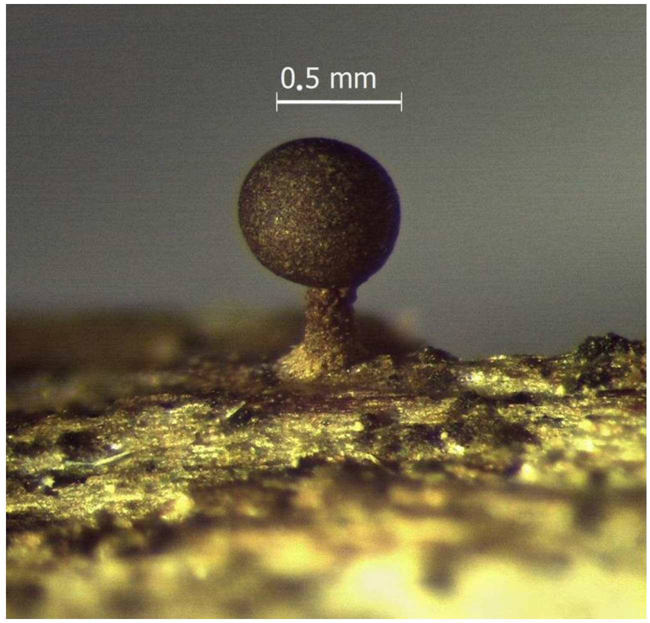

Figure 71. ***Trichia subfusca*** sporangium, a slime mold known to grow on mosses. Photo from Flora of Russia, Moscow State University, through Creative Commons.

Figure 72. ***Ceratiomyxa fruticulosa*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 73. ***Ceratiomyxa fruticulosa*** on mosses. Photo by MK, through Hiveminer.

Figure 74. ***Stemonitopsis typhina*** sporangia on rotting wood. Photo by George Barron, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 75. ***Cribraria*** sp. fruiting on bryophytes. Photo by Sarah Lloyd, with permission.

Figure 76. ***Cribraria cancellata*** fruiting bodies. Photo by Lawrence Leonard, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 77. ***Hemitrichia calyculata***. Young fruiting bodies on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 78. ***Hemitrichia calyculata***. Young fruiting bodies. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 79. ***Hemitrichia calyculata***. Mature sporophyte dispersing spores and showing capillitium. Photo by Lawrence Leonard, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 80. ***Leocarpus fragilis*** with young sporangia on moss. Photo by Boris Loboda, with permission.

Figure 81. ***Leocarpus fragilis*** mature fruiting bodies. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 82. Mature fruiting bodies of ***Physarum braunianum***. Photo by Denver Botanical Garden, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Others, collected in Maine, USA, that may have a moss preference are ***Trichia subfusca*** (Figure 85), cultured from mosses in a moist chamber, and ***Paradiachea rispaudii*** (Figure 86), a rather rare species that Stephenson collected only twice in 30 years, both times with mosses on the forest floor (Zoll & Stephenson 2013).

Figure 83. ***Physarum rubiginosum*** on moss, possibly **Hylocomiaceae**. Photo by Scott Darbey, through Creative Commons.

Figure 84. ***Physarum rubiginosum*** fruiting on moss. Photo by John Davis, with permission.

Figure 85. ***Trichia subfusca*** fruiting on bark. Photo by Alain Michaud, Eumycetozoan Project, DiscoverLife.org, with online permission.

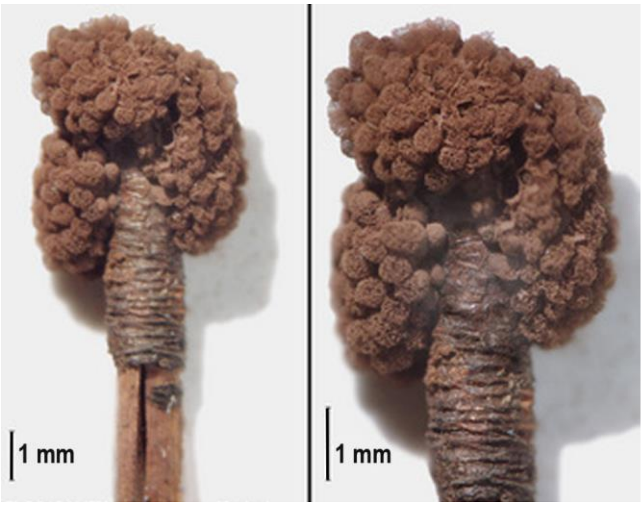

Figure 86. ***Paradiachea rispaudii***, possibly an obligate moss dweller. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Lado *et al*. (2003) examined slime molds in two Neotropical forest reserves in Mexico. ***Physarum alvoradianum*** occurred on mosses along with the slime mold ***Diderma rugosum*** (Figure 87). Other slime molds are sometimes associated with dead or living bryophytes, including ***Diderma chondrioderma*** (Figure 88), ***Didymium bahiense*** (Figure 89), ***Licea*** sp. (Figure 29-Figure 30, Figure 90-Figure 91), ***Physarum album*** (Figure 92), ***P. crateriforme*** (Figure 93), ***P. didermoides*** (Figure 94), and ***Stemonitis flavogenita*** (Figure 95-Figure 96).

Figure 87. ***Diderma rugosum*** fruiting structure, a slime mold that is often associated with bryophytes. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 88. ***Diderma chondrioderma*** on moss. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 89. ***Didymium bahiense*** fruiting on bryophyte detritus. Photo from EOL, through Creative Commons.

Figure 90. ***Licea retiformis*** plasmodium on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 91. ***Licea floriformis*** fruiting bodies on moss leaves. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 92. ***Physarum album***, a slime mold sometimes associated with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission..

