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# CHAPTER 3-1
# SLIME MOLDS: BIOLOGY AND DIVERSITY

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# CHAPTER 3-1
# SLIME MOLDS: BIOLOGY AND DIVERSITY

Figure 1. Orange slime mold on moss, Blue Lake Creek valley, Washington, USA. Photo by Matt Goff, Sitka Nature, with permission.

## What are Slime Molds?

Slime mold or slime mould is an informal name given to three kinds of unrelated eukaryotic organisms. While the bryophytes were undergoing classification changes at the familial and ordinal levels, **Protista** were jumping to new kingdoms and phyla. Hence, anyone whose knowledge about these organisms is as old as mine needs a road map to understand who now belongs where. Slime molds are no longer considered fungi, but instead seem to be protozoa.

The protozoa have been joined by other groups to form the current concept of the paraphyletic kingdom **Protista**, also known as **Protozoa**, a grouping that is one of convenience. One such group to join them is the slime molds (Figure 1). Once classified as fungi, they have been booted out of that kingdom due to their lack of chitin and their feeding by engulfing food. They are now considered **Protista** due to their motile stages that look and behave like protozoa. Within the **Protozoa**, we will consider here the phylum known as **Eumycetozoa** or **Amoebozoa** (Shadwick *et al*. 2009; Kang *et al*. 2017).

The slime molds are comprised of more than 1000 species from all seven continents (Lloyd 2011). The life cycle is one reason for their current classification position. They can live freely as single cells, but in dictyostelids they can later aggregate to form multicellular reproductive structures.

Using 18S rDNA and cladistics, Leontyev *et al*. (2019) revised the classification of the **Myxomycetes**. Noting that "Myxomycetes show a higher within-group genetic divergence than true fungi, higher animals, or vascular plants," they divide the slime molds into three classes, giving the groups taxonomic status according to the International Code of Nomenclature:

- **CLASS MYXOMYCETES** (Figure 2-Figure 9)

  The **Myxomycetes**, also known as **Myxogastria**, are the **acellular** slime molds, referring to the plasmodium that is multinucleate with no cell separation. These form the largest group of slime molds and contain almost all of the slime molds that associate with bryophytes. Based on the list of genera in nomen.eumycetozoa.com (5 May 2019), I have found all but three of the genera with at least one species that has been found on bryophytes to be in this class. The **plasmodium** (Figure 22, Figure 24) moves by amoeboid movement with rapidly streaming protoplasm, reaching speeds up to 1.35 mm per second (Alexopoulos 1962, 1964). The mass can migrate when it streams to an advancing position and

withdraws its protoplasm from the rear area. When food becomes scarce, this mass will migrate to the surface of the substrate and form its rigid fruiting bodies. These produce spores that hatch into amoebae to continue the life cycle (Ling 1999).

Figure 2. ***Physarum decipiens*** young fruiting bodies on leafy and thallose liverworts. Photo by David Mitchell, from The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 3. ***Physarum decipiens*** mature fruiting bodies on leafy liverwort. Photo by Alain Michaud, from The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 4. ***Physarum cinereum*** immature fruiting bodies. Photo from Denver Botanical Garden, from The Eumycetozoan Project, DiscoverLife.org, with permission.


Figure 5. ***Physarum cinereum*** mature fruiting bodies. Photo by David Mitchell, from The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 6. ***Physarum globuliferum*** with immature fruiting bodies. Photo by Ray Simons, from The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 7. ***Physarum globuliferum*** with mature fruiting bodies releasing spores. Photo by Dmitry Leontyev, from The Eumycetozoan Project, DiscoverLife.org, with permission

Figure 8. ***Physarum leucophaeum*** with immature fruiting bodies. Photo by Denver Botanical Garden, from The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 9. ***Physarum leucophaeum*** with mature fruiting bodies emitting spores. Photo by Alain Michaud, from The Eumycetozoan Project, DiscoverLife.org, with permission.

- **CLASS DICTYOSTELIOMYCETES** (Figure 12)

  **Dictyostelids** are cellular slime molds. I have found only two genera with any species reported on these slime molds. The **Dictyosteliomycetes** do not form huge plasmodia (Figure 22, Figure 24) and remain as individuals, feeding on microorganisms. When they run out of food, they form fruiting bodies, first releasing signal molecules that enable them to find each other and then aggregating as swarms. They join to form a tiny multicellular coordinated slug-like creature (Figure 10). They can aggregate about 100,000 cells in ***Dictyostelium discoideum*** (Figure 11-Figure 12) (Kessin *et al*. 1996). This aggregate crawls to an open place in the light to form a fruiting body (Kakiuchi *et al.* 2001). While some of the amoeboid cells actually become spores, others become part of the dead stalk that lifts the spores upward. About 20% of the cells of the ***Dictyostelium discoideum*** die as they form the stalk (Kessin *et al*. 1996). This group is largely unrecorded from bryophytes. The only record I found was for ***Dictyostelium quercibrachium*** from the margin of a small bog in Ohio, USA (Cavender *et al*. 2005), and it is not clear if was actually on a moss.

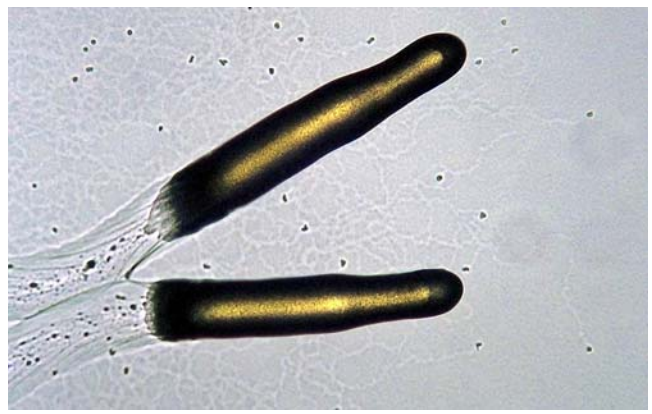

Figure 10. ***Dictyostelium mucoroides*** pseudoplasmodial slug on agar. Note their slug-like appearance. Photo by Dmitry Leontyev, through Creative Commons.

Figure 11. ***Dictyostelium discoideum*** development. Photo by Usman Bashir, through Creative Commons.

Figure 12. ***Dictyostelium discoideum*** fruiting in an open place. Photo by Usman Bashir, through Creative Commons.

- **CLASS CERATIOMYXOMYCETES**

The **Ceratiomyxomycetes** is a small group of only three genera (Leontyev *et al.* 2019). Their typical substrates are dead plant material, especially decaying wood. The genus ***Ceratiomyxa*** has at some time been in each of these three classes. It is the only genus of this new class that I have found reported from bryophytes. These slime molds have a complex life cycle, usually with a sexual phase, and the cycle includes amoeboflagellates that do not divide but instead convert into amoebae or to form a plasmodium (Spiegel *et al.* 2018). The plasmodium most likely follows sexual reproduction and formation of a zygote, although the sexual reproduction has not been verified in all genera. Fructification produces one, two, four, or eight spores at the top of a relatively long stalk.

## Identification Difficulties

Identification of species can be difficult for a number of reasons. Not only are there different color phases during the development of the sporangia, but there are different sexual strategies within currently perceived species (Clark & Haskins 2010; Feng & Schnittler 2015). One example of this is the widespread ***Trichia varia*** (Figure 13-Figure 17; **Myxomycetes**), an occasional bryophyte dweller (Feng & Schnittler 2015). Within this "species" there are three distinct sexual biospecies that are reproductively isolated from each other, based on 197 specimens collected from throughout Eurasia. In this case, the genotypes are distinct, but the phenotypes are not. Furthermore, there appear to be numerous sibling species that are biologically distinct, unable to mate, but morphologically indistinguishable, and these are spread throughout the world (Clark & Haskins 2010).

Figure 13. ***Trichia varia*** with white young sporangia on mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 14. ***Trichia varia*** with orange sporangia. Photo by Lebrac, through Creative Commons.

Figure 15. ***Trichia varia*** with yellow sporangia on moss. Photo from Bite.Your.Bum Photography, through Creative Commons.

Figure 16. ***Trichia varia*** with brown sporangia. Photo from EOL, through Creative Commons.

Figure 17. ***Trichia varia*** with mature brown sporangia, dehiscing and dispersing spores. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.com, with online permission

## Reproduction and Colonization

Slime molds sound like nasty things that grow in the corners of your refrigerator, but in fact they are beautiful and fascinating organisms that really aren't molds at all. For centuries we thought they were, but unlike true fungi, they eat bacteria and other micro-organisms. Hence, they have been reclassified into the **Protista**. Stephenson and Stephenson (2022) found that although bryophyte mats are appropriate substrata for slime molds in temperate deciduous forests, the species richness and abundance are both relatively low. Their unique call to fame is their rather strange life cycle in which they try to be fungi when fruiting and protozoa when active.

### General Life Cycle

The **Myxomycetes** are the **plasmodial slime molds** and with few exceptions are the only group large enough to be noticed easily (Wikipedia: Slime Molds 2019). In these **acellular** slime molds, the **plasmodia** (Figure 18, Figure 22, Figure 24) have many nuclei with no dividing cell membranes and can form a plasmodial mass that may be several meters in size. One of the most obvious of these is the slimy yellow plasmodium of ***Fuligo septica*** (Figure 19-Figure 20) on rotting logs – a species that also can occur on bryophytes (Figure 18). Both the amoeboid and the plasmodial stages can engulf microorganisms as food.

Figure 18. ***Fuligo muscorum*** on **Polytrichaceae**. Photo by James K. Lindsey, with permission.

Figure 19. ***Fuligo septica*** plasmodium on log. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 20. ***Fuligo septica*** on mosses (**Polytrichaceae**) in Orekhovo, Russia. Photo by Alexey Sergeev <asergeev@asergeev.com>.

When slime mold spores germinate, amoeba-like cells form (**myxamoebae**; Figure 21, Figure 24) (Wikipedia: Slime Molds 2019). These are typically **haploid** (have one set of chromosomes), can move about, and feed on bacteria. If these amoebae encounter the correct mating type, they can mate to form **zygotes** that develop into **plasmodia** (Figure 19, Figure 22, Figure 24). The protoplasm within the plasmodium can stream at speeds up to 1.35 mm per second, the fastest rate known for any organism (Alexopoulos 1962). When food becomes limiting, the plasmodium moves to the surface and begins to form its rigid fruiting bodies (**sporangia**; Figure 6-Figure 12, Figure 24) (Wikipedia: Slime Molds 2019). It is this stage that caused us to originally think they were fungi, but it lacks the chitin that is present in fungi. The life cycle is completed when these sporangia produce spores, usually by meiosis, for the next generation of amoebae. Some of these species go from spore to fruiting structure very quickly (Alexopoulos 1964).

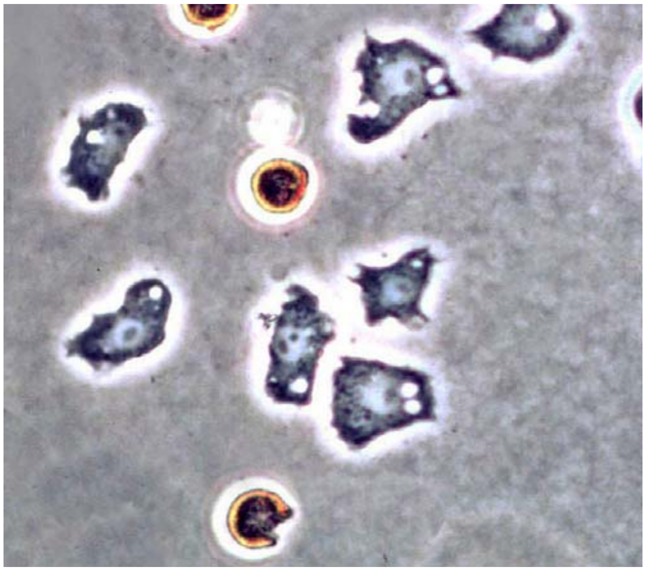

Figure 21. ***Didymium*** myxamoebae hatched from spores. Brown structures are spores. Photo by George Barron, modified, with permission.

Figure 22. ***Fuligo aurea*** plasmodium. Photo through Creative Commons.

If free water is available, **myxamoebae** (Figure 21) form **swarm cells** (Figure 24) by developing flagella – one long and one very short (Myxomycota 2019). Some species mate as myxamobae (Figure 24) and others as swarm cells. Although adjoined myxamoebae are ready to mate, they generally cannot mate with the same strain, *i*.e. no sibling mating.

If conditions become too dry for the plasmodium (Figure 22), it will form a **sclerotium** (Figure 23, Figure 24), which is a dry dormant state (Wikipedia: Slime Molds 2019) and sometimes resembles the slime left by a slug. When this sclerotium once again becomes moist, it returns to the active plasmodium state. An alternative to this is that some species can form a **microcyst** (Figure 24) (Myxomycota 2019). This stage occurs when the amoeboid cells or swarm cells round up and form a thin wall, then become dormant, surviving unfavorable conditions.

Figure 23. Sclerotium. Photo courtesy of Steve Stephenson.

The multinucleate, diploid plasmodium (Figure 22) moves and feeds until conditions are right (or wrong) and it reorganizes into sporangia (Myxomycota 2019). The spores that are produced generally undergo meiosis to produce four nuclei. Three of these abort, leaving a single haploid nucleus, in a cell that becomes the haploid spore.

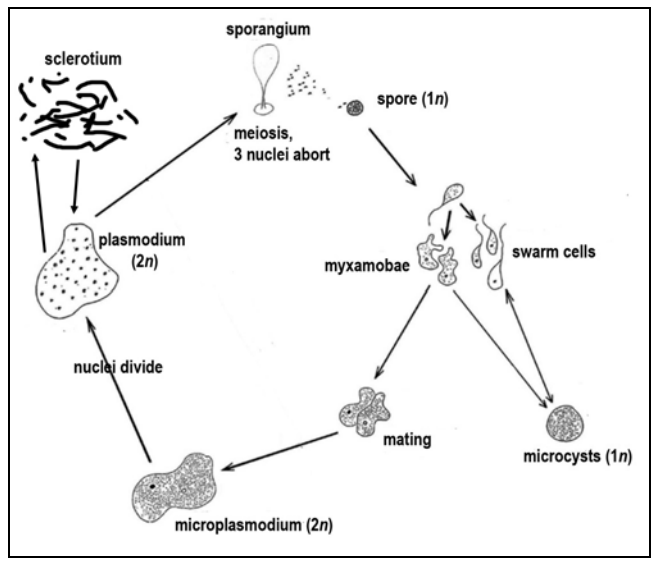


Figure 24. Generalized slime mold life cycle. Modified from Hoppe & Schwippert 2014.

Some species can produce **diploid** (having 2 sets of chromosomes) **amoeboflagellates** (includes flagellated cells and amoeboid cells) that develop directly into the plasmodium (Figure 22) without having any crossing with another cell (Clark & Haskins 2010). This appears to be the result of a failure of meiosis, resulting in **diploid** spores (**apomixis**). Thus a single spore of some species can complete a life cycle without any mating occurring.

## Seasonal Changes

Reproduction in the **Myxomycetes** is typically seasonal. Eliasson (1980) recorded the times of **fructification** (producing sporangia) in several Swedish species over the course of four years. Those **Myxomycetes** fruiting in May-June include ***Amaurochaete atra*** (Figure

25), ***A. tubulina*** (Figure 26; not known from bryophytes), ***Reticularia jurana*** (Figure 27-Figure 28; a species close to the sometimes bryophyte dweller ***R. lycoperdon*** and that sometimes occurs close to bryophytes), and ***Symphytocarpus flaccidus*** (Figure 29-Figure 30; sometimes occurs on bryophytes). Those fruiting in June-August include ***Ceratiomyxa fruticulosa*** (Figure 31-Figure 32), ***Fuligo septica*** (Figure 33), ***Stemonitis axifera*** (Figure 34), ***S. fusca*** (Figure 35-Figure 36), and ***Stemonitopsis hyperopta*** (Figure 37; image on moss seen, but further documentation not available), all of which are known sometimes to associate with bryophytes. In September-October, those fruiting include ***Colloderma oculatum*** (Figure 38), ***Fuligo muscorum*** (Figure 39), ***Trichia botrytis*** (Figure 40-Figure 42), and ***T. decipiens*** (Figure 43-Figure 45). ***Lycogala epidendrum*** (Figure 46) spans May to October. Some of the species fruiting in spring may fruit again in autumn. All of these species occasionally occur associated with bryophytes.

Figure 25. ***Amaurochaete atra***, a slime mold that fruits in May-June in Sweden. Photo from UkrBIN.com, with online permission.

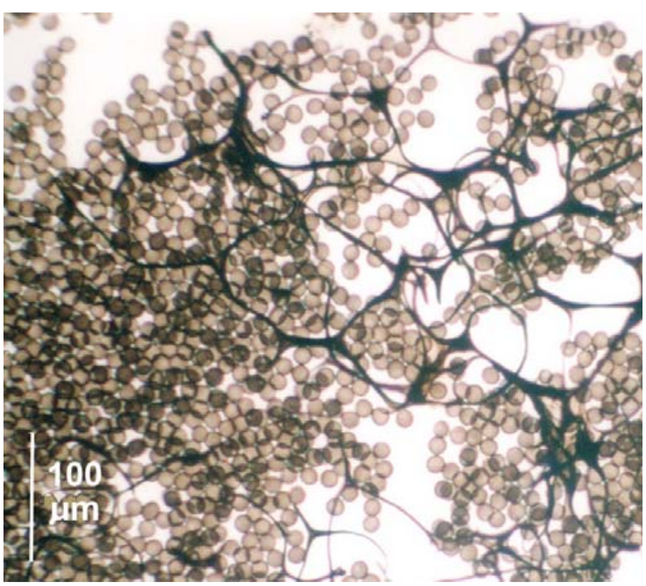


Figure 26. ***Amaurochaete tubulina*** spores and capillitium, a slime mold that fruits in May-June in Sweden. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 27. ***Reticularia jurana***, a species that fruits in May to June in Sweden. From Amadej Trnkoczy, through Creative Commons.

Figure 28. Habitat of ***Reticularia jurana*** on a mossy bank. Photo by Amadej Trnkoczy, through Creative Commons.

Figure 29. ***Symphytocarpus flaccidus*** on mosses. Photo by Dmitry Leontyev, with online permission.

Figure 30. ***Symphytocarpus flaccidus*** with maturing capsules. Photo by Thomas Laxton, through Creative Commons.

Figure 31. ***Ceratiomyxa fruticulosa*** fruiting bodies on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 32. ***Ceratiomyxa fruticulosa*** fruiting bodies. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 33. ***Fuligo septica*** plasmodia growing on mosses at the base of a tree. Photos by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 34. ***Stemonitis axifera*** fruiting bodies growing on moss. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 35. ***Stemonitis fusca*** fruiting bodies on log. Photo from Encyclopedia of Life, through Creative Commons.

Figure 36. ***Stemonitis fusca* var. *fusca*** on mosses. Photo from Denver Botanical Gardens, with online permission.

Figure 37. ***Stemonitopsis hyperopta*** on rotting wood. Photo through Creative Commons.

Figure 38. ***Colloderma oculatum*** fruiting bodies on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.


Figure 39. ***Fuligo muscorum*** fruiting structure on bryophyte. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

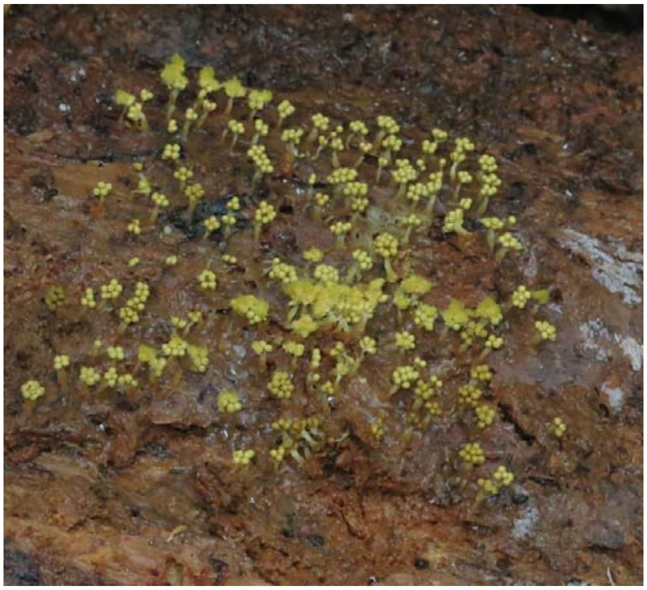

Figure 40. ***Trichia botrytis*** cf. **var. *flavicoma*** fruiting on rotten wood. Photo by John Barkla, through Creative Commons.

Figure 41. ***Trichia botrytis*** fruiting on wood. Photo by Sarah Lloyd, with permission.

Figure 42. ***Trichia botrytis*** old and dry fruiting structures on wood. Photo by Bernard Dupont, through Creative Commons.

Figure 43. ***Trichia decipiens*** young fruiting bodies. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 44. ***Trichia decipiens***. Mature fruiting bodies. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 45. ***Trichia decipiens*** empty fruiting bodies. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 46. Fruiting bodies of ***Lycogala epidendrum*** (wolf's milk; toothpaste slime) on mosses. The plasmodia are composed of small, red amoeboid cells (Wikipedia: *Lycogala epidendrum* 2019). When the conditions change, these rarely seen cells find each other by chemical signals and aggregate into the fruiting body, as seen here. Photos by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Some of the other seasonal records for the occasional **Myxomycetes** bryophyte dwellers include ***Arcyria ferruginea*** (Figure 47; known from bryophytes – based on photos by Iyp-tala at <https://hiveminer.com/Tags/arcyria>; Dawn & Jim at <https://hiveminer.com/Tags/arcyria>), ***A. obvelata*** (Figure 48; known from bryophytes – based on photo from <https://www.alamy.com/stock-photo-arcyria-obvelata-slime-mold-73514471.html>, ***Collaria arcyrionema*** (Figure 49; syn=***Lamproderma arcyrionema***; known from bryophytes – Ranade *et al*. 2012), and ***Physarum viride*** (Figure 50; known from bryophytes – Stephenson & Studlar 1985), all of which appeared early in the year. ***Stemonitopsis hyperopta*** (Figure 37; known from bryophytes based on online image; attribution not available), ***Cribraria intricata*** (Figure 51; known from mosses – Ranade *et al*. 2012), ***Cribraria cribrarioides*** (Figure 52; on bryophytes in photograph), ***Lamproderma columbinum*** (Figure 53; known from bryophytes – Stephenson & Studlar 1985), ***Tubifera ferruginosa*** (Figure

54-Figure 55; known from bryophytes – Stojanowska & Panek 2004), and ***Trichia verrucosa*** (Figure 56; known from bryophytes based on image) appeared later in the year.

Figure 47. ***Arcyria ferruginea*** fruiting bodies. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 48. ***Arcyria obvelata***, a species that has been photographed elsewhere growing on bryophytes. Photo by Patrick Schifferli, through Creative Commons.

Figure 49. ***Collaria arcyrionema*** fruiting, a species reported from bryophytes. Photo by Guang-Bao Xiang and Quan-Nian Jun, through Creative Commons.

Figure 50. ***Physarum viride*** fruiting bodies. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 51. ***Cribraria intricata***, a species known to grow on bryophytes. Photo by Clive Shirley, The Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 52. ***Cribraria cribrarioides*** on bryophytes, and fruiting late in the year. Photo from Myxotropic, through Creative Commons.

Figure 53. ***Lamproderma columbinum*** growing with bryophytes, showing the slime mold's fruiting bodies. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 54. ***Tubifera ferruginosa*** on mossy wood. Photo by Sarah Lloyd, with permission.

Figure 55. Mature sporangia of ***Tubifera ferruginosa*** on moss. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 56. ***Trichia verrucosa*** with liverworts, and fruiting late in the year. Photo by Sarah Lloyd, with permission.

## Environmental Stimuli

Kazunari (2010) examined the succession of slime mold communities in a forest setting in southwestern Japan and found that the seasonal factors of the slime mold communities were related to the decay state of the wood. Kazunari also showed that certain species were visible at only certain times of the year. But what are the factors that trigger these responses?

### Light

Many of the slime molds migrate to light before initiating development of sporangia. Loss of bark during decay could provide a light signal for amoeboid and swarm cells under the loose bark of a decaying log. Reinhardt (1968) explored the effect of light on the cellular slime mold ***Acrasis rosea*** (Figure 57-Figure 58), a taxon that might not be representative of the **Myxomycetes** of interest here. Both continuous light and continuous dark failed to stimulate the production of sporangia. Reinhardt was able to stimulate sporangia production by exposing the cultures to light, followed by a minimum of 7-8 hours of darkness. Hence, we see that seasonal changes in day length could synchronize the fruiting of the slime molds.

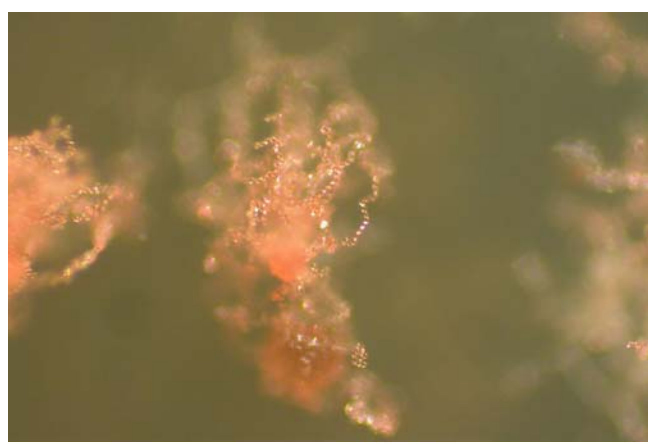

Figure 57. ***Acrasis rosea*** sporangia; this cellular slime mold responds to light to produce sporangia. Photo from Biology of Fungi Lab UC Berkeley, California, through Creative Commons.

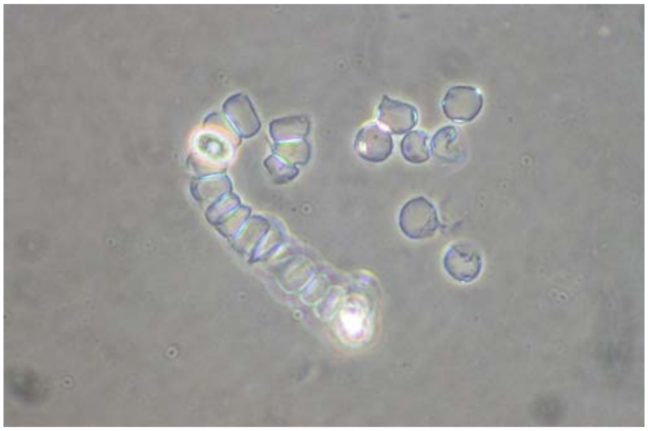

Figure 58. ***Acrasis rosea*** amoebae, a cellular slime mold, emerging from spores. Photo by Chirley Chio at Mushroom Observer, California, through Creative Commons.

Kakiuchi *et al.* (2001) demonstrated the role of the colors of light in the initiation of reproduction in the **Myxomycetes** slime mold ***Physarum polycephalum*** (Figure 59). Light initiates the breakup of the plasmodium (Figure 22) into equal-sized spherical pieces within about five hours. Blue and far-red light both initiate this behavior, whereas red light (but not blue) inhibits the far-red induction. These fragments develop the sporangia and spores. When it is time to develop sporangia, plasmodia can creep out from under bark or the bases of bryophytes and seek higher ground and more light.

Figure 59. ***Physarum polycephalum*** on leafy liverworts. Photo by Bernard Spragg, through Creative Commons.

### *p*H and Volatile Substances

Researchers have found that bark *p*H is important in determining slime mold distribution on bark, but that it might be masked by geographic location (Everhart *et al.* 2008; Keller & Everhard 2010). It is reasonable to ask, then, if substrate *p*H is important in the reproductive cycle.

Early work by Reinhardt (1968) demonstrated that *p*H was important for fruiting in ***Acrasis rosea*** (Figure 57-Figure 58); a cellular slime mold in an entirely different clade), with growth occurring at *p*H 3.5-7.6, but fruiting only at 5.0-6.6. Such differences in *p*H could occur as a result of changes in the decay state of a log or litter. Of course this is only one species, and not even in the **Myxomycetes**, but it illustrates the mechanisms that might be used by other slime molds as well.

Gray (1939) found that temperature and *p*H are closely interrelated, at least in the **Myxomycetes** slime mold ***Physarum polycephalum*** (Figure 59). When *p*H remains constant, the time required for fruiting varies directly with the temperature, requiring longer times at higher temperatures. Furthermore, the higher the temperature, the fewer cultures produce fruiting bodies. When *p*H also varies, higher temperatures require greater acidity to produce fruiting bodies. At a constant temperature, the greatest fruiting occurs at *p*H 3.0. The maximum temperature at which this species will produce sporangia is 32.5º-35.0ºC. **Sclerotia** will not form at low temperatures (8º-12ºC) or high temperatures (32.5º-35.0ºC). Light still seems to be necessary for fruiting at all temperatures.

While the change in *p*H could be a seasonal phenomenon, research by Newell *et al.* (1969) suggests a different relationship. In the slime mold ***Dictyostelium discoideum*** (Figure 11-Figure 12; **Dictyosteliomycetes)**, a dweller of shallow soil, also known from bryophytes and litter, the amoebae form multicellular aggregates from which they are able to form fruiting bodies with stalks and spores. This change of state may occur at the same microsite, or it can change its structure into a form that can migrate to a more favorable location. This migration can be stimulated by the accumulation of metabolites from the slime mold or a low ionic strength in its substrate. This migration is inhibited by the presence of a buffer or overhead illumination. In an unbuffered system, the stimulus for fruiting is "appreciably volatile." In the presence of a buffer, the slime molds transformed from a migrating **slug** (Figure 10) and sat still, producing fruiting bodies on that spot. The strong base NaOH was completely ineffective in preventing the formation of the moving slug. Furthermore, the transformation into a moving slug was inversely related to the density of the slime mold cells, indicating that it was something produced by the slime mold that signalled the migration. Others (Bonner *et al.* 1950; Francis 1964) have observed that this species moves toward heat, following a very low temperature change gradient (as little as 0.05º C per cm). This behavior could decrease the volatile substance produced by the slime mold – an indicator that it is not too dense a population. But a heat gradient also would lead the moving slug form toward the light, which would then stop the migration and cause it to form the fruiting bodies.

Using the unicellular slime mold ***Dictyostelium mucoroides*** (Figure 10; **Dictyosteliomycetes**), Filosa (1979) similarly demonstrated the presence of a volatile substance by using charcoal as an absorbent. In the dark, this species produced **macrocysts** (encysted, resting plasmodium), but in the light it produced fruiting bodies. But if the dark cultures were grown over activated charcoal, they likewise would form fruiting bodies. When grown in light with KOH (a $CO_2$ absorbent), they produced macrocysts, but if activated charcoal was added, they again only produced fruiting bodies.

All of these responses to heat, light, *p*H, and an exudate from the slime molds themselves could optimize their reproductive potential. These stimuli cause the slime molds to move to a location where spores are more easily dispersed and will have less competition for space during fruiting and food for the next generation.

### Water

In the cellular slime molds, surface water is a key factor as well (Bonner *et al*. 1982). When the plasmodial slug tip reaches above the water film, it usually causes the slime mold to shift gears and produce the fruiting structures. Among the cellular slime molds, light seems to be less important, promoting fructification only in those phototactic slugs that orient away from the surface.