Figure 93. ***Physarum crateriforme*** fruiting bodies on moss leaves. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

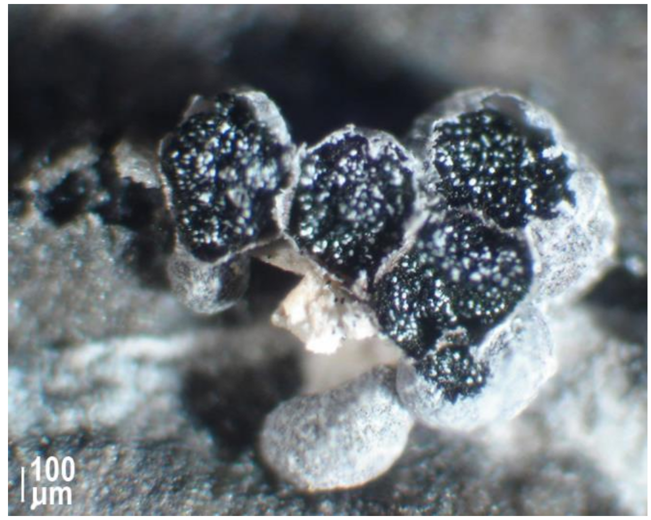

Figure 94. ***Physarum didermoides*** fruiting bodies, a slime mold sometimes associated with mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 95. ***Stemonitis flavogenita*** early sporangial development on log and mosses. Photo by Chris Wagner, through Creative Commons.

Figure 96. ***Stemonitis flavogenita*** fruiting on decaying wood. Photo by Kathawk, through Creative Commons.

Even in the Antarctic, bryophytes, in this case the leafy liverwort ***Lepidozia*** (Figure 97), support the growth of the slime mold ***Lamproderma*** (Figure 6) (Stephenson *et al*. 1992).

Figure 97. ***Lepidozia glaucophylla***; the genus ***Lepidozia*** is a substrate for slime molds in the genus ***Lamproderma*** in the Antarctic. Photo by Janice Glime.

Collection Records in Floras

Most of the records of slime molds associated with bryophytes are in floristic treatments where species are listed, described, and known habitat affinities provided. Hence, I was able to add a number of bryophyte associates to this chapter by searching this body of literature, albeit not extensively. Unfortunately, these usually fail to state where the bryophyte is growing, much less the species. Thus we cannot separate those that expand from a log onto the moss from those that become established on the moss by preference or even restriction. When the more specific substrate is known, the relationship is in the Slime Mold subchapter on Ecology and Habitat.

A further difficulty is that the plasmodial stage may reside in a different place from the fruiting stage. The plasmodial stage can usually only be identified by culturing it until it produces sporangia. Even then, beginners will be confounded by the many color phases seen in some species (Figure 98-Figure 104).

Figure 98. ***Arcyria affinis***, a known log species, on liverworts. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 99. ***Arcyria affinis*** 1 October. This and the following series of this species indicate the color changes as the slime mold matures on the same rock. Photo by Sarah Lloyd, with permission.

Figure 100. ***Arcyria affinis*** 2 October. Photo by Sarah Lloyd, with permission.

Figure 101. ***Arcyria affinis*** 3 October. Photo by Sarah Lloyd, with permission.

Figure 102. ***Arcyria affinis*** 4 October as the color darkens. Photo by Sarah Lloyd, with permission.

Figure 103. ***Arcyria affinis*** 6 October as the outer covering (**periderm**) begins to break. Photo by Sarah Lloyd, with permission.

Figure 104. ***Arcyria affinis*** 9 October, with capsules dehiscing and revealing the capillitium. Photo by Sarah Lloyd, with permission.

Among the early North American records, Sturgis (1893) in Massachusetts, USA, reported that ***Paradiachea caespitosa*** (syn=*Comatricha caespitosa*; Figure 105-Figure 111) occurred on moss and the lichen ***Cladonia*** (Figure 112). Ricker (1902) reported ***Craterium obovatum*** (Figure 113) on moss and sticks, ***Physarum leucophaeum*** (Figure 46) on moss, ***Lepidoderma tigrinum*** (Figure 5) in moss on tree, ***Diachea thomasii*** (Figure 114) on moss, and ***Cribraria argillacea*** (Figure 115) among mosses in Maine, USA. Gilbert (1927) reported ***Physarum virescens*** (Figure 116) on moss in eastern Massachusetts, USA. Greene (1929) reported ***Diderma deplanatum*** (Figure 56-Figure 58), ***Diderma radiatum*** (Figure 117), ***Didymium melanospermum*** (listed in publication as *D. melanosporum*; Figure 118), ***Physarum bivalve*** (syn=*Physarum sinuosum*; Figure 45), and ***P. contextum*** (Figure 119) on moss in western Washington, USA. Gray (1938) added ***Physarum gyrosum*** (Figure 120) as a species fruiting on living moss in Indiana, USA.

Figure 105. ***Paradiachea caespitosa*** 6:11 am 12 December. Photo by Sarah Lloyd, with permission.

Figure 106. ***Paradiachea caespitosa*** 4:42 pm 12 December. Photo by Sarah Lloyd, with permission.

Figure 107. ***Paradiachea caespitosa*** 6:48 am 13 December. Photo by Sarah Lloyd, with permission.

Figure 108. ***Paradiachea caespitosa*** 4:16 pm 13 December. Photo by Sarah Lloyd, with permission.

Figure 109. ***Paradiachea caespitosa*** 7:06 am 15 December. Photo by Sarah Lloyd, with permission.