### Reproduction in Myxomycetes

Some slime molds are particularly associated with bryophytes (Ing 1994), and almost all of these are in the **Myxomycetes**, the acellular or plasmodial slime molds. ***Myxo*** means slime. They gain their energy by engulfing and digesting bacteria, yeasts, fungal spores, and decaying material in their amoeboid stage (Wikipedia: Slime Molds 2019), food sources that are often available on bryophytes. Spores are formed in a capsule-like structure. When the spores germinate, they release the amoeboid cells, referred to as the **myxamoebae** (Figure 21). If there is sufficient water for swimming, the myxamoeba may develop flagella and become a **swarm cell**. This process can be reversed, the flagellum retracted, and the amoeboid stage returned. Unlike the **Dictyosteliomycetes**, the **Myxomycetes** are sexual. When two different mating strains find each other, they join to form a **zygote**. Even in forming the **plasmodium** (Figure 22), the **Myxomycetes** differ from the **Dictyosteliomycetes**. In **Myxomyceyes**, the zygote does not form an amoeba, but instead divides only its nucleus. These nuclei continue to divide to form the **plasmodium** – a large, multinucleate body composed of a single cell.

In their **plasmodium** (Figure 22) stage, the **Myxomycetes** can flow like an amoeba, feeding as they traverse their substrate (Wikipedia: Slime Molds 2019). The plasmodium prefers darkness, and when it ventures into the light it is likely to go into its **sclerotium** (Figure 23, Figure 24) stage – a dormant stage that can remain so for years; this stage is also imitated by drying conditions. That shiny dry covering that looks like a slug's slime trail on the surface of a moss might be a sclerotium. The sclerotium is particularly likely to form if the plasmodium dries out. If, on the other hand, it runs short on food first, it goes into its fruiting stage. Such factors as light and temperature can induce the plasmodium to transform into fruiting structures (Figure 61 that produce **meiospores**, hence returning the organism to its 1*n* state (having only one set of chromosomes). The subsequent spores may germinate into flagellated cells or amoeboid cells that multiply vegetatively and engulf food to gain energy.

Figure 60. ***Didymium squamulosum*** sporangia. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 61. ***Trichia subfusca*** mature fruiting bodies on bark. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

**Temperature** plays an important role in maintaining the active state of the amoeboid stage, and any habitable site must have sufficient moisture, making bryophytes necessary for survival of any that venture onto rocks (Ing 1994). The behavior of the slime mold under adverse conditions is reminiscent of the bryophytes and many of the fauna found there. When the going gets rough, they sleep like Rip Van Winkle! For the slime molds, it is the sclerotium (Figure 23, Figure 24); for many fauna it is a cyst; and for the bryophytes it is a simple dormancy without any change of state.

The **Physarales** (Figure 2-Figure 9; Figure 60-Figure 68), and especially ***Diderma*** (Figure 62-Figure 68), frequently fruit extensively where bryophytes and lichens cover the bark (Brooks *et al*. 1977). We know substrate is important for finding food in the mobile stages, but is it important for fruiting? Do the bryophytes offer the advantage of a higher perch for dispersal of these tiny beings?

Figure 62. ***Diderma*** sp. on liverwort. Ken-ichi Ueda, through Creative Commons.

Figure 63. ***Diderma cinerea*** sporangia on moss. Photo by Sarah Lloyd, with permission.


Figure 64. ***Diderma imperialis*** fruiting bodies on moss. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 65. ***Diderma montanum*** fruiting bodies on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 66. ***Diderma sessile*** fruiting bodies on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 67. ***Diderma sessile***. fruiting bodies on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 68. ***Diderma umbilicatum*** fruiting bodies on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

## Dispersal

Using 18S rDNA variants from 125 specimens from 91 localities of the myxomycete ***Badhamia melanospora*** (sometimes a moss dweller; Figure 69-Figure 70), Aguilar (2014) set out to determine if the Baas-Becking hypothesis of "everything is everywhere" can be applied to **Myxomycetes**. They found two distinct groups within this

species: one group comprises all populations from Argentina and Chile; the other is formed by populations from North America together with human-introduced populations from other parts of the world. For this species, they concluded that everything is not everywhere. Instead, the taxon consists of a complex that has at least two cryptic species that probably diverged as **allopatric** (having non-overlapping distributions) in North and South America. But as will be seen in this chapter, many of the slime molds do have widespread distributions on several continents.

Figure 69. ***Badhamia melanospora***, a species that sometimes grows on bryophytes. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

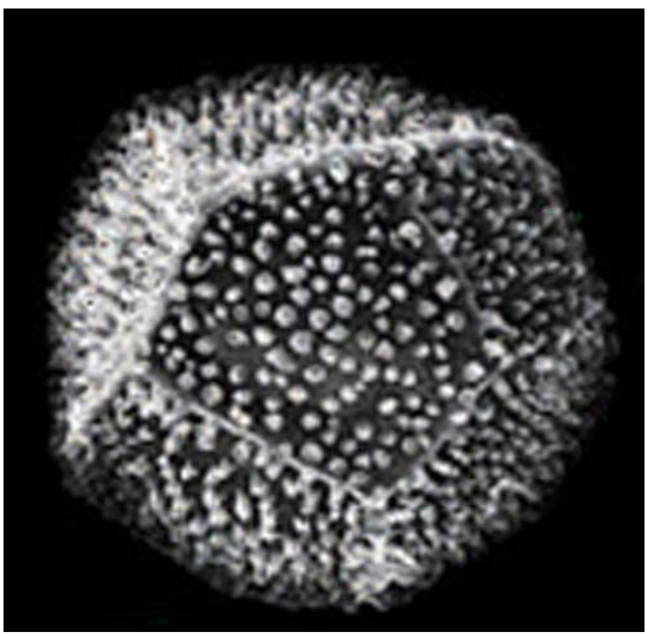

Figure 70. ***Badhamia melanospora*** spore SEM. Can it travel around the world? The Eumycetozoan Project, DiscoverLife.org, with permission.

It appears that some slime molds occur in the same places for multiple years, but their propensity for living on logs and even living trees means that at some time they must disperse to survive. Schnittler and Tesmer (2008) asked if the habitat colonization model for spore-dispersed organisms works for slime molds. They found spore numbers per sporangium ranging from 1 to 106. Average spore size ranges 10.3 µm to 14.8 µm in the studied taxa. Culture data suggest that the number of spores required to create the observed frequencies (as a percent of successfully colonized habitat islands) is generally three orders of magnitude higher. Species with sexual reproductive systems typically produce more spores than do asexual ones.

The presence of individual species is limited not by dispersal, which seems to be efficient, but by suitable substrate (Ing 1994). We have seen that the species are seasonal, but as we might expect, the time of year for the conspicuous fruiting varies with climatic zone. The dispersal is primarily tied to the onset of rain after a long warm period. This is typically autumn in the temperate regions, whereas in parts of the tropics it begins with the monsoon season. Dispersal does not determine species presence, except perhaps among the corticolous species. Rather, it is suitable substrates that determine presence.

One factor in dispersal of the spores is their surface structure. Three types exist in the **Myxomycetes**: spiny, reticulate, and smooth surfaces (Hoppe & Schwippert 2014). Using spores from 17 species, including ***Metatrichia floriformis*** (Figure 71) (reticulate; see Figure 72), ***Fuligo septica*** (Figure 33) (spiny; see Figure 73), and ***Licea parasitica*** (smooth; see Figure 74) as well as ***Ceratiomyxa fruticulosa*** (Figure 31-Figure 32; **Ceratiomyxomycetes**) (smooth) (all known from bryophytes as well as other substrata), they determined the wettability of the spores. Spiny spores would half sink into the water but nevertheless they floated. Reticulate spores are superhydrophobic and float on the surface tension of the water. Spores with no ornamentation sink to the bottom rather quickly.

Figure 71. ***Metatrichia floriformis*** sporangia. Photo by Clive Shirley, The Hidden Forest, with permission.

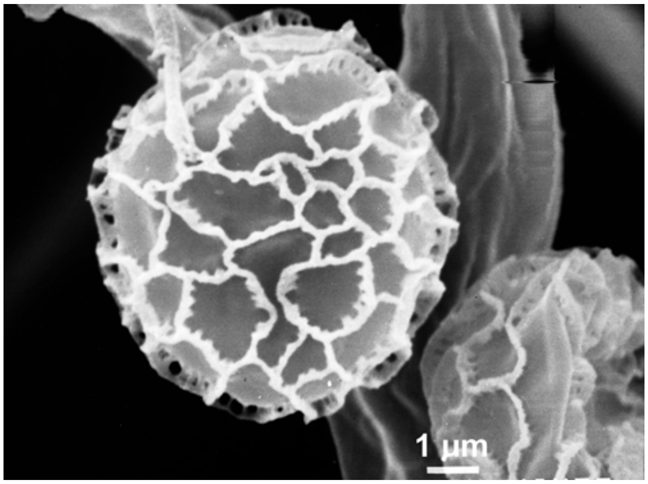


Figure 72. ***Stemonitis fusca***, sometimes a moss dweller, reticulate spores. SEM photo courtesy of Yuri Novozhilov.

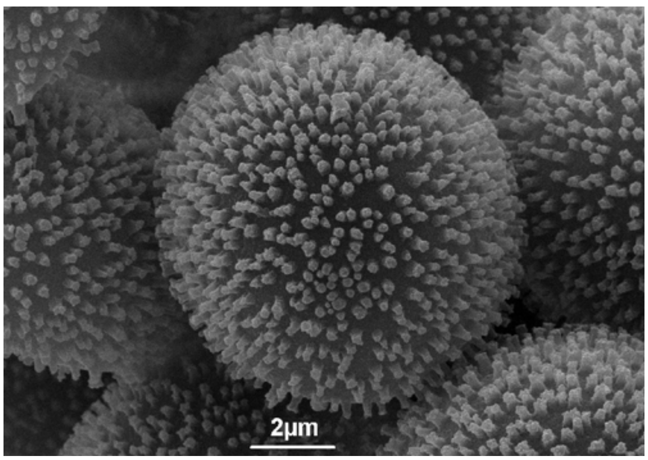


Figure 73. ***Physarum notabile***, sometimes a moss dweller, spiny spores. SEM photo courtesy of Yuri Novozhilov.

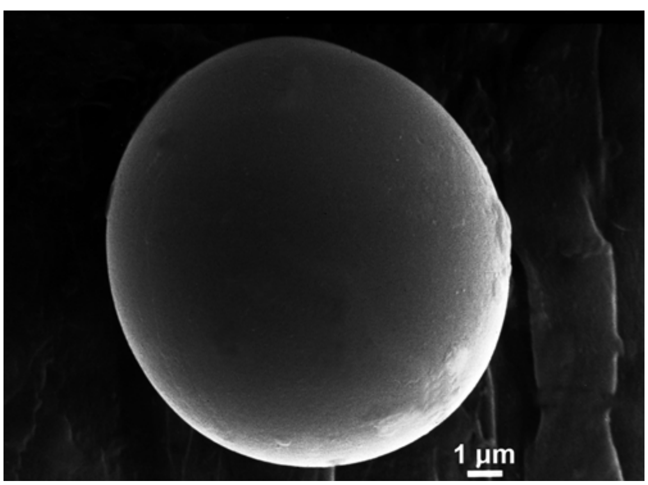


Figure 74. ***Licea deplanata***, not a known bryophyte dweller, smooth spore. SEM photo courtesy of Yuri Novozhilov.

Dispersal by wind seems to predominate (Keller & Smith 1978). Underlying bryophytes can become covered in spores (Figure 75). Dispersal may be aided by the **capillitium** (Figure 76) that in some species twists in response to changing moisture conditions. The capillitium also is likely to act like a salt shaker, doling out a few spores at a time instead of releasing all of them in a single burst of wind, a function similar to that of the peristome in mosses.

Figure 75. ***Tubulifera ferruginosa***. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

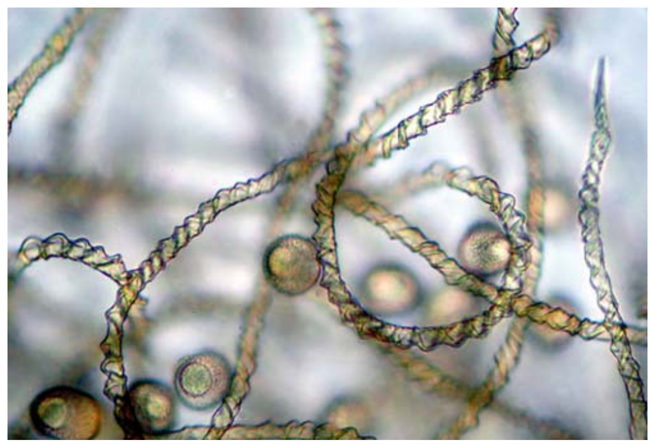

Figure 76. ***Trichia varia*** spores and capillitium. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

In some species, insects and mites seem to be important dispersal agents (Keller & Smith 1978; Eliasson 1977). Beetles are abundant on ***Amaurochaete*** (Figure 25) species and spores that cling to the body and legs would get a free ride for dispersal (Eliasson 1977).

Eliasson (1980) indicated that invertebrates are important in the dispersal of several species of slime molds. This is sometimes accomplished through predation by snails and insects that carry the spores on their bodies or in their digestive tracts (Ing 1967; Angela Newton, Bryonet, 20 November 2006).

The isopod ***Philoscia muscorum*** (Figure 77) appears to spread the cellular slime mold ***Didymium bahiense*** (Figure 78) (Ing 1004). Huss (1989) verified the potential of dispersal by earthworms (Figure 79) and pillbugs (**Isopoda**; Figure 77). Some of these invertebrate species are bryophyte dwellers, although typically not the ones used in the experiments. These invertebrates were fed both spores and myxamoebae of slime molds. Although percentages of both survived, the spores survived better

than the myxamoebae. When invertebrate feces were cultivated, the species the invertebrates had eaten developed in the cultures.

Figure 77. The isopod ***Philoscia muscorum***, a likely dispersal agent for the cellular slime mold ***Didymium bahiense***. Photo by Malcolm Storey, through Creative Commons.


Figure 78. ***Didymium bahiense*** on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 79. The earthworm ***Octolasion cyaneum***; some species in this genus ingest slime molds and disperse them. Photo by Chih-Han Chang, through Creative Commons.

A similar relationship was found between the cellular slime mold ***Dictyostelium discoideum*** (Figure 11-Figure 12; **Dictyosteliomycetes**), an occasional bryophyte dweller, and the nematode ***Caenorhabditis elegans*** (Figure 80) (Kessin *et al*. 1996). This nematode is an inhabitant of the moss ***Sphagnum*** (Figure 81) (Glatzer & Ahlf 2001) and feeds on slime molds, including consumption of the spores. It kills the amoeboid stage, but the spores survive the digestive tract, making this another organism capable of moving the spores from one place to a new location for germination.

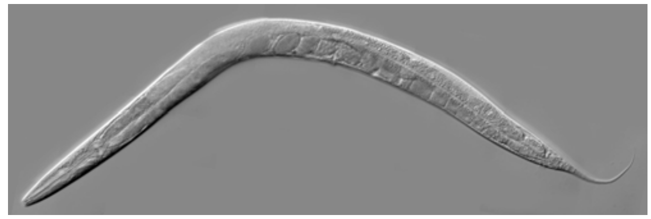

Figure 80. ***Caenorhabditis elegans***, a nematode that seems to benefit from some properties of ***Sphagnum***, and that also can disperse slime molds living there. Photo by Kbradnam, through Creative Commons.

Figure 81. ***Sphagnum recurvum***, in a genus that is home for the nematode ***Caenorhabditis elegans***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

## Habitat Needs

Publications on slime molds are in no short supply. Gray and Alexopoulos (1968) published a treatise on the biology. Martin and Alexopoulos (1969) wrote a general treatise on the group. Ing (1994) summarized the phytosociology, arranged according to major vegetation types. Rollins and Stephenson (2011) summarized the global distribution and ecology.

As of 2011, Sarah Lloyd reported that only 1000 species of slime molds had been described. Their greatest abundance is in temperate forests, where they occur on living and dead trees and rotting wood, but also in some unusual habitats, including on dung and on living animals (Stephenson & Rojas 2017).

### Moisture

Ing (1994) related the slime molds to their habitat factors, surmising that temperature is an important limiting factor in tropical, subtropical, Mediterranean, and alpine species. There is a consistent distinction between the corticolous, lignicolous, and epiphyllous species, and the lignicolous species have a preference for either conifers or deciduous trees. Ing even referred to bryophyte associations, noting that a few slime molds are particularly

associated with them. This may be due to water relations, with Ing noting that water and water-retaining substrates are of prime importance. The presence of fruiting structures (sporangia) is dependent on the arrival of rain after a prolonged warm period, making their presence most common in autumn in temperate regions. In the tropics, capsules form when the monsoon season begins. Fruiting seems to be independent of substrate.