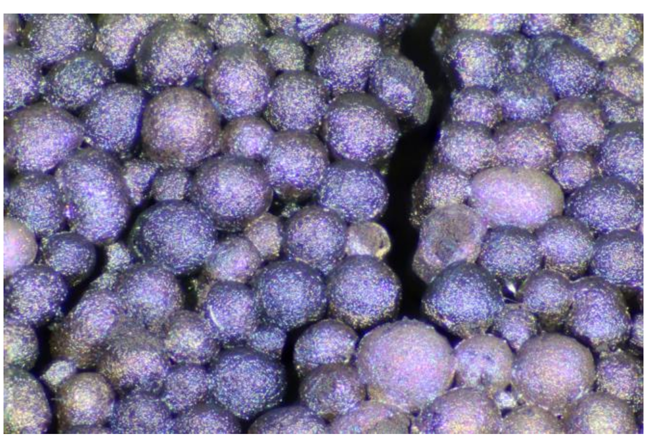

Figure 110. ***Paradiachea caespitosa*** sporangia 26 January. Photo by Sarah Lloyd, with permission

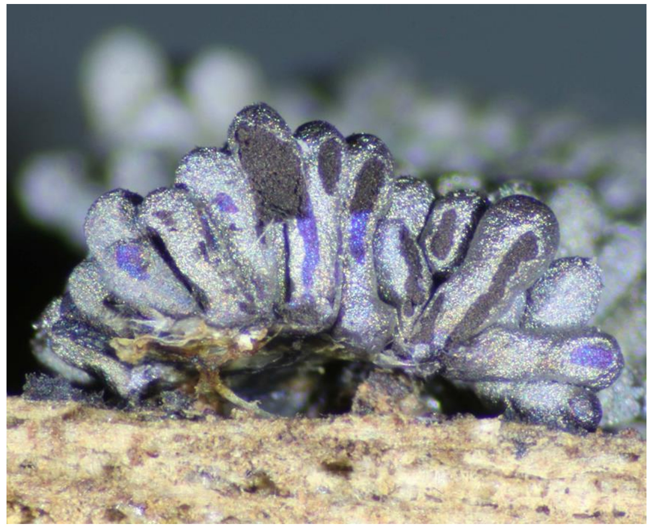

Figure 111. ***Paradiachea caespitosa*** sporangia. Photo by Sarah Lloyd, with permission.

Figure 112. ***Cladonia chlorophaea*** with ***Polytrichum***; the genus ***Cladonia*** can serve as a substrate for the slime mold ***Paradiachea caespitosa***. Photo by Tim Sage (NMNR), through Creative Commons.

Figure 113. ***Craterium obovatum*** or ***Trichia erecta*** yellow plasmodium. Kim Fleming, through Creative Commons.

Figure 114. ***Diachea thomasii*** sporangia, sometimes a moss dweller in Maine, USA. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 115. ***Cribraria argillacea*** sporangia on moss on log. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 116. ***Physarum virescens*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 117. ***Diderma radiatum*** on wood with bryophytes. Photo by Clive Shirley, <www.hiddenforest.co.nz>, with permission.

Figure 118. ***Didymium melanosporum*** sporangia on mosses. Photo by J. C. Schou, with permission.

Figure 119. ***Physarum contextum*** on wood, a slime mold known to inhabit mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

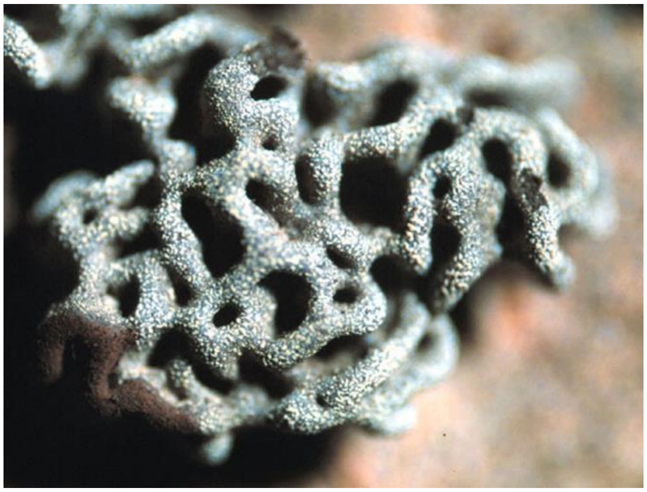

Figure 120. ***Physarum gyrosum***, a slime mold that sometimes occurs on bryophytes. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Lister (1917) cultured the slime mold ***Colloderma*** sp. (Figure 4) from mosses in the UK, maintaining it until the slime mold produced spores. More recent references include a greater number of records of moss dwellers, and often more details of the habitat. Doidge (1950) reported ***Lamproderma scintillans*** (Figure 12) growing on mosses and roots of epiphytic orchids in a greenhouse.

Based on collections from Lake ltasca State Park, Minnesota, USA, Palm *et al*. (1979) listed bryophytes as the substrate for a number of slime molds, but they did not give the substrate of the bryophytes. These bryophyte-dwelling slime molds included ***Arcyria oerstedtii*** (Figure 121), ***Craterium leucocephalum*** (Figure 122), ***C. minutum*** (Figure 123-Figure 124), ***Diderma crustaceum*** (Figure 125), ***Didymium melanospermum*** (Figure 48), ***D. nigripes*** (Figure 126), ***D. squamulosum*** (Figure 127), ***Fuligo septica*** (Figure 53, Figure 62), ***Hemitrichia serpula*** (Figure 128-Figure 129), ***Leocarpus fragilis*** (Figure 81), ***Metatrichia vesparia*** (Figure 42), ***Mucilago crustacea*** (Figure 130), ***Physarum bivalve*** (Figure 45), ***P. cinereum*** (Figure 22-Figure 23), ***P. notabile*** (Figure 131), ***P. album*** (Figure 49), ***Stemonitis fusca*** (Figure 14), and ***Tubifera ferruginosa*** (Figure 65).

Figure 121. ***Arcyria oerstedti*** on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 122. ***Craterium leucocephalum*** sporangia ready to dehisce. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 123. ***Craterium minutum*** immature sporangia on mosses in New Zealand. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 124. ***Craterium minutum*** with dehiscing sporangia. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 125. ***Diderma crustaceum*** sporangia. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 126. ***Didymium nigripes*** sporangia, a species known from bryophytes. Photo by Sarah Lloyd, with permission.

Figure 127. ***Didymium squamulosum*** on mosses. Photo by James K. Lindsey, with permission.

Figure 128. ***Hemitrichia serpula***, a known moss dweller. Photo by John Carl Jacobs, through Creative Commons.

Figure 129. ***Hemitrichia serpula*** with moss and snail. Photo by Amadej Trnkoczy, through Creative Commons.

Figure 130. ***Mucilago crustacea*** on bryophytes. Photo by Drew Henderson, through Creative Commons.

Figure 131. ***Physarum notabile*** sporangia. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with permission.

New records continue to appear. Baba and Er (2018) added ***Craterium dictyosporum*** (Figure 132) to the records from Turkey by finding this species on mosses. In 2013, Mishra and Phate added the new species ***Badhamiopsis stipitata*** to the slime molds of Maharashtra, India, noting its fruiting occurrence on living mosses, but that species does not seem to appear in any checklists or nomenclatural lists.

Figure 132. ***Craterium dictyosporum*** sporangia on moss. Photo by John Davis, with permission.

Perhaps the most interesting recent study for bryologists (since that of Stephenson and Studlar in 1985) is that of Yatsiuk *et al*. (2018) in the Ukraine. They not only noted the species of slime molds, but also identified the moss species substrate in many cases. They found ***Didymium melanospermum*** (Figure 48) on the living moss ***Atrichum undulatum*** (**Polytrichaceae**; Figure 133). ***Didymium ovoideum*** (Figure 134) and ***Stemonitis axifera*** (Figure 135) were restricted to species of ***Sphagnum*** (Figure 136) and/or **Polytrichaceae**.

Figure 133. ***Atrichum undulatum***, substrate for ***Didymium melanospermum*** in peatlands. Photo by Hugues Tinguy, through Creative Commons.

Figure 134. ***Didymium ovoideum*** sporangium on wood. Photo by Thomas Laxton, through Creative Commons.

Figure 135. ***Stemonitis axifera***, a species that has been reported from bryophytes several times and is restricted to them in a Ukrainian peatland. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 136. ***Sphagnum palustre***; the genus ***Sphagnum*** is a known substrate for slime molds. Photo by Bob Klips, with permission.

Ranade *et al*. (2012) also reported ***Stemonitis axifera*** (Figure 135; as ***S. smithii***) from bryophytes in India. ***Didymium*** species are typically organisms of litter and parts of living plants (Liu *et al.* 2015), but several species have already been reported in this subchapter as living on bryophytes. Furthermore, ***D. melanospermum*** seems to prefer acid substrates (Stephenson & Studlar 1985; Ing 1994), explaining its presence in a ***Sphagnum*** habitat. Yatsiuk *et al*. (2018) found ***Stemonitis axifera*** (Figure 61) not only on living mosses, but also on litter and wood debris, as was the case for ***Arcyria cinerea*** (Figure 16).

Photographic Indicators

One way to determine which slime molds are able to live on bryophytes is to search for images that show them with bryophytes. This doesn't work for most animal relationships because photographers are likely to pose their animals on bryophytes to provide a pleasing background, but it seems unlikely that this happens with slime molds, particularly when it appears to be taken in the field.

The following images (Figure 137-Figure 173) provide such pictures to increase our knowledge of slime molds one might find on bryophytes. Some of these are adjacent, but not intermingled, suggesting that they do well in similar habitats and on the same substrate, frequently indicating similar moisture and *p*H requirements.

Figure 137. ***Alwisia bombarda*** with sporangia on mosses. Photo by Sarah Lloyd, with permission.

Figure 138. ***Arcyria stipata***, a known log species, associated with leafy liverworts and mosses on wood, but not actually growing on the bryophytes. This suggests they both might simply like the same habitats. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 139. Fruiting bodies of ***Badhamia delicatula*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 140. ***Badhamia macrocarpa*** sporangia on mosses. Photo by David Mitchell, with permission.

Figure 141. ***Badhamia melanospora*** fruiting bodies with mosses on bark. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 142. ***Badhamiopsis ainoae*** open fruiting body, growing with mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 143. ***Brefeldia maxima*** plasmodium with moss. Photo through Creative Commons.

Figure 144. ***Comatricha alta*** sporangia on mosses. Photo by Sarah Lloyd, with permission.

Figure 145. ***Cribraria confusa*** sporangia with bryophytes. Photo by Sarah Lloyd, with permission.

Figure 146. ***Cribraria macrocarpa*** on bark with mosses, possibly ***Neckera*** sp. Photo by Alejandro Huereca, through Creative Commons.

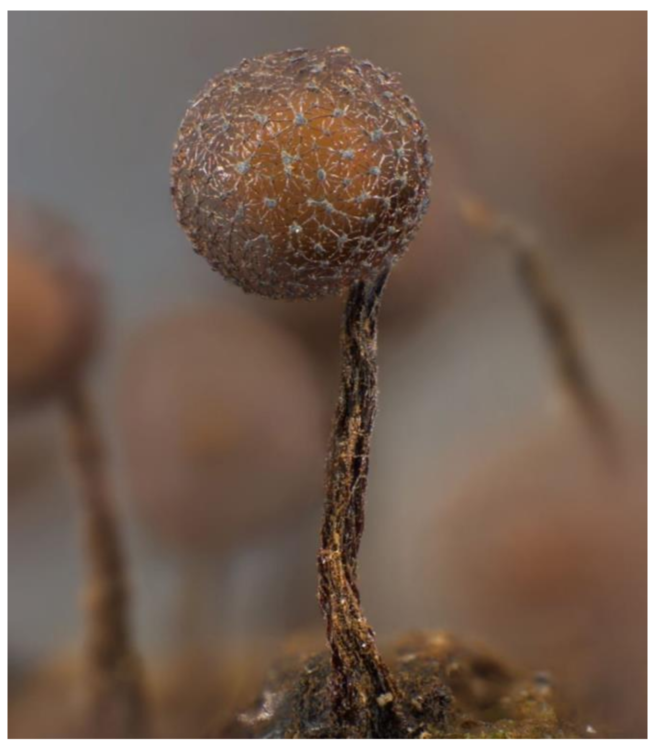

Figure 147. ***Cribraria piriformis*** sporangium, a species that sometimes fruits on bryophytes. based on image from <http://www.gorjanski-gobar.si/wp/?p=14163>. Photo from Myxotropic, through Creative Commons.