Eliasson (1980) noted that species that have large plasmodia (Figure 22) typically are rare under arid conditions. This would suggest that the slime molds on bryophytes are the larger species in most habitats because of the moisture-holding capacity of the bryophytes.

On the other hand, Schnittler *et al*. (2013), based on observations in Xinjiang Province, China, concluded that corticolous **Myxomycetes** are some of the most drought-tolerant organisms in that habitat. They are opportunistic, permitted by their ability to survive in a dormant state for decades and to complete their life cycles in a few days of appropriate conditions.

### Latitude

Stephenson *et al*. (1993) found recognizable patterns in the latitudinal variation of slime molds. The species assemblages in the tropical-subtropical regions is distinctly different from that found in temperate regions. Furthermore, the species differ in their substrate usage at different latitudes. Some species that are rare outside the Arctic and subArctic can be relatively common in these northern regions (Stephenson *et al*. 2000).

### Food and Light

Naturally, available food is of importance in the location of active slime molds. Slime molds frequently make "decisions" for location based on the quality of food available. The common **Myxomycetes** slime mold ***Physarum polycephalum*** (Figure 59, Figure 82; sometimes a bryophyte dweller), in its amoeboid phase and if both locations are shaded, will choose the higher food quality 100% of the time (Latty & Beekman 2010). When a much higher quality food is in the light, it is selected, but when the difference in quality is small, the slime mold will select the shade over the light location, even if its food is of lesser quality.

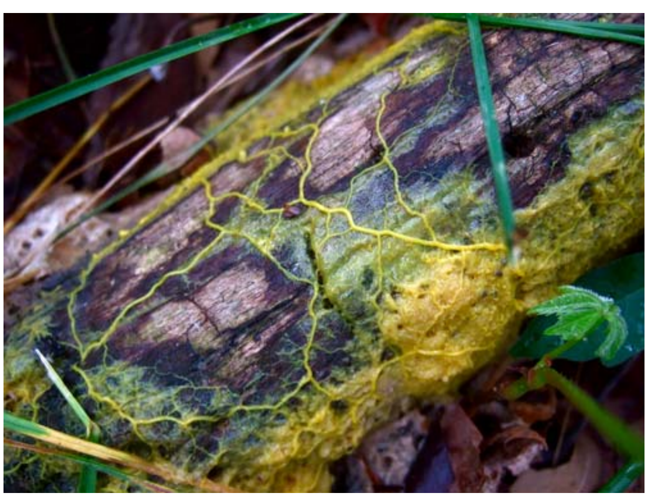

Figure 82. ***Physarum polycephalum*** plasmodium or rotting wood. Photo by Frankenstoen, through Creative Commons

## Role of Bryophytes as Slime Mold Habitat

Stephenson and Studlar (1985) found representatives of all six orders (at that time) of slime molds, exclusive of the **Labyrinthulomycota** and the **Plasmodiophorids** in their study of bryophyte-dwellers in the United States and Canada. The **Physarales** (Figure 2-Figure 9; Figure 60-Figure 68) (38% of all collections) were the most abundant, but members of the **Stemonitales** (Figure 34-Figure 37) (23%), **Trichiales** (Figure 13, Figure 40-Figure 45) (18%), and **Liceales** (Figure 83-Figure 84) (17%) were also commonly bryophyte associates. The order **Echinosteliales** (Figure 99-Figure 100) and the class **Ceratomyxomycetes** (Figure 31-Figure 32) comprised only 4% and 1%, respectively. All four of the major types of slime mold fruiting bodies (sporangia, aethalia, plasmodiocarps, and pseudoaethalia) were represented in their 170 collections.

Figure 83. ***Licea floriformis*** fruiting bodies on moss leaves. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 84. ***Licea retiformis*** plasmodium. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

But are these slime molds preferential colonists of bryophytes? Stephenson and Studlar (1985) set out to try to answer this question. By examining 170 collections throughout North America, they found that three species were particularly common: ***Fuligo septica*** (Figure 33), ***Stemonitis axifera*** (Figure 34), and ***S. fusca*** (Figure 35).

Furthermore, they found that some bryophytes were more likely than others to be suitable substrata: ***Nowellia curvifolia*** (Figure 85), ***Brotherella recurvans*** (Figure 86), ***Thuidium delicatulum*** (Figure 87), and ***Hypnum imponens*** (Figure 88). The slime mold order **Physarales** (Figure 2-Figure 9; Figure 60-Figure 68) was the most commonly represented. Taxa producing sporangia were the most abundant, representing 79% of the collections, but this is also the most common type of slime mold fruiting body (Gray & Alexopoulos 1968).

Figure 85. ***Nowellia curvifolia*** on log, a leafy liverwort that is a suitable substrate for some slime molds. Photo from <www.aphotofauna.com>, with permission.

Figure 86. ***Brotherella recurvans***, one of the more common moss substrata for the slime molds ***Fuligo septica***, ***Stemonitis axifera***, and ***S. fusca***. Photo by Bob Klips, with permission.

Figure 87. ***Thuidium delicatulum***, one of the more common moss substrata for the slime molds ***Fuligo septica***, ***Stemonitis axifera***, and ***S. fusca***. Photo by Janice Glime.


Figure 88. ***Hypnum imponens***, one of the more common moss substrata for the slime molds ***Fuligo septica***, ***Stemonitis axifera***, and ***S. fusca***. Photo by Jason Hollinger, through Creative Commons.

Most of the slime molds examined by Stephenson and Studlar (1985) occurred only one or two times among the 170 bryophyte collections that had slime molds, suggesting that there is little specificity involved. They suggest that three cases warrant further examination: ***Stemonitis axifera*** (Figure 34) with ***Thuidium delicatulum*** (Figure 87), ***Barbeyella minutissima*** (Figure 89) with ***Nowellia curvifolia*** (Figure 85) and ***Lepidozia reptans*** (Figure 90), and ***Lepidoderma tigrinum*** (Figure 91) with ***Nowellia curvifolia***. Certainly ***S. axifera*** (Figure 34) is not specific for bryophytes; 78% of those examined were from decorticated areas of logs. Likewise, the second and third most common species were more commonly collected from other substrata. ***Barbeyella minutissima*** was only associated with liverworts, but it is so small that it was not seen in the field. Therefore, it was found only on liverwort samples that were examined in the lab. In the Stephenson and Studlar study, **smooth mats** support more slime molds than other life forms. And slime molds that live on rotten wood seem to be the most common bryophyte associates.


Figure 89. ***Barbeyella minutissima*** on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, with permission.

Figure 90. The liverwort ***Lepidozia reptans***. Photo by Michael Lüth, with permission.

Figure 91. ***Lepidoderma tigrinum*** immature on moss with slug. Photo by Marianne Meyer, through Creative Commons.

But other studies suggest there really are some bryophyte-specific slime molds. ***Fuligo muscorum*** (Figure 39), named for a mossy habitat, is common on ***Polytrichum*** (Figure 92), ***Dicranum*** (Figure 93), and ***Hypnum*** (Figure 88) species (Ing 1994). ***Elaeomyxa cerifera*** (Figure 94), although very rare, is known only from terrestrial bryophytes, including the liverwort ***Pellia epiphylla*** (Figure 95) (Hadden 1921).

Figure 92. ***Polytrichum juniperinum***; the slime mold ***Fuligo muscorum*** is common on the genus ***Polytrichum***. Photo by Bob Klips, with permission.

Figure 93. ***Dicranum scoparium***; the slime mold ***Fuligo muscorum*** is common on the genus ***Dicranum***. Photo by Janice Glime.

Figure 94. ***Elaeomyxa cerifera*** fruiting bodies on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 95. ***Pellia epiphylla*** is a suitable substrate for ***Elaeomyxa cerifera***, a species only known from bryophytes. Photo by Bernd Haynold, through Creative Commons.

If bryophytes are indeed a preferred substrate for some species, the next question is why. Stephenson and Studlar (1985) suggest that bryophytes serve as spore traps, increasing the chances of the trapped species becoming residents here. The bryophytes then provide a moist habitat, again favoring growth of slime molds. These same conditions provide a habitat for numerous protozoa and bacteria, providing food for the slime molds, and even the detritus produced by tardigrades, annelids, and arthropods can serve as food sources (Gerson 1969, 1982; Richardson 1981).

In a single study, Bovee (1979) reported 68 species of protozoa (particularly shelled amoebae and ciliates) among mosses, mostly the mosses ***Brachythecium salebrosum*** (Figure 96), ***Plagiomnium cuspidatum*** (Figure 97), and ***Pylaisiella selwynii*** (Figure 98) on a rotten log in Minnesota. Many of these protozoa provide suitable food for the slime molds in their mobile phase.

Figure 96. ***Brachythecium salebrosum***, home of many protozoa. Photo by Michael Lüth, with permission.

Figure 97. ***Plagiomnium cuspidatum***, home of many protozoa. Photo by Janice Glime.

Bryophytes may provide a preferred location for forming sporangia. Slime molds migrate to the highest position available before making sporangia (Stephenson & Studlar 1985), and bryophytes on a log could very well be that place.

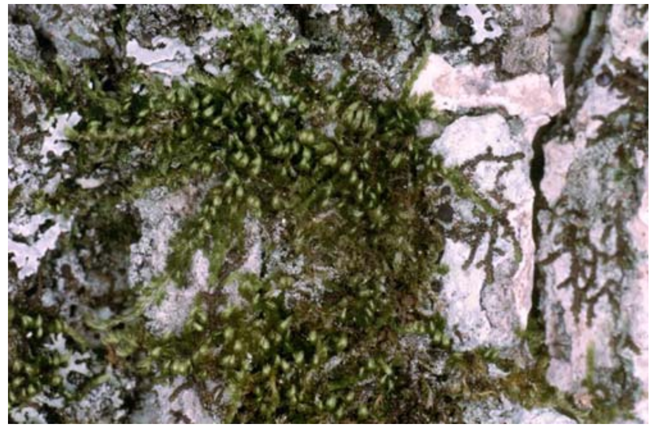

Figure 98. ***Pylaisia selwynii***, home of many protozoa. Photo by Jan-Peter Frahm, with permission.

In any case, the slime molds, like the tardigrades, rotifers, and protozoa, seem to be well-adapted to the **poikilohydric** (having no mechanism to prevent desiccation) existence of living among bryophytes (Gerson 1982). When the bryophyte and the slime mold dry out, the myxamoebae and swarm cells of the slime mold can form **microcysts**; plasmodia (Figure 22) are able to form **sclerotia** (Figure 23, Figure 24). These structures are all resistant and survive well under desiccating conditions. They can quickly resume activity when water becomes available. The tolerance of slime molds to alternate wetting and drying that typically accompanies the bryophytes provides us with another reason to suspect that they can live within, as well as sporulate upon, bryophyte clumps.

But not all slime molds benefit from the moist environment of the bryophytes. The genus ***Echinostelium*** (Figure 99-Figure 100) is comprised of tiny slime molds that live on bark (Keller & Brooks 1976). But in areas that support the growth of algae, mosses, and leafy liverworts, larger aphano- and phaneroplasmodial slime molds are favored. Keller and Brooks surmised that the tiny protoplasmodial ***Echinostelium*** species were unable to compete.

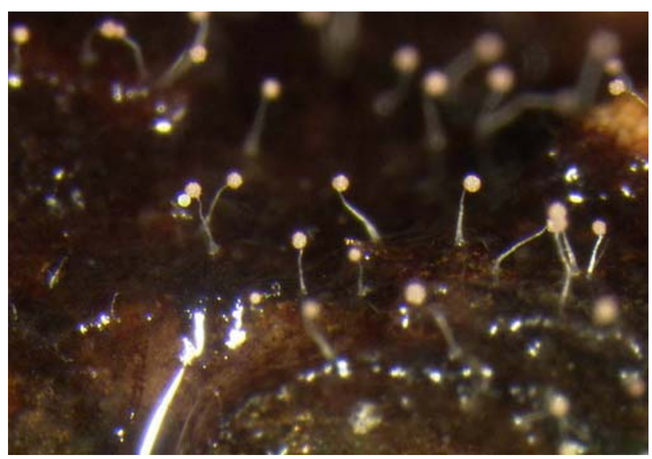

Figure 99. ***Echinostelium minutum***, a tiny species that is probably unable to compete. Photo by Satyendra Rajguru, The Eumycetozoan Project, DiscoverLife.org, with online permission.

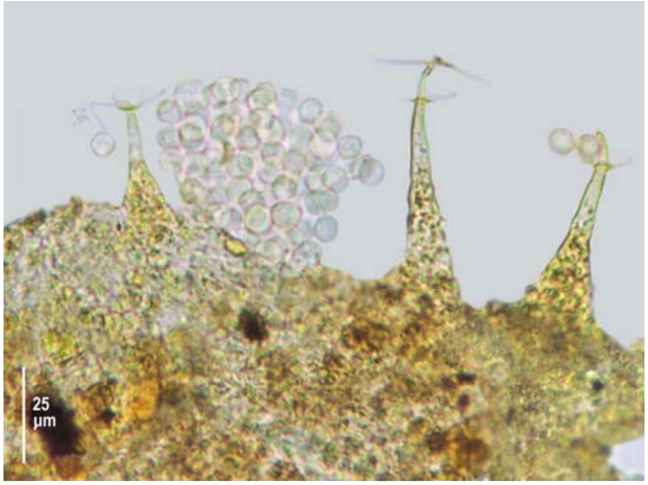


Figure 100. ***Echinostelium arboreum*** showing stalks left when spores are dispersed. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

## Slime Mold Effects on Bryophytes

A takeover by slime molds on mosses is apparently a rare occurrence (Coker 1966). Nevertheless, at least one example exists. Coker reported that the slime mold ***Cribraria rufa*** (Figure 101) had apparently destroyed a patch of the moss ***Orthodontium lineare*** (Figure 102-Figure 103) on a rotten conifer stump.

Figure 101. ***Cribraria rufa*** fruiting, a species that apparently can destroy the moss ***Orthodontium lineare***. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 102. ***Orthodontium lineare*** on rotting log, a moss that can be destroyed by the slime mold ***Cribraria rufa***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 103. ***Orthodontium lineare*** with capsules, a moss that can be destroyed by the slime mold ***Cribraria rufa***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Almost 100 compounds have been identified from the slime molds (Dembitsky *et al*. 2005). These include lipids, fatty acid amides (pigments) and derivatives, alkaloids, amino acids and peptides, naphthoquinone pigments, aromatic compounds, carbohydrate compounds, terpenoid compounds, and arcyriaflavin derivatives (alkaloids). Some of these give the slime molds their unique colors. But some have antimicrobial activity against bacteria like ***Bacillus cereus*** (Figure 104) (Pereira *et al*. 1996). These compounds might permit them to compete with other slime molds, but do they have any effect on the bryophytes?

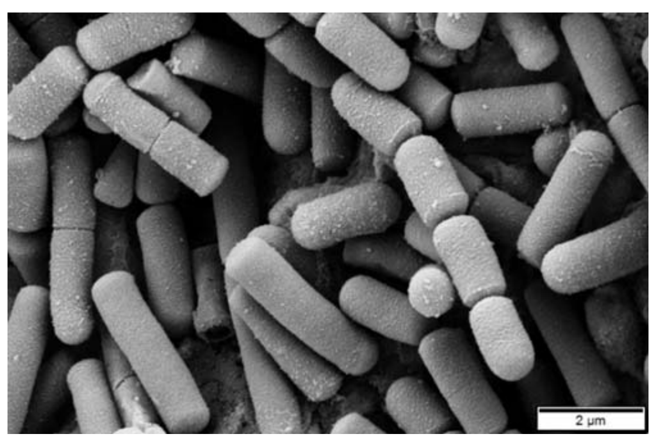


Figure 104. ***Bacillus cereus*** SEM, a species that is inhibited by some of the secondary compounds produced by slime molds. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

Slime molds do not usually appear to be any threat to the bryophytes. However, in some cases, it appears that the slime molds are aggressive enough to overgrow and destroy the bryophytes (Coker 1966). ***Fuligo intermedia*** (Figure 105) seems to be harmful (Pant & Tewari 1982), most likely due to its density of fruiting bodies that can cover patches several centimeters in diameter. Such growths would deprive the moss of light and may interfere with gas exchange.