Figure 148. ***Dictydiaethalium plumbeum*** on bryophytes. Photo by Ray Simons, The Eumycetozoa Project, DiscoverLife.org, with online permission.

Figure 149. ***Diderma*** sp. on liverwort. This is a common genus on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 150. ***Diderma globosum*** fruiting on mosses. Photo from Mushroom Observer.org, through Creative Commons.

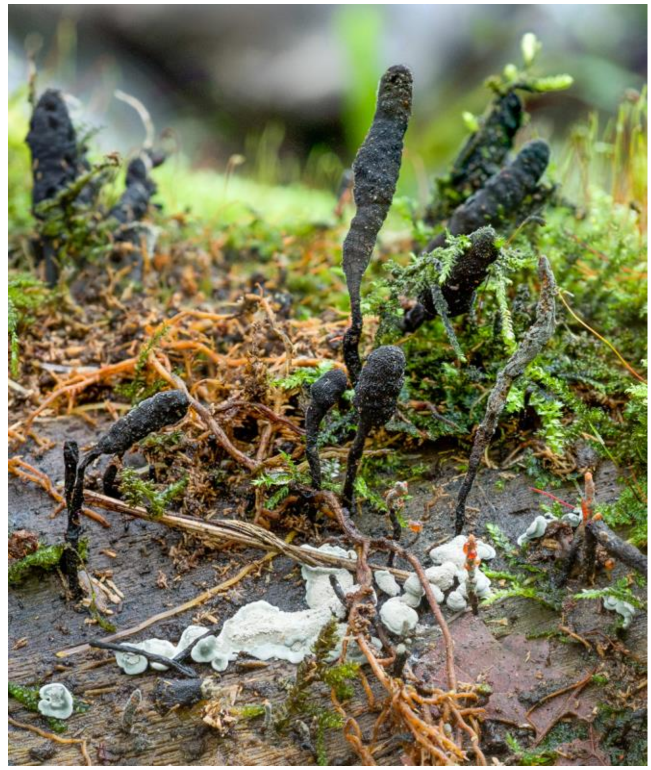

Figure 151. ***Diderma globosum*** fruiting on mosses. Photo from Mushroom Observer.org, through Creative Commons.

Figure 152. ***Diderma*** *cf.* ***niveum*** sporangia on mosses. Photo by Sarah Lloyd, with permission.

Figure 153. ***Diderma*** *cf* ***subincarnatum*** with capsules on mosses. Photo by Sarah Lloyd, with permission.

Figure 154. ***Fuligo septica*** on moss. Photo by Mikel A. Tapia, with permission.

Figure 155. ***Fuligo septica*** on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 156. ***Lamproderma piriforme*** sporangia on bryophytes. Photo by Sarah Lloyd, with permission.

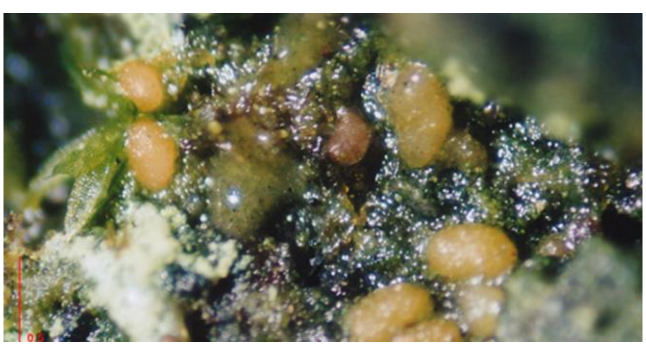

Figure 157. ***Licea sambucina*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 158. ***Lindbladia tubulina*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 159. ***Lindbladia tubulina***; upper image is on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 160. ***Lindbladia tubulina*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 161. ***Lycogala conicum*** on decaying wood with a leafy liverwort. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 162. ***Lycogala conicum*** on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 163. ***Physarum bogoriense*** with mosses. Photo from the Denver Botanical Garden, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 164. ***Physarum flavidum*** on moss. Photo from Denver Botanical Garden, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 165. ***Physarum leucopus*** on moss. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 166. ***Stemonitis herbatica*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 167. ***Stemonitis herbatica*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 168. ***Stemonitopsis typhina*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 169. ***Stemonitopsis typhina*** sporangia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 170. ***Symphytocarpus amaurochaetoides*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 171. ***Trichia contorta*** on mosses. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 172. ***Trichia munda*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 173. ***Tubifera microsperma*** with mosses. Photo by Lawrence Leonard, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Generalists – Bryophytes Are Okay