Figure 105. ***Fuligo intermedia*** fruiting bodies on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

## Bryophytes Growing on Slime Molds

In some species, the fruiting bodies of slime molds can persist. That can lead to a reverse relationship with bryophytes. It gives the bryophytes sufficient time to grow over the slime molds, as observed by Sarah Lloyd (2011). She found a growth of leafy liverworts on the stalk of a slime mold on decaying wood, undoubtedly a very rare occurrence.

## Epizooites

One of the most unusual habitats for slime molds is on living lizards, ***Corytophanes cristatus*** (Figure 106), in Mexico and Costa Rica (Lloyd 2011). This lizard is a sit-and-wait predator and therefore moves around little. It uses its head to dig its nest and often has residual soil in the scoop on the top of its head. This microenvironment is home to the tiny liverwort ***Lejeunea obtusangula*** (see Figure 107) (Gradstein & Equihua 1995). But this lizard is also sometimes home to the slime mold ***Physarum pusillum*** (Figure 108). The co-occurrence of the liverwort and the slime mold, if at all, is most likely one of chance resulting from the scooping behavior of the lizard.

Figure 106. ***Corytophanes cristatus***, the crested lizard that sometimes has the slime mold ***Physarum pusillum*** or the leafy liverwort ***Lejeunea obtusangula*** growing on it. Photo by Simon J. Tonge, through Creative Commons.

Figure 107. ***Lejeunea*** sp. from the Neotropics; ***L. obtusangula*** sometimes occurs on the lizard ***Corytophanes cristatus***. Photo by Michael Lüth, with permission.

Figure 108. ***Physarum pusillum*** fruiting bodies, a species known to live on the lizard ***Corytophanes cristatus***. Photo by Gustavo F. Morejón J., through Creative Commons.

## Potential for Symbiosis?

In sharp contrast to the casual and accidental associations of most slime molds with their substrates and neighbors, some relationships might be more directly beneficial. In pure cultures of the slime mold ***Fuligo cinerea*** (Figure 109; sometimes a bryophyte dweller) (and the green alga ***Chlorella xanthella*** – Figure 110), sodium radiophosphate accumulated in them both from the medium. When these were separately mixed with the opposite species, both species were able to accumulate the radiophosphorus from the other species cultured with it. While this suggests the potential for a symbiosis, it fails to demonstrate any dependency or benefit. Nevertheless, a **protocooperation** could exist with nutrients, moisture, or other conditions that enhance the environment created by a bryophyte and a slime mold living together. Adding algae or **Cyanobacteria** to the mix might make it even better.

Figure 109. ***Fuligo cinerea*** on lichens and leafy liverworts, a slime mold that is able to exchange substances with the alga ***Chlorella xanthella***. Photo by Alexey Sergeev, with permission.


Figure 110. ***Chlorella*** sp.; ***C. xanthella*** is able to exchange substances with the slime mold ***Fuligo cinerea***. Photo by Barry H. Rosen, through Creative Commons.

## Interactions with Invertebrates

Both bryophytes and slime molds often host a variety of invertebrates. Among the inhabitants of slime molds, nematodes can be numerous, as they are among some bryophytes. In ***Dictyostelium discoideum*** (Figure 12; **Dictyosteliomycetes**), the aggregate of slime mold cells protects the formation from nematode predation, whereas nematodes readily feed on the individual cells (Kessin *et al*. 1996). Nematodes are also known from the **Myxomycetes** slime molds ***Trichia varia*** (Figure 13-Figure 17) and ***Stemonitopsis typhina*** (Figure 111; both can occur on bryophytes) on rotten wood (Ing 1967).

Figure 111. ***Stemonitopsis typhina*** sporangia, a species where nematodes can thrive. Photo from George Barron, with online permission.

Snails (Figure 112) and slugs (Figure 113) also can feed on slime molds, and these slime molds may be moss inhabitants. Snails and other invertebrates feed on the fruiting bodies of ***Lycogala epidendrum*** (Figure 46) (Eliasson 1980; Pant & Tewari 1982).

Some tardigrades (water bears) feed selectively on slime molds (Kylin 1991). Since tardigrades are common on bryophytes, it is likely that this three-way association occurs, with bryophytes providing the substrate for the slime molds and the slime molds providing food for the tardigrades. ***Milnesium tardigradum*** (Figure 114), used in the experiments, is a moss inhabitant (see Chapter 5 in this volume). Kylin demonstrated that it not only will consume some slime molds and spurn others, those consumed can be moss inhabitants. These include the **Myxomycetes** ***Diderma*** cf. ***testaceum*** (Figure 115; an inhabitant of species of mosses, leaves, and twigs), ***Trichia botrytis*** (Figure 40-Figure 42), and ***Clastoderma debaryanum*** (Figure 116-Figure 117). The response of ***D.*** cf. ***testaceum*** is interesting. The tardigrade typically attacks the vein where protoplasm is streaming. The slime mold responds by streaming away from the bite. The tardigrade seldom takes a second bite, causing little damage to the slime mold. But when the slime mold begins forming sporangia, the tardigrade once again attacks, burrowing into the developing sporangium. This causes the sporangial development to cease. Occasionally the sporangium will collapse onto the tardigrade, trapping it. ***Trichia botrytis*** elicits similar responses when the plasmodium (Figure 22)

is attacked, usually feeding for about 12 hours, but has a sporangium that is too small for the tardigrade to burrow into it. ***Clastoderma debaryanum*** is a much smaller slime mold and the tardigrade usually consumes the entire plasmodium.

Figure 112. Fruiting bodies of ***Arcyria stipata*** with one of its enemies – a snail. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 113. Slug and the slime mold ***Lamproderma*** on mosses. Photo by Keller, through Creative Commons.

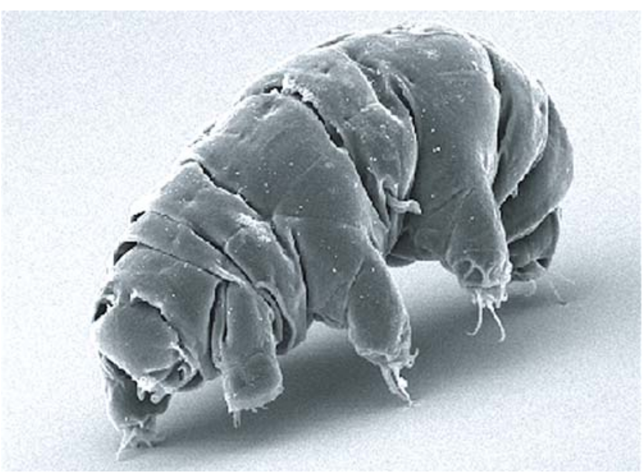

Figure 114. ***Milnesium tardigradum*** SEM, a species that feeds on the moss-inhabiting slime molds ***Diderma*** cf. ***testaceum***, ***Trichia botrytis***, and ***Clastoderma debaryanum***. Photo from Schokraie *et al.* 2012, through Creative Commons.

Figure 115. ***Diderma testaceum*** fruiting structures, with lichens, a slime mold that serves as food for the tardigrade ***Milnesium tardigradum***. Masse (1892) indicated that this species grows on leaves, mosses, and twigs. Photo by James K. Lindsey, through Creative Commons.

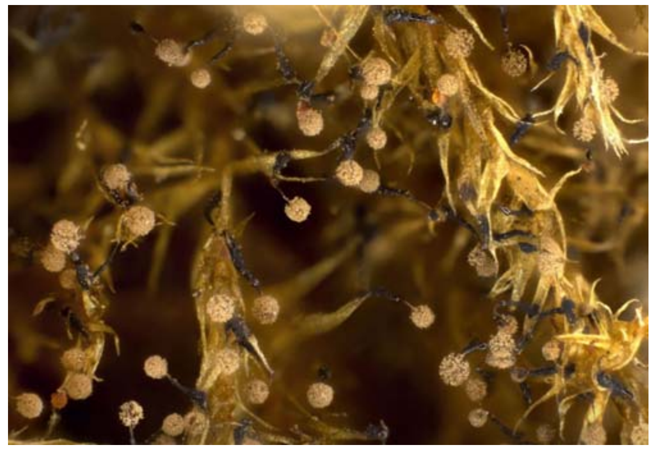

Figure 116. ***Clastoderma debaryanum*** on moss, a slime mold that serves as food for the tardigrade ***Milnesium tardigradum***. Photo from Myxotropic, through Creative Commons.

Figure 117. ***Clastoderma debaryanum*** fruiting body on moss, a slime mold that serves as food for the tardigrade ***Milnesium tardigradum***. Photo from Myxotropic, through Creative Commons.

Isopods are common inhabitants on bryophytes and will readily consume them (Hames & Hopkin 1989). They likewise can occur on slime molds (Ing 1967). They eat both plasmodia (Figure 22) and fruiting bodies of the **Myxomycetes** slime molds. The isopods ***Trichoniscus pusillus*** (Figure 118) and ***Oniscus asellus*** (Figure 119) feed on the slime molds ***Trichia varia*** (Figure 13-Figure 17) and ***Arcyria denudata*** (Figure 120). The isopod ***Androniscus dentiger*** (Figure 121) eats both plasmodia and sporangia of ***Didymium iridis*** (Figure 122), at the same time dispersing this species across the substrate. Spores have been found in the isopod digestive tracts undigested. All of these three slime molds are known from bryophytes.

Figure 118. ***Trichoniscus pusillus***, an isopod that feeds on the slime molds ***Trichia varia*** and ***Arcyria denudata***. Photo by Malcolm Storey, EOL, through Creative Commons.

Figure 119. ***Oniscus asellus*** with moss on log, an isopod that feeds on the slime molds ***Trichia varia*** and ***Arcyria denudata***. Photo by Kurt Kulac, through Creative Commons.

Figure 120. ***Arcyria denudata*** fruiting bodies. Photo by Kim Fleming, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 121. ***Androniscus dentiger***, an isopod that feeds on the slime mold ***Didymium iridis***. Photo by Gilles San Martin, through Creative Commons.

Figure 122. ***Didymium iridis*** sporangia, food for the isopod ***Androniscus dentiger***. Photo by through Creative Commons.

Millipedes are likely known from both bryophytes and slime molds. The millipede ***Cylindroiulus punctatus*** (Figure 123) consumes the sporangia of the slime mold ***Trichia varia*** (Figure 13-Figure 17) on wet, rotten wood (Ing 1967).

Figure 123. ***Cylindroiulus punctatus***, a millipede that feeds on the slime mold ***Trichia varia***. Photo by Saxifraga-Ab H Baas, through Creative Commons.

**Collembola** (springtails; Figure 124) are avid consumers of small slime molds on bark (Ing 1967). Some of these springtails eat ***Stemonitopsis typhina*** (Figure 111; sometimes a bryophyte dweller) and ***Cribraria piriformis*** (Figure 125-Figure 126) on rotten wood. Both ***Stemonitopsis typhina*** and ***Cribraria piriformis*** can occur on or with bryophytes, making it likely that a 3-way association sometimes occurs among the bryophytes, slime molds, and springtails.

Figure 124. ***Isotoma caerulea*** on moss and a potential consumer of slime molds. Photo by Andy Murray, through Creative Commons.

Figure 125. ***Cribraria piriformis*** sporangia with contained spores, food for springtails. Photo from Myxotropic, through Creative Commons.

Figure 126. ***Cribraria piriformis*** sporangia with spores gone, perhaps being eaten by springtails. Photo by Myxotropic, through Creative Commons.

Insects are common on both bryophytes and slime molds. Some **Coleoptera** (beetles) may be occasional or accidental feeders on **Myxomycetes** (Ing 1967). Among these, the beetle ***Anisotoma humeralis*** (Figure 127) seems to be confined to large slime molds such as ***Fuligo septica*** (Figure 33), ***Reticularia lycoperdon*** (Figure 128-Figure 129), ***Stemonitis fusca*** (Figure 35-Figure 36), ***Symphytocarpus flaccidus*** (Figure 29-Figure 30), and ***Tubifera ferruginosa*** (Figure 55); all of these slime molds can sometimes be found associated with bryophytes. The spores are held in the capillitium and are relatively accessible (Figure 130).

Figure 127. ***Anisotoma humeralis***, a beetle that feeds on slime molds that are known to inhabit mosses. Photo by Boris Loboda, through Creative Commons.

Figure 128. Pink ***Reticularia lycoperdon*** on mossy log. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 129. White ***Reticularia lycoperdon*** on mossy bark. Photo by Marion Zãller, through Creative Commons.

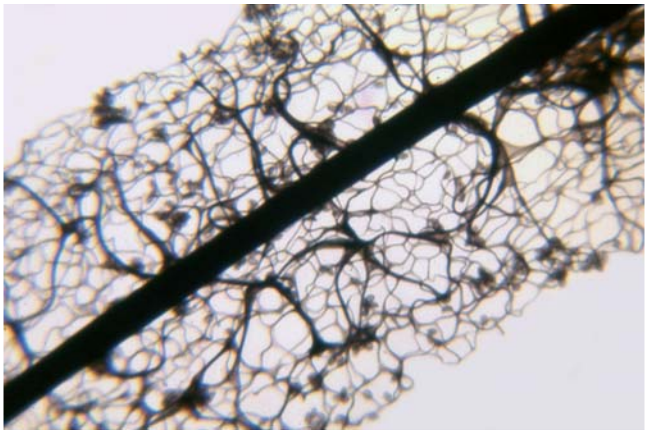

Figure 130. Capillitium of sporangium of ***Stemonitis***. Photo by Janice Glime.

Some beetles even seem to be obligate feeders on slime molds (Dudka & Romanenko 2006). Lawrence and Newton (1980) reported on about 35 beetle species, mostly from North American, that feed on slime mold spores. Dudka and Romanenko (2006) found that slime mold spores occurred in 19 of the 25 beetle (**Latridiidae**) guts they examined from Crimea. These included ***Latridius hirtus*** (Figure 131), ***Enicmus rugosus*** (Figure 132), and ***E. fungicola*** (Figure 133) as obligate slime mold feeders. On the other hand ***Corticarina truncatella*** (Figure 134) is a facultative slime mold feeder. The most common 13 species of slime molds, including ***Fuligo septica*** (Figure 33), ***Mucilago crustacea*** (Figure 135), ***Stemonitis axifera*** (Figure 34), ***S. fusca*** (Figure 35), and ***S. splendens*** (Figure 136), were inhabited by five species of **Latridiidae**; all of these slime molds can occur on bryophytes.

Figure 131. ***Latridius hirtus*** adult, a beetle that feeds on slime mold spores. Photo by Stefan Schmidt, through Creative Commons.

Figure 132. ***Enicmus rugosus*** adult, a beetle that feeds on slime mold spores. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 133. ***Enicmus fungicola*** adult, a beetle that feeds on slime mold spores. Photo by Tim Faasen, with permission.

Figure 134. ***Corticarina truncatella*** adult, a beetle that facultatively feeds on slime mold spores. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 135. ***Mucilago crustacea*** on mosses. Photo by Drew Henderson, through Creative Commons.

Figure 136. ***Stemonitis splendens***, one of the slime molds eaten by the beetle family **Latridiidae**. Photo by Dan Molter, through Creative Commons.

Some **Coleoptera** (beetles) in the **Leiodidae** can be considered slime mold beetles (Wheeler & Miller 2005). ***Stetholiodes*** sp. (Figure 137) is a slime mold beetle that was originally described from moss in northern Indiana (Blatchley 1910). Several species of ***Agathidium*** (Figure 138) are known moss inhabitants, including ***A. brevisternum***, ***A. rhinocerellum***, and ***A. cavisternum*** (Figure 139) (Wheeler & Miller 2005). The only known host for ***Agathidium rhinocerellum*** is the **Myxomycetes** slime mold ***Fuligo septica*** (Figure 33, Figure 140), a widespread generalist species that includes bryophytes among its substrates. It is likely that other moss dwellers in this family also feed on slime molds.