Many of the slime molds that occur with or on bryophytes are **generalists**. This is not to be confused with those species that prefer bryophytes and that are typically **specialists**. Lado and de Basanto (2008) highlighted the abundance and widespread distribution of generalist ***Arcyria cinerea*** (Figure 16) in their review of Neotropical slime molds, indicating its presence in 28 of 30 countries. Tropical generalists include ***Arcyria denudata*** (Figure 174; known from bryophytes – Stojanowska & Panek 2004), ***Cribraria cancellata*** (Figure 175; known to associate with bryophytes on logs – Schnittler & Novozhilov 1998), ***Didymium nigripes*** (Figure 126; known from bryophytes – Palm *et al*. 1979), ***D. squamulosum*** (Figure 127; known from bryophytes – Palm *et al*. 1979), ***Fuligo septica*** (Figure 53, Figure 62; known from bryophytes – Stephenson & Studlar 1985), ***Hemitrichia calyculata*** (Figure 77-Figure 79; known from bryophytes – Stephenson & Studlar 1985), ***H. serpula*** (Figure 128-Figure 129; known from mosses – Ranade *et al*. 2012), ***Lycogala epidendrum*** (Figure 15; known from bryophytes – Stephenson & Studlar 1985), ***Perichaena chrysosperma*** (Figure 31; known from liverworts – Dudka & Romanenko 2006), ***Physarum album*** (Figure 92; known from bryophytes – Lado *et al*. 2003), ***Ph. viride*** (Figure 66; known from bryophytes – Stephenson & Studlar 1985), ***Stemonitis fusca*** (Figure 14; known from bryophytes – Palm *et al*. 1979; Dudka & Romanenko 2006), and ***Trichia favoginea*** (Figure 63; known from bryophytes – Stephenson & Studlar 1985).

Figure 174. ***Arcyria denudata*** on bryophytes. Photo by Sarah Lloyd, with permission.

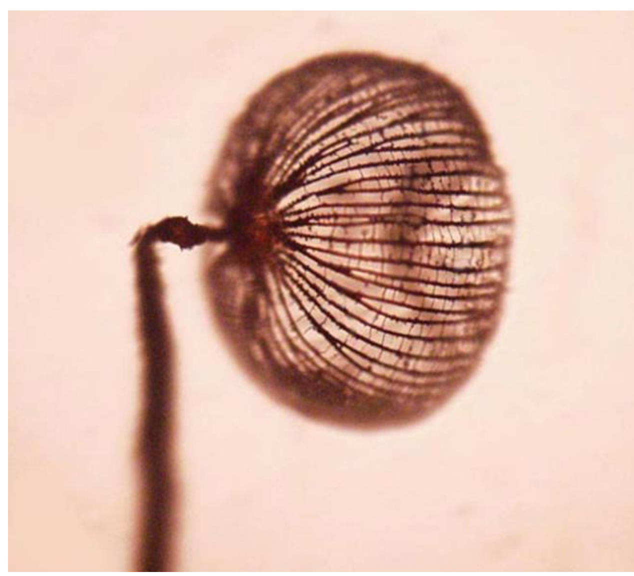

Figure 175. ***Cribraria cancellata*** fruiting body showing threadlike capillitium. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Härkönen and Ukkola (2000) considered the occasional moss dwellers ***Arcyria cinerea*** (Figure 16), ***A. pomiformis*** (Figure 176) and ***Echinostelium minutum*** (Figure 19) to be indifferent to substrate.

Figure 176. ***Arcyria pomiformis*** with mosses. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Interactions Can Be Helpful or Hindering

Despite the number of associations between bryophytes and slime molds, the relationship is often negative. Schnittler and Stephenson (2000) found that the higher the epiphytic coverage was, the lower the number of slime mold records obtained in culture (Figure 177). In Costa Rica, both slime mold species diversity and abundance decreased with increasing elevation, as well as with higher moisture levels, relationships that suggest they should not correlate well with bryophytes, which typically increase with altitude. Furthermore, on litter, the slime mold species with robust plasmodia increased with increasing elevation, further supporting the hypothesis of a negative relationship with bryophytes. On the other hand, Schnittler and Stephenson suggest that excess moisture of tropical forests does not favor the slime mold development. This conclusion is supported by the observation that the two seasonal dry forest types accounted for 90% of the total slime mold diversity. Nevertheless, the typical wood inhabitant ***Ceratiomyxa fruticulosa*** (Figure 72) was recorded twice from mossy bark in the wet forest. Schnittler and Stephenson suggested that a possible explanation for the decreasing slime molds with altitude (Figure 177) is that a closed epiphyte (bryophytes and lichens) cover interferes with slime mold growth.

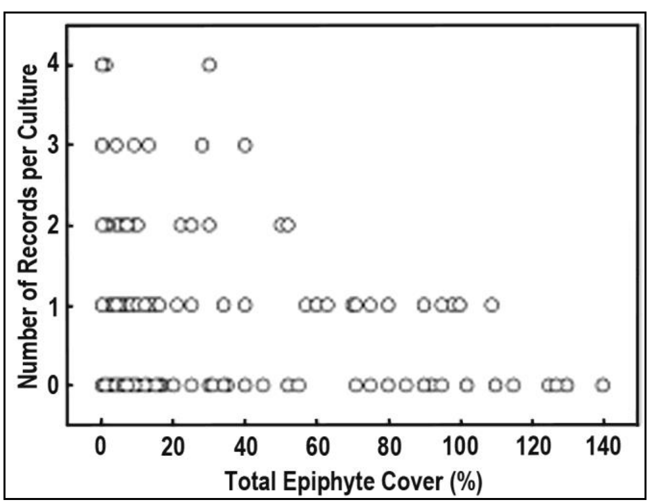

Figure 177. Myxomycete species richness vs epiphyte (including bryophyte) cover. Modified from Schnittler & Stephenson 2000.

Novozhilov *et al*. (2000) considered that the bryophilous slime molds, or at least the plasmodial slime molds (**Myxogastria**), albeit associated with mosses, were probably there due to slime algae (Figure 178), wood, or rocks that occurred where moisture was maintained by humid ravines. The ravine taxa include less than 5% of the slime molds and are mostly macroscopic taxa of temperate and boreal zones. Their fructification and spore release typically occurs in late autumn. The ravine species are all but impossible to grow in culture, making it likewise all but impossible to identify those not fruiting at the time of collection.

Figure 178. ***Cribraria persoonii*** fruiting bodies; the substrate appears to have algae with the slime molds growing on them. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

On the other hand, Landolt *et al*. (1992) suggested that the antibiotic properties of bryophytes might inhibit the growth of slime molds on or among many kinds of bryophytes. This could be particularly important for those slime molds that might use the bryophytes as feeding grounds for bacteria and other micro-organisms (Banerjee & Sen 1979). Landolt and coworkers observed that slime molds exhibited greater numbers in forests with a groundcover of deciduous litter than in those with a bryophyte ground cover. But is that due to inhibition or to differences in habitat requirements?

Schnittler and Stephenson (2000) commented further on the decreasing abundance and diversity of slime molds with elevation, whereas bryophytes increase in both. They suggested that competition for nutrients could cause bryophytes, especially in the tropics, to outcompete the slime molds for nutrients.

But as also noted by Schnittler and Stephenson (2000), slime mold species diversity is positively correlated with substrate *p*H on both litter and bark. Since conifer litter and conifer forests tend to be acidic, could that explain the absence of slime molds on bryophytes there, as observed by Landolt *et al*. (1992)? On the other hand, studies in the conifer *Cryptomeria japonica* forests in Japan indicate a negative correlation between slime mold abundance and *p*H, particularly for some species (Takahashi 2018; Takahashi & Harakan 2018).

Summary

Few bryophytes seem to be restricted to bryophytes (**bryophiles**). These include ***Barbeyella minutissima*** on leafy liverworts (especially ***Nowellia curvifolia***), ***Colloderma oculatum***, and ***Lepidoderma tigrinum***, the latter two often in association with ***B. minutissima***. This raises so many questions about the relationship between bryophytes and slime molds. Why is ***Barbeyella minutissima*** so restricted in its substrate? Does it derive some benefit from the liverworts? Could it really be elsewhere but in a form we have recognized as a different species?

And why do some slime molds seem to grow to the edges of moss mats and stop? Does the moss produce an inhibitory substance? Or is it the darkness at the base of the moss mat that stops the plasmodium in its tracks?

Other slime molds with a preference for bryophytes include ***Lamproderma columbinum*** and ***L. scintillans***. But most of the associations seem to be coincidental – the bryophytes are in the preferred habitat and nothing stops the expansion of the slime molds simply grow onto the bryophytes. And how many associations are we missing in the amoeboid, swarm cell, and plasmodial stages because they are hard to find and require culturing for identification? And even if they grow in culture and produce identifiable sporangia, would they do this in nature on or among the bryophytes?

Stemonitis axifera may be a candidate that prefers bryophytes, being restricted to ***Sphagnum*** and **Polytrichaceae** in a peatland study.

Checklists and photographs can be used to find some of those species that sometimes occur on bryophytes. From these, one can surmise that most of the bryophyte dwellers are **generalists** that can live on a bryophyte, whereas those that prefer or only live on bryophytes are **specialists**.

Evidence from elevational studies suggests that bryophytes might actually inhibit or outcompete the slime molds at higher altitudes by overgrowing them, shading them, or competing for nutrients. Antibiotics produced by the bryophytes could inhibit the micro-organisms needed by the slime molds as food or even inhibit the slime molds themselves. In some cases, *p*H is a deterrent for many slime mold species. Presence of algae and Cyanobacteria, as well as protozoa and bacteria, may enhance the suitability of bryophytes as a substrate for slime molds.

Acknowledgments

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Literature Cited

Baba, H. and Er, A. 2018. *Craterium dictyosporum*: A new record of Myxomycetes from Hatay, Turkey. Acta Biol. Turc. 31: 33-35.

Banerjee, R. D. and Sen, S. P. 1979. Antibiotic activity of bryophytes. Bryologist 82: 141-153.

Doidge, E. M. 1950. Myxomycetes. Bothalia 5(1): 83-94.

Dudka, I. O. and Romanenko, K. O. 2006. Co-existence and interaction between Myxomycetes and other organisms in shared niches. Acta Mycol. 41: 99-112.

Eliasson, U. H. and Adamonyte, G. 2009. Species of Myxomycetes new to Sweden with additional records of some rarely collected species. Karstenia 49: 33-39.

Gilbert, F. A. 1927. Notes on Myxomycetes from eastern Massachusetts. Rhodora 29: 165-173.

Gray, W. D. 1938. Myxomycetes of Clark County, Indiana, II. Proc. Ind. Acad. Sci. 48: 71-73.

Greene, H. C. 1929. Myxomycetes of western Washington. Mycologia 21(5): 261-273.

Hadden, N. G. 1921. Mycetozoa at Porlock in October 1920. Trans. Brit. Mycol. Soc. 7: 13-16.

Härkönen, M. and Ukkola, T. 2000. Conclusions on Myxomycetes compiled over twenty-five years from 4793 moist chamber cultures. Biologiezentrum Linz, Austria, pp. 105-112.

Härkönen, M., Rikkinen, J., Ukkola, T., Enroth, J., Virtanen, V., *et al.* 2002. The communities of bryophytes, lichens and Myxomycetes on bark of living trees in Hunan, Southern China. 4th International Congress on Systematics and Ecology of Myxomycetes (August 4-9, 2002). Abstract. Scripta Bot. Belg. 22: 36 37.

Ing, B. 1994. The phytosociology of Myxomycetes. Tansley Review No. 62. New Phytol. 126: 175-201.

Ing, B. 1999. The Myxomycetes of Britain and Ireland. An identification Handbook. The Richmond Publishing Co. Ltd., Slough, UK, 374 pp.

Lado, C. and Basanta, D. W. de. 2008. A review of Neotropical Myxomycetes (1828-2008). An. Jardín Bot. Madrid 65: 211-254.