Figure 137. ***Stetholiodes laticollis*** adult; some members of this genus are slime mold beetles that live on mosses. Photo by Museum of Comparative Zoology, Harvard University, through Creative Commons.

Figure 138. ***Agathidium*** sp. adult; some members of this genus are both moss and slime mold inhabitants. Photo by Joyce Gross, with permission.


Figure 139. ***Agathidium cavisternum***, a moss dweller and possible slime mold feeder. Photo from Museum of Comparative Zoology, Harvard University, through Creative Commons.

Figure 140. ***Fuligo septica*** on moss, a slime mold that is host for the beetle ***Agathidium rhinocerellum***. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Some **Diptera** larvae live on the slime mold plasmodia (Figure 22) and feed on them, with some remaining there as pupae. ***Bradysia*** (Figure 141) species feed on plasmodia of ***Fuligo septica*** (Figure 33) and sporangia of ***Lycogala epidendrum*** (Figure 46) and ***Arcyria incarnata*** (Figure 142-Figure 143), all occasional bryophyte dwellers. In fact, some flies can be reared on slime molds as their only food.

Figure 141. ***Bradysia*** larvae, a species that feeds on slime mold plasmodia of ***Fuligo septica*** and sporangia of ***Lycogala epidendrum*** and ***Arcyria incarnata***. Photo by David Cappaert, through Creative Commons.

Figure 142. ***Arcyria incarnata*** fruiting bodies, food for ***Bradysia***. Photo by Stu's Images, through Creative Commons.

Figure 143. ***Arcyria incarnata*** fruiting bodies on mosses, food for ***Bradysia***. Photo by Dan Molter, through Creative Commons.

## Summary

Slime molds are really not molds, but protozoa, with an amoeboid feeding stage and a spore-producing, non-feeding stage. They also lack chitin, a compound found in true molds. The bryophyte dwelling members are included in the **Eumycetozoa** or **Amoebozoa** and classified into the classes **Myxomycetes**, **Dictyosteliomycetes**, and **Ceratiomyxomycetes**.

The life cycle has a dormant spore that will germinate when adequate water is available and develop into **swarm cells** or **amoeboid cells**. This stage feeds like an amoeba. In **Myxomycetes**, either of these cell types can form a zygote that divides to form a **plasmodium**. This stage likewise feeds on bacteria, algae, and protozoa. It can dry out to form a **sclerotium** that can remain dormant for years, or move to higher ground in the light to form sporangia and spores. Either stage can occur on bryophytes, but the plasmodium stage is likely to be unnoticed. The life cycle is usually keyed to seasons, with autumn being the more favorable fruiting season for most species. Dispersal is most likely primarily by wind, but animals are also dispersal vectors, either by carrying spores on the outside or by digesting them or plasmodia and dispersing them in the feces.

The slime molds respond to light, *p*H, volatile substances, temperature, and water availability to trigger fruiting. We know most slime molds seek higher positions with more light before forming sporangia. Do bryophytes provide a more suitable location for that event? Do slime molds benefit in their dispersal by the activities of moss fauna?

The slime molds known to associate with mosses are predominantly in the **Myxomycetes**. The mosses may provide prolonged moisture and a place to get above the prevailing substrate for better dispersal, or they may be dispersed by some of the invertebrates living among the bryophytes. Little is known about the effect the slime molds have on the bryophytes. Some slime molds live on animals, and these may be the same animals that have bryophytes growing on them. The potential for symbiosis exists, but little evidence supports any symbiotic relationship.

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# CHAPTER 3-2
# SLIME MOLDS: BRYOPHYTE ASSOCIATIONS

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# CHAPTER 3-2 SLIME MOLDS: BRYOPHYTE ASSOCIATIONS

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.

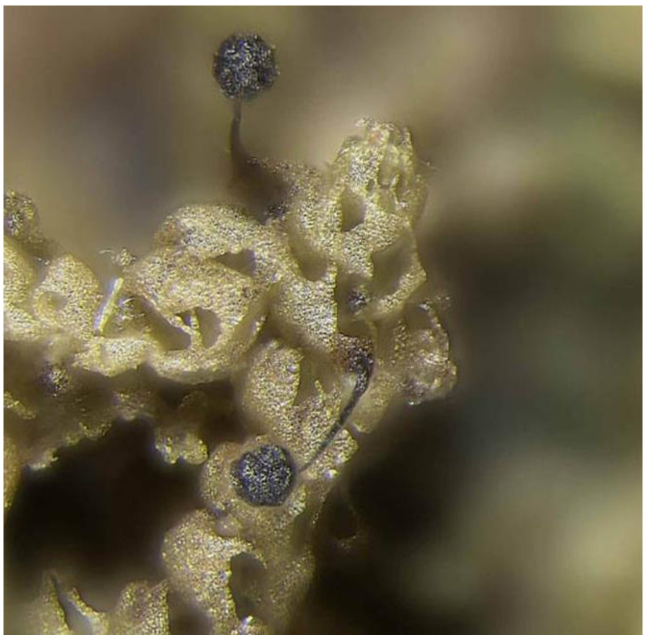

Figure 3. Fruiting bodies of ***Barbeyella minutissima*** on a leafy liverwort. Photo by Steve Stephenson, The Eumycetozoan Project, DiscoverLife.org, with online permission.

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.

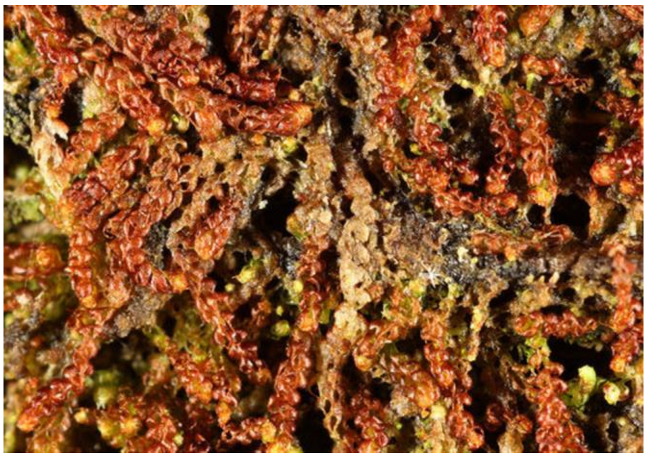

Figure 8. ***Nowellia curvifolia***, a leafy liverwort substrate for the slime mold ***Barbeyella minutissima***. Photo from Bioimages, through Creative Commons.

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.

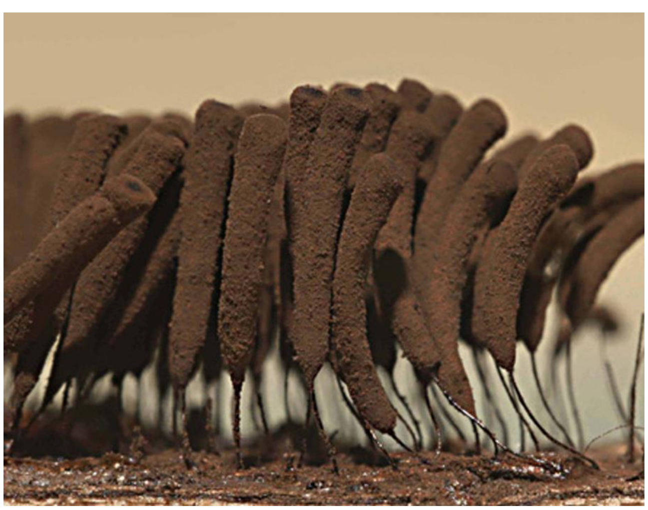

Figure 14. ***Stemonitis fusca*** with mature sporangia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

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.

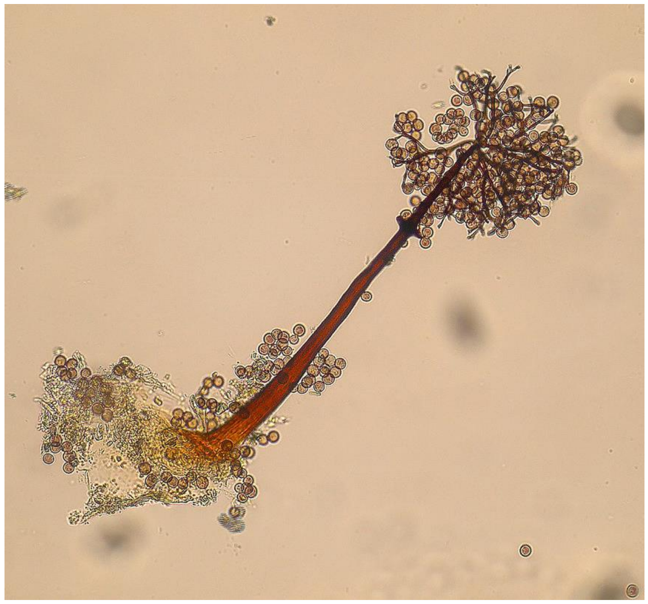

Figure 20. ***Macbrideola cornea***, a species frequently associated with bryophytes. Photo by Shirokikh, through Creative Commons.

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.

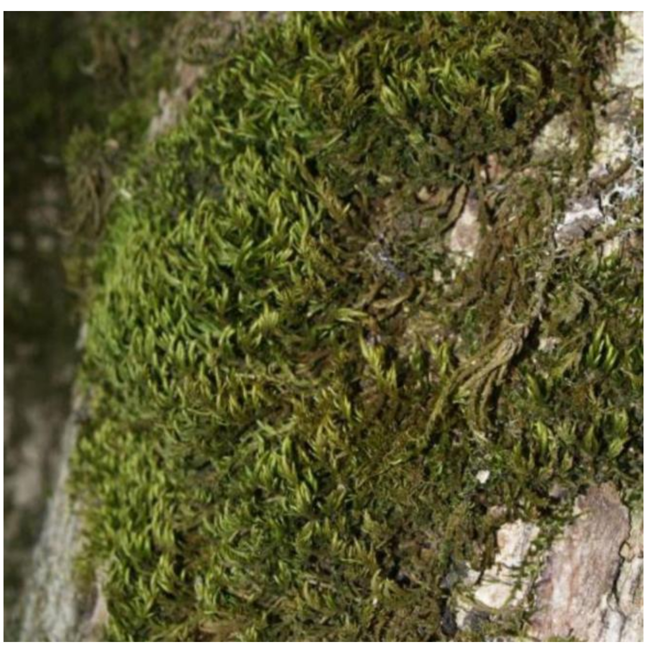

Figure 25. ***Leucodon sciuroides*** dry, a moss that often provides the substrate for a number of slime mold species. Photo by Kai Vellak, through Creative Commons.

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.

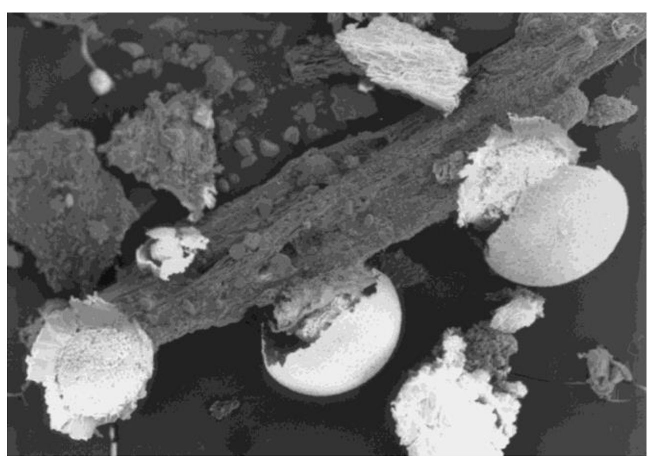

Figure 27. ***Didymium trachysporum***, a species known from the moss ***Ctenidium molluscum***. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

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.

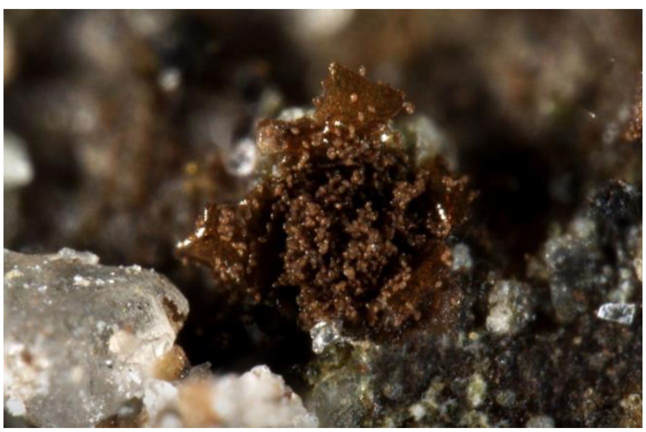

Figure 30. ***Licea minima*** fruiting body showing spores. Photo from Myxotropic, through Creative Commons.

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.

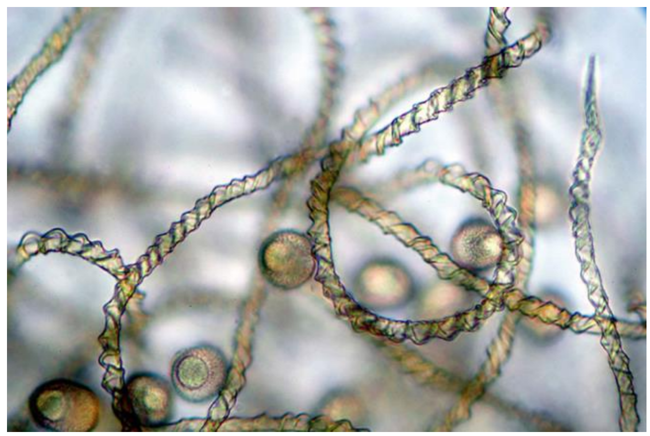

Figure 39. ***Trichia varia*** capillitia and spores. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

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.

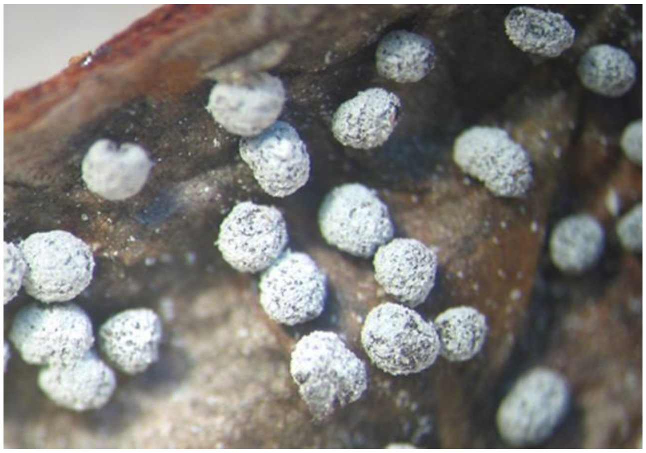

Figure 47. ***Didymium melanospermum*** fruiting bodies. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

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.

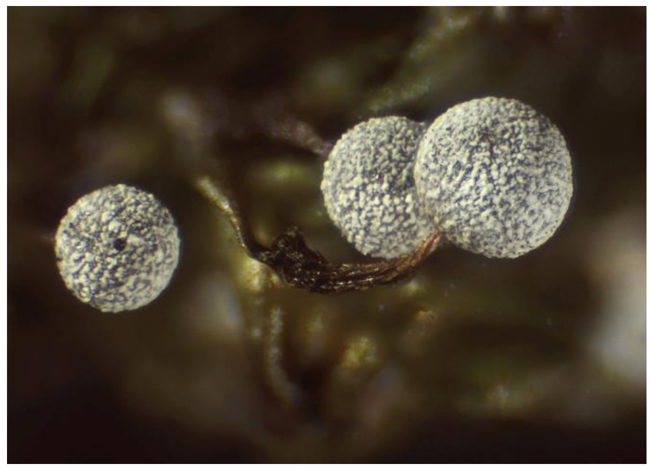

Figure 51. ***Physarum pusillum*** sporangium on mosses. Photo by TAO92, through Creative Commons.

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.

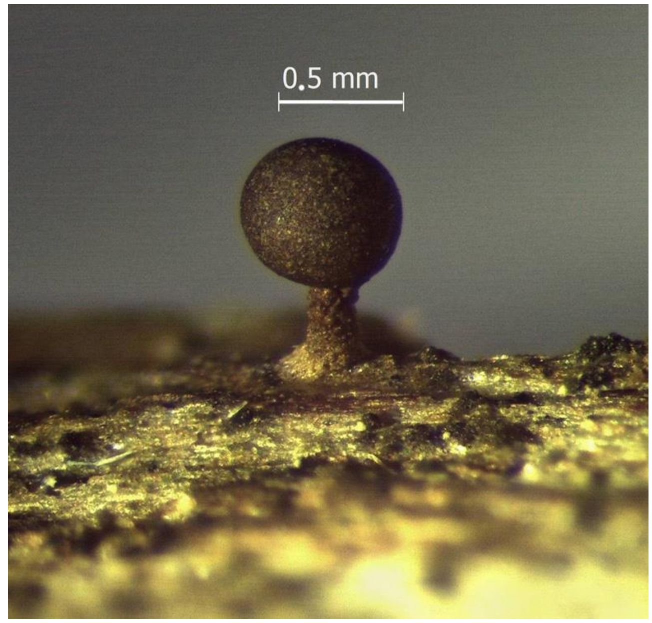


Figure 71. ***Trichia subfusca*** sporangium, a slime mold known to grow on mosses. Photo from Flora of Russia, Moscow State University, through Creative Commons.

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.

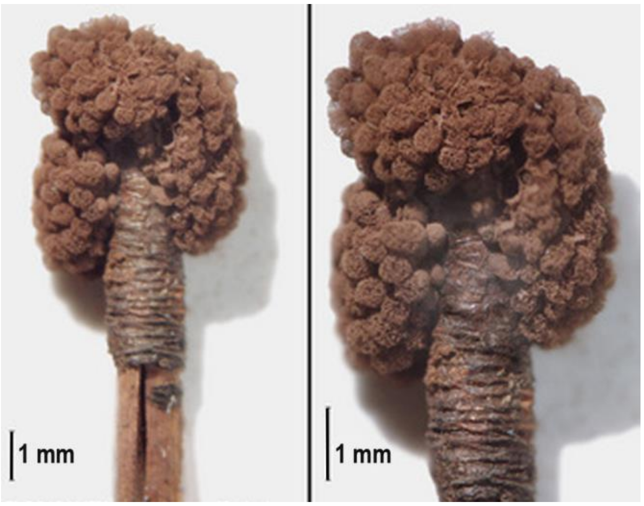


Figure 86. ***Paradiachea rispaudii***, possibly an obligate moss dweller. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

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.

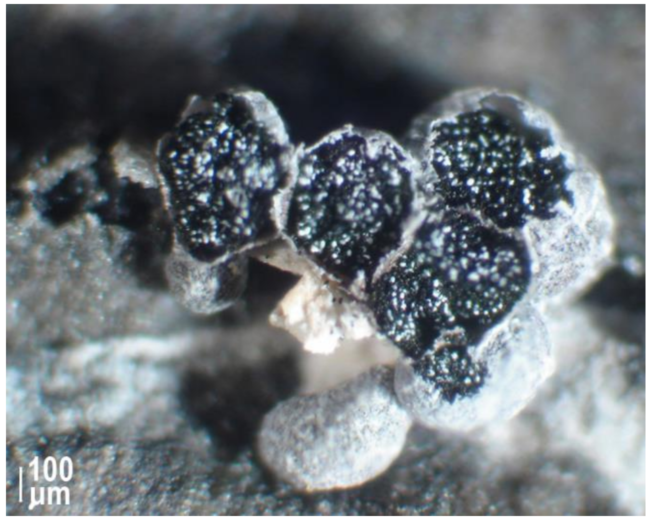


Figure 94. ***Physarum didermoides*** fruiting bodies, a slime mold sometimes associated with mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

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.

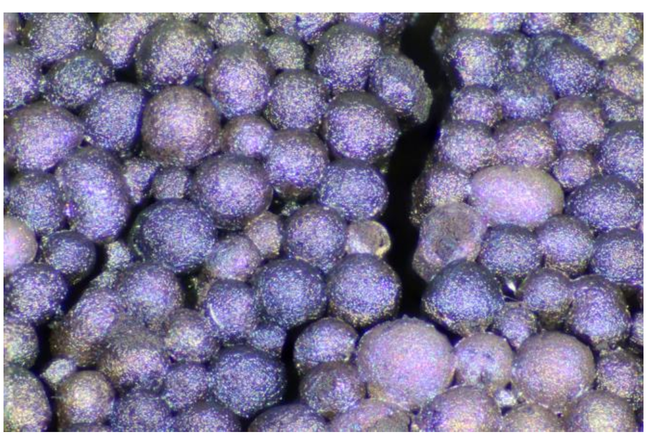

Figure 110. ***Paradiachea caespitosa*** sporangia 26 January. Photo by Sarah Lloyd, with permission

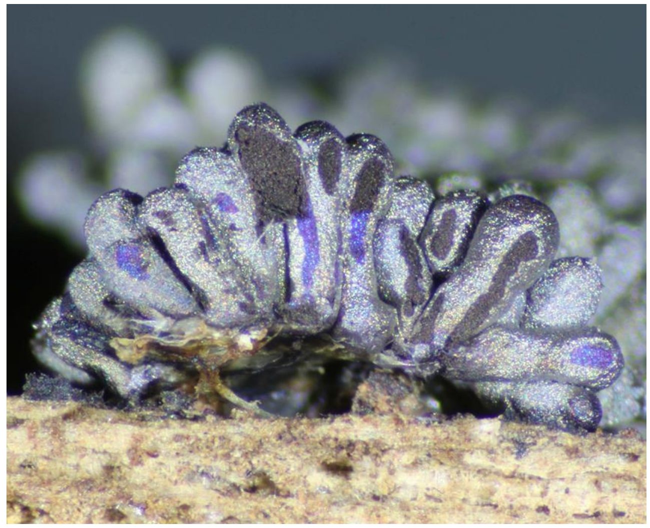

Figure 111. ***Paradiachea caespitosa*** sporangia. Photo by Sarah Lloyd, with permission.

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.

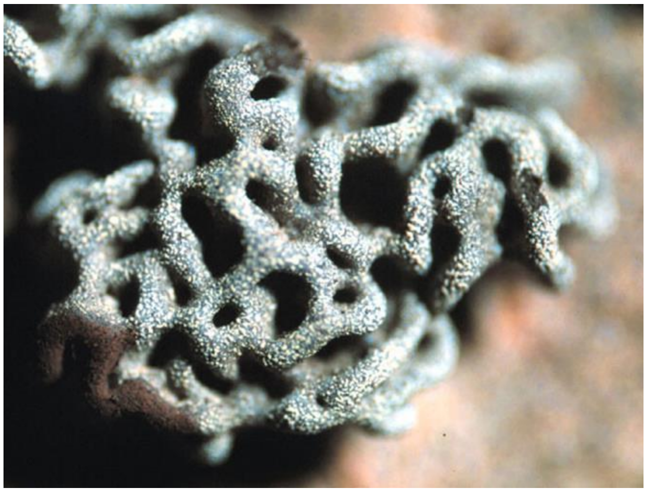

Figure 120. ***Physarum gyrosum***, a slime mold that sometimes occurs on bryophytes. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

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.

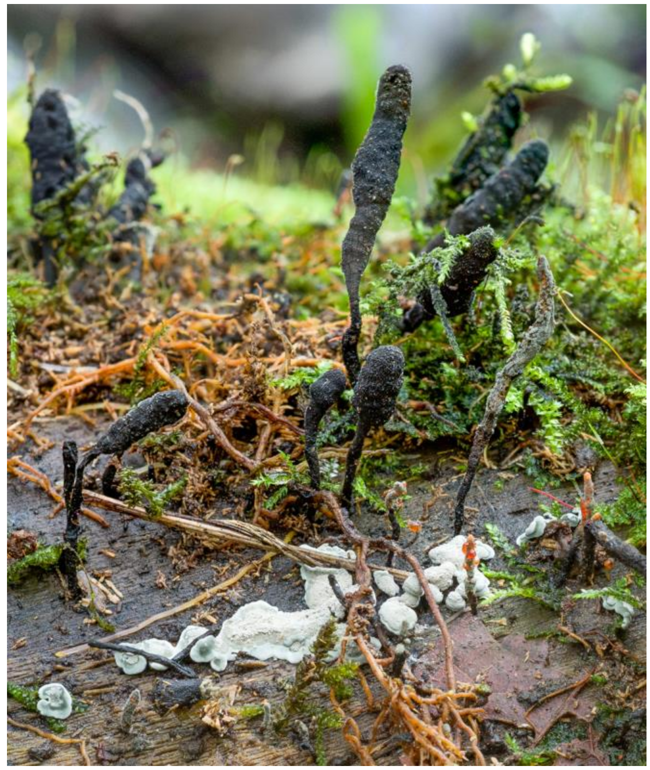

Figure 151. ***Diderma globosum*** fruiting on mosses. Photo from Mushroom Observer.org, through Creative Commons.

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.

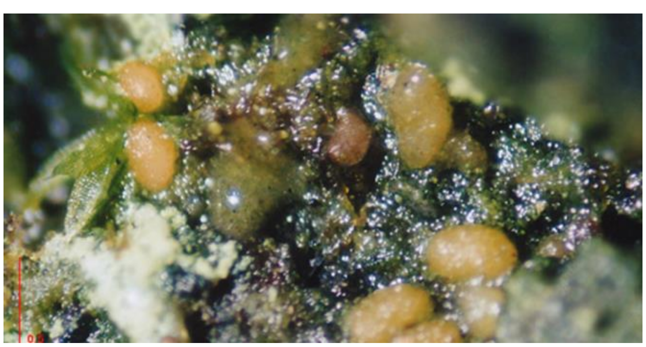

Figure 157. ***Licea sambucina*** on mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.


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.

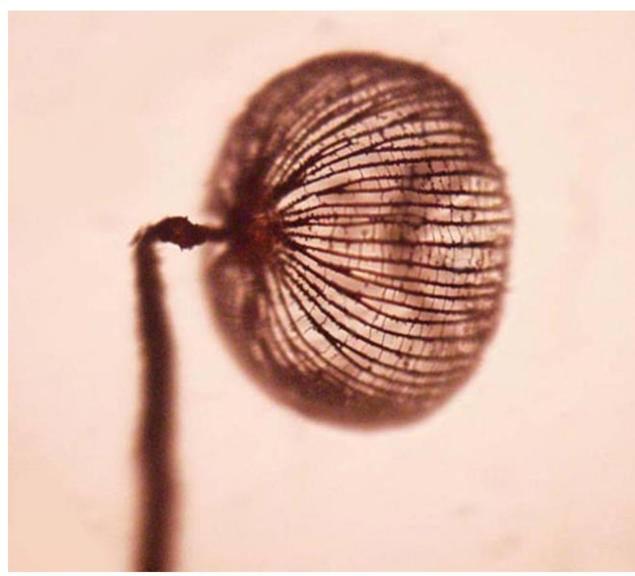

Figure 175. ***Cribraria cancellata*** fruiting body showing threadlike capillitium. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

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.

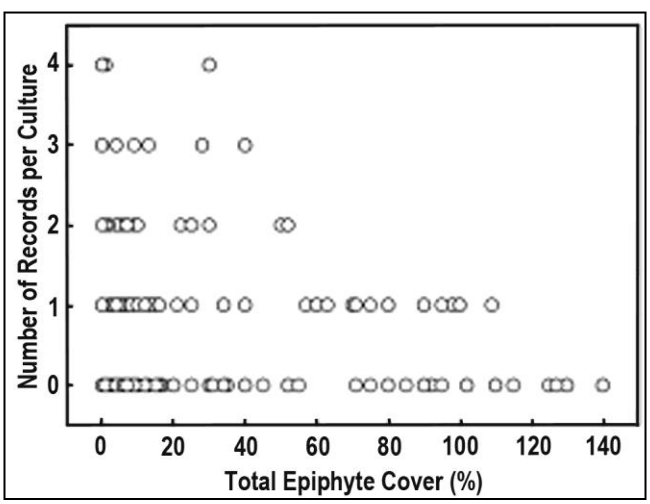


Figure 177. Myxomycete species richness vs epiphyte (including bryophyte) cover. Modified from Schnittler & Stephenson 2000.

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

Thank you to Sarah Lloyd for early inspiration in writing this chapter and for her generous help with images and knowledge. The Eumycetozoan Project has been invaluable in providing images.

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# CHAPTER 3-3
# SLIME MOLDS: ECOLOGY AND HABITATS – BARK AND LOGS

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# CHAPTER 3-3
# SLIME MOLDS: ECOLOGY AND HABITATS – BARK AND LOGS

Figure 1. ***Fuligo*** *cf.* ***septica*** growing on bryophytes on a log. Photo by Janice Glime.

## Habitats

It is well known that many slime molds have a substrate preference (Eliasson 1980), including dead wood, bark, twigs, dead leaves, and dung (Stephenson *et al*. 2000). But are there truly species that prefer bryophytes? It would appear that some may prefer leaves with bryophyte associations, as described in the ecology subchapter. But there are a number of species that are likely to be found in bryophyte associations, particularly in the high latitudes of the Northern Hemisphere (Kaiser 1913; Gray & Alexopoulos 1968; Farr 1979; Ing 1994; Stephenson *et al*. 2000). Martin and Alexopoulos (1969) reported 49 different species on some sort of mossy substrate.

Rollins and Stephenson (2011) identified five substrate types for slime molds: soil, leaf litter, twigs, bryophytes, and snow. For some reason, they did not list logs as a habitat/substrate, although the paper did discuss slime molds on logs.

Döbbeler & Nannenga-Bremekamp (1979) suggest that some slime molds may indeed be unique to bryophytes, or at least use them as primary substrate. Similarly, Ing (1994), in studying the phytosociology of slime molds, reported that a few species are "particularly associated" with bryophytes. Likewise, several other authors have reported that some (few) bryophytes appear almost invariably in association with bryophytes (Gray & Alexopoulos 1968; Ing 1983, 1994).

However, the majority of slime mold associates most frequently encountered by Stephenson and Studlar (1985) in the USA and Canada include ***Brotherella recurvans*** (Figure 2), ***Thuidium delicatulum*** (Figure 3), ***Hypnum imponens*** (Figure 4), and ***Hypnum curvifolium*** (Figure 5) – species that show a broad ecological amplitude, and characteristically grow not only on rotten wood but also on soil, living trees, and rocks.

Figure 2. ***Brotherella recurvans***, a frequent slime mold substrate in North America. Photo by Bob Klips, with permission.

Figure 3. ***Thuidium delicatulum***, a frequent slime mold substrate in North America. Photo by Hermann Schachner, through Creative Commons.


Figure 4. ***Hypnum imponens***, a frequent log dweller and slime mold substrate in North America. Photo by Jason Hollinger, through Creative Commons.

Figure 5. ***Hypnum curvifolium***, a frequent slime mold substrate in North America. Photo by Bob Klips, through Creative Commons.

Stephenson and Studlar (1985) found that most of the bryophyte species that support the development of slime mold colonies are low-growing. Their life forms include **smooth mat**s (58%) > **short turfs** (19%) > **rough mat**s (13%) > **wefts** (9% ) > **tall turf**s (2%) > **turfs with creeping primary stem** (1%) > **small cushion** (1%). The only species that exceeded 2 cm in height were ***Polytrichum commune*** (Figure 6) and ***Sphagnum recurvum*** (Figure 7) (both **tall turfs**) and ***Pleurozium schreberi*** (Figure 8) (**weft**). Longton (1980) determined that **short turfs** retain more capillary water than do the other life forms, perhaps explaining that these were the second most abundant life form.

Figure 6. ***Polytrichum commune***, one of the few taller moss species used as a substrate by slime molds. Photo by Bob Klips, with permission.

Figure 7. ***Sphagnum recurvum***, one of the few taller moss species used as a substrate by slime molds. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 8. ***Pleurozium schreberi***, one of the few taller moss species used as a substrate by slime molds. Photo by Bob Klips, with permission.