Lado, C., Estrada-Torres, A., Stephenson, S. L., Wrigley de Basanta, D., and Schnittler, M. 2003. Biodiversity assessment of Myxomycetes from two tropical forest reserves in Mexico. Fung. Divers. 12: 67-110.

Landolt, J. C., Stephenson, S. L., Laursen, G. A., and Densmore, R. 1992. Distribution patterns of cellular slime molds in the Kantishna Hills, Denali National Park and Preserve, Alaska, U.S.A. Arct. Alp. Res. 24: 244-248.

Leontyev, D. V. 2010. Plant community preferences of some Myxomycete species in Gomolsha forests. Nauka Studia (Poland). 4(28): 14-24.

Lister, G. 1917. Mycetozoa found during the selby foray. Trans. Brit. Mycol. Soc. 6: 88-91.

Liu, Q.-S., Yan, S.-Z., and Chen, S.-L. 2015. Species diversity of Myxomycetes associated with different terrestrial ecosystems, substrata (microhabitats), and environmental factors. Mycol. Progr. 14: 1-13.

Mishra, R. L. and Phate, P. V. 2013. Two new Myxomycetes from Maharashtra, India. Biosci. Guard. 3: 431-435.

Moreno, G. Singer, H., and Stephenson, S. L. 2008. A study of *Lamproderma australiensis* and *L. reticulosporum*. Bol. Soc. Micol. Madrid 32: 113-120.

Novozhilov, Y. K., Schnittler, M., Zemlianskaia, I. V., and Fefelov, K. A. 2000. Biodiversity of plasmodial slime moulds (Myxogastria): measurement and interpretation. Protistology 1: 161-178.

Novozhilov, Y. K., Zemlianskaia, I. V., Schnittler, M., and Stephenson, S. L. 2006. Myxomycete diversity and ecology in the arid regions of the Lower Volga River Basin (Russia). Fungal Divers. 23: 193-241.

Palm, M. E., Stewart, E. L., and Haskins, E. 1979. Lake ltasca State Park Myxomycetes: An Annotated Checklist. Minn. Acad. Sci. 45: 24-26.

Pant, G. and Tewari, S. D. 1982. A myxomycete, *Fuligo intermedia* Macbr. on mosses from Nainital. Curr. Sci. 51: 478.

Ranade, V. D., Korade, S. T., Jagtap, A. V., and Ranadive, K. R. 2012. Checklist of Myxomycetes from India. Mycosphere 3: 358-390.

Ricker, P. L. 1902. A Preliminary List of Maine Fungi. University of Maine Studies #3, Orono, Maine, 86 pp.

Robbrecht, E. 1974. The genus *Arcyria* Wiggers (Myxomycetes) in Belgium. Bull. Jardin Bot. Natl. Belgique / Bull. Natl. Plant. België 44: 303-353.

Rojas, C., Valverde, R., Stephenson, S. L., and Vargas, M. J. 2010. Biogeographical and ecological patterns of Costa Rican Myxomycetes. Fungal Ecol. 3: 39-147.

Schnittler, M. 2001. Foliicolous liverworts as a microhabitat for Neotropical Myxomycetes. Nova Hedw. 72: 259-270.

Schnittler, M. and Novozhilov, Y. 1996. The Myxomycetes of boreal woodlands in Russian northern Karelia: A preliminary report. Karstenia 36: 19-40.

Schnittler, M. and Novozhilov, Y. K. 1998. Late-autumn Myxomycetes of the Northern Ammergauer Alps. Nova Hedw. 66: 205-222.

Schnittler, M. and Stephenson, S. L. 2000. Myxomycete biodiversity in four different forest types in Costa Rica. Mycologia 92: 626-637.

Schnittler, M. and Stephenson, S. L. 2002. Inflorescences of Neotropical herbs as a newly discovered microhabitat for Myxomycetes. Mycologia 94: 6-20.

Schnittler, S., Stephenson, L., and Novozhilov, Y. K.. 2000. Ecology and world distribution of *Barbeyella minutissima* (Myxomycetes). Mycol. Res. 104: 1518-1523.

Stephenson, S. L. and Stempen, H. 1994. Myxomycetes: A Handbook for Slime Molds. Timber Press, Portland, Oregon, 183 pp.

Stephenson, S. L. and Studlar, S. M. 1985. Myxomycetes fruiting upon bryophytes: Coincidence or preference? J. Bryol. 13: 537-548.

Stephenson, S. L., Seppelt, R. D., and Laursen, G. A. 1992. The first record of a Myxomycete from sub Antarctic Macquarie Island. Antarct. Sci. 4: 431-432.

Stojanowska, W. and Panek, E. 2004. Myxomycetes of the nature reserve near Wałbrzych (SW Poland). II. Dependence on the substrate and seasonality. Acta Mycol. 39: 147-159.

Sturgis, W. C. 1893. On two new or imperfectly known Myxomycetes. Bot. Gaz. 18(5): 186-187.

Takahashi, K. 2018. Distribution pattern of corticolous Myxomycetes on different size classes of living *Cryptomeria japoinca* trees. Hikobia 17: 273-283.

Takahashi, K. and Harakon, Y. 2018. Biogeographical assessment of corticolous Myxomycetes on Cryptomeria japonica in Japanese mainland and satellites. Hikobia 17: 285-297.

Ukkola, T., Härkönen, M., and Zeng, Z. 2001. Myxomycetes of Hunan, China. I. Ann. Bot. Fennici 38: 305-328.

Yatsiuk, I. I., Leontyev, D. V., and Shlakhter, M. L. 2018. Myxomycetes of the National Nature Park Slobozhanskiy (Ukraine): Biodiversity and noteworthy species. Nord. J. Bot. 36(1-2), njb-01605.

Zoll, V. and Stephenson, S. L. 2013. Myxomycete records from Eagle Hill in Maine. Mycosphere 4: 532-537.