## Bark Associations

Ing (1994) concluded that slime molds are more likely to be found on bryophytes in woodlands having high humidity. This is probably more important on standing tree bark associations than on fallen logs. Bryophytes on the bark can help to retain moisture and to trap airborne spores, thus making it likely that at least some slime molds should be favored by or restricted to mossy areas. This affinity might also differ with the moisture availability in the habitat.

In addition to water-holding capacity of bark, the general shape of the tree, surface texture of the tree bark, (fibrous, furrowed, ridged, scaly, smooth) along with epiphytic cover of algae, mosses, liverworts, and lichens may also influence the presence of corticolous slime molds (Brooks *et al*. 1977).

***Diderma corrugatum*** (Figure 9) is a slime mold that seems to be restricted to moss-covered bark, occurring in the southeastern United States (Brooks *et al*. 1977). It typically occurs in the top part of the canopy on branches and on the upper trunk, in both places where bryophytes form extensive cover. It has a watery white phaneroplasmodium often associated with mosses and liverworts (Brooks *et al*. 1977). Although it can live on several kinds of trees, elms (***Ulmus***; Figure 10) seem to be the more common substrate. Everhart and Keller (2008) suggested that bryophytes may contribute to the necessary moisture for this species.

Figure 9. ***Diderma corrugatum*** sporangia, a species that seems to be restricted to moss-covered bark when it grows in the southeastern USA. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 10. ***Ulmus americana*** bark, a preferred substrate for ***Diderma corrugatum***. Photo by Downtowngal, through Creative Commons.

The closely related ***Diderma rugosum*** (Figure 11) differs in microhabitat from ***D. corrugatum*** (Figure 9), but still is often associated with mosses (Brooks *et al*. 1977). It occupies leaf litter and the basal part of tree trunks. Unlike ***D. corrugatum***, it seems to prefer mossy bark of the sycamore (***Platanus occidentalis***; Figure 12) along streams. Ing (1982) reported ***Diderma chondrioderma*** (Figure 13) as a rare species from mossy bark of living trees in the UK. Ranade *et al*. (2012) contributed to our knowledge of bryophyte-***Diderma*** associations in India. In their checklist, they reported ***Diderma badhamioides*** on mosses growing on the bark of a tree; ***Diderma chondrioderma*** occurs on live mosses as well tree bark in India.

Figure 11. ***Diderma rugosum*** fruiting structure, a species that seems to prefer mossy bark of the sycamore (***Platanus occidentalis***). Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

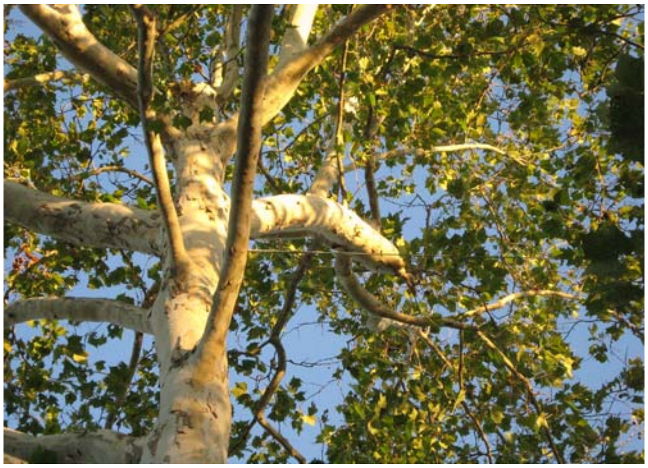

Figure 12. ***Platanus occidentalis*** (sycamore); ***Diderma rugosum*** seems to prefer the bark of this tree, often with mosses. Photo by Bill McChesney, through Creative Commons.

Figure 13. ***Diderma chondrioderma***, a rare species in the UK, living on the mossy bark of trees. Photo by James K. Lindsey, with permission.

***Diderma cinereum*** likewise lives on bark, including sometimes living on the epiphytic mosses (Figure 14-Figure 15). So far I have found only a photographic record of this.

Figure 14. ***Diderma cinereum*** sporangia on bryophytes. Photo by James K. Lindsey, with permission.

Figure 15. ***Diderma cinereum*** sporangia on bryophytes. Photo by James K. Lindsey, with permission.

Doidge (1950) noted ***Badhamia affinis*** (Figure 16-Figure 17) on both mosses and bark of dead and living trees in Africa. ***Badhamia versicolor*** (Figure 18) usually occurs on bark of living trees, and similarly it often uses mosses and lichens as a substrate (Ing 1982; Poulain *et al*. 2011). Ing (1982) reported that ***Badhamia versicolor*** is a rare species on mossy bark of living trees in the UK. Keller and Brooks (1975) described ***Badhamia rugulosa*** from bark and moss-covered tree substrata and grape vines (***Vitis***). They noted that this slime mold tends to occur in flowways and in areas of the bark that retain moisture, with both mosses and liverworts, as well as algae, satisfying that need for moisture retention. In Taiwan, ***Badhamia formosana*** occurs on bark of living trees where it often appears also on the epiphytic mosses (Liu *et al.* 2002).

Figure 16. Fruiting bodies of ***Badhamia affinis*** with bryophytes. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 17. Mature fruiting bodies of ***Badhamia affinis*** with bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 18. Fruiting bodies of ***Badhamia versicolor*** on a moss. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org with online permission.

Figure 20. ***Physarum tesselatum*** sporangia, a species of bark and living mosses. Photo from Myxotropic, through Creative Commons.

Ranade *et al*. (2012) contributed to our knowledge of bryophyte-slime mold associations on bark in India. In their checklist, they reported ***Physarum mortonii*** (Figure 19) and ***P. tesselatum*** (Figure 20) on bark and living mosses, whereas ***Physarum album*** (Figure 21) occurs not only on moss growing on bark of trees, but also on dead twigs; this species is also known from moss-covered rotting logs in China (Ukkala *et al*. 2001). Ukkala *et al*. (2001) found that in Hunan, China, the slime mold ***Physarum pusillum*** (Figure 22) is sometimes associated with mosses on the bark of broad-leaved trees.

Figure 21. ***Physarum album*** sporangia on decaying wood, a species that also lives on mosses of bark and dead twigs. Photo by George Shepherd, through Creative Commons.

Figure 19. ***Physarum mortonii*** sporangia, a species of bark and living mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

***Stemonitis axifera*** (Figure 23-Figure 24) and ***Trichia botrytis*** (Figure 25) both occur on bark of trees and mosses growing on them in India (Ranade *et al*. 2012).

Figure 22. ***Physarum pusillum*** sporangia, a species that sometimes is associated with epiphytic mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 23. ***Stemonitis axifera*** sporangia on decorticated log, a species that also occurs on bark and epiphytic mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 24. ***Stemonitis axifera*** with liverworts, a species of bark and epiphytic mosses. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 25. ***Trichia botrytis*** on mosses, a species that occurs both on bark and bark mosses. Photo by Dragiša Savić, with permission.

Gilert and Neuendorf (1991) reported ***Elaeomyxa reticulospora*** (Figure 26; as *Lamproderma reticulosporum*) from its type locality in western Java in Indonesia, where it was found on the moss-covered trunk of a huge evergreen tree.

Figure 26. ***Elaeomyxa reticulospora***, a species known from moss-covered bark. Photo by Sarah Lloyd, with permission.

Large colonies of ***Colloderma oculatum*** (Figure 27) occur on the moss-covered bark of living trees in coastal Central Europe (Schnittler & Novozhilov 1996). ***Clastoderma pachypus*** occurs on bark covered with mosses in Lithuania (Adamonytė 2007).

Figure 27. ***Colloderma oculatum*** on bryophytes, a typical habitat for it on bark of living trees. Photo by The Eumycetozoan Project, DiscoverLife.org, with online permission.

Schnittler *et al*. (2002) reported ***Didymium floccosum*** (Figure 28) from the densely moss-covered bark of a living tree. The single large colony grew among mosses and small amounts of leafy debris.

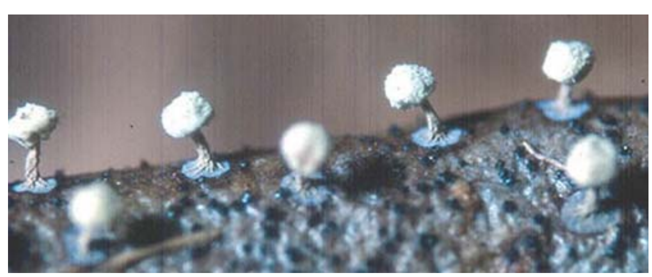

Figure 28. ***Didymium floccosum*** sporangia, a species that can occur on dense moss cover on bark. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

The slime mold ***Paradiacheopsis solitaria*** (Figure 29; syn.=*Comatricha solitaria*) occurs on bark, often with mosses and lichens, in the UK (Ing 1982). Eliasson and Gilert (2007) found ***Paradiacheopsis solitaria*** on mosses and lichens on bark of living ***Malus*** (apple) in Sweden. ***Perichaena chrysosperma*** (Figure 30) occurs in Sweden as solitary, globose or subglobose sporangia on bark or mosses on bark of living trees.

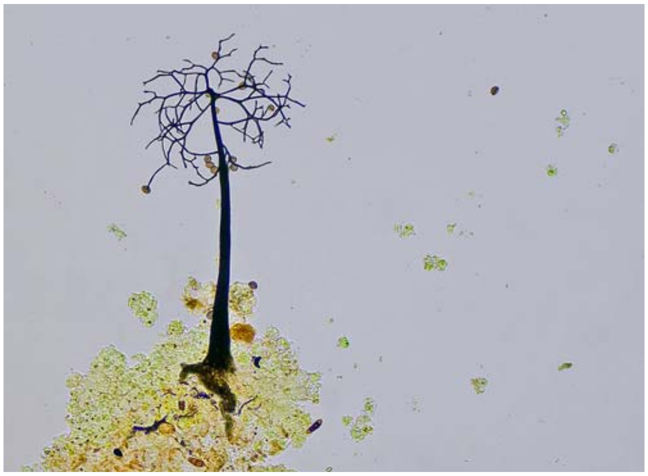

Figure 29. ***Paradiacheopsis solitaria*** sporangium that has lost its spores, a bark and moss-dwelling species. Photo by Dmitry Leontyev, through Creative Commons.

Figure 30. ***Perichaena chrysosperma***, a species of bark and mosses on living trees. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Some corticolous species of slime molds may invade the bryophytes from their bark substrate (Brooks *et al.* 1977). On the other hand, some taxa may start on mosses and then invade the bark. If a plasmodium lives under the bark, it may sometimes be difficult to avoid mosses when it crawls out to produce sporangia (Figure 31).

In their study of corticolous taxa in Costa Rica, in four different forest types, Schnittler and Stephenson (2000) found that those species found on bark at higher elevations also occurred on lush bryophyte mats that covered the bark: ***Arcyria cinerea*** (Figure 32-Figure 33), ***Physarum*** *cf.* ***roseum*** (Figure 34-Figure 35), ***Ceratiomyxa fruticulosa*** (Figure 36), ***Cribraria oregana*** (Figure 37), and ***Didymium iridis*** (Figure 38). Nevertheless, they found that when no bare bark was present, the growth of slime molds was diminished. But, in culture, bark with no epiphytes failed to provide successful slime mold cultures. Perhaps the bryophytes act as a trap, but the sporelings quickly migrate to a more open surface in this habitat.

Figure 31. ***Brefeldia maxima*** on mosses on bark. With mosses everywhere, plasmodia emerging from bark crevices will undoubtedly crawl onto mosses. Photo by Dick Culbert, through Creative Commons.

Figure 32. Fruiting bodies of ***Arcyria cinerea***. Photo by Kim Fleming, The Eumycetozoan Project, DiscoverLife.org, with permission.

Figure 33. ***Arcyria cinerea*** fruiting on mosses. Photo by Dan Molter, through Creative Commons.

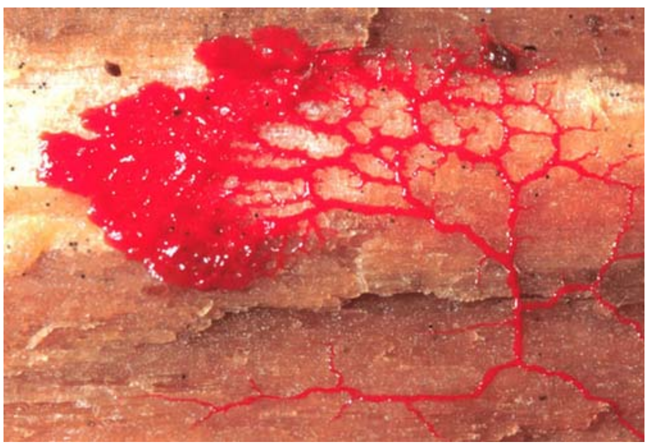

Figure 34. ***Physarum roseum*** plasmodium, a species that occurs on lush moss mats at higher elevations in North America. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 35. ***Physarum roseum*** sporangia. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 36. ***Ceratiomyxa fruticulosa*** fruiting bodies on bryophytes. Photo by Richard Droker, through Creative Commons.

Figure 37. ***Cribraria oregana*** sporangia, a species that can occur on lush bryophyte mats. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 38. ***Didymium iridis*** on decaying log. Photo by Willa Schrlau, through Creative Commons.

Among these Costa Rican bryophyte inhabitants, only ***Arcyria cinerea*** (Figure 32-Figure 33) was also present in Virginia (Schnittler & Stephenson 2000). The most common species in each of these two areas were absent in the other. ***Arcyria cinerea*** is a widespread species tolerant of an array of substrates, including mossy bark of living trees, especially oak (Ing 1982). Furthermore, as elevation increased, the number of species of slime molds decreased (Schnittler & Stephenson 2000), contrasting with the elevational relationship of bryophytes in the Colombian Andes (Gradstein *et al*. 1989; Wolf 1993).

Everhart and Keller (2008) examined the life history strategies of slime molds that live on bark, including six tree species and two vine species in Kentucky and Tennessee, USA. They cultured 580 samples and found 46 slime mold species in 20 different genera. The majority of

these had stalked sporangia. They concluded that the corticolous slime molds in the tree canopy are **r-selected** (optimized for high reproduction). Their resistant, dormant, resting stages permit them to survive the irregular wet periods interspersed with prolonged dry periods in their habitat. The most abundant species, especially the **Echinosteliales** (Figure 39-Figure 40), have a plasmodial stage that exhibits the smallest surface to volume ratio (**protoplasmodium**) and produces spores quickly over 2-4 days by producing a single, tiny, stalked sporangium (Figure 40). Their spore release is efficient, with an rapidly disappearing **periderm** (outer covering of the sporangium).

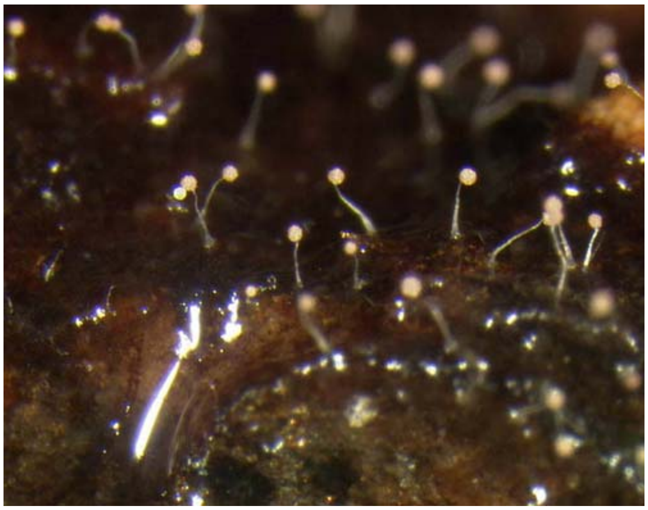

Figure 39. ***Echinostelium minutum***, showing the tiny, stalked sporangia. Photo by Satyendra Rajguru, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 40. ***Echinostelium minutum*** sporangium showing absence of periderm when spores are dispersing. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Slime mold specialists are using rope-climbing techniques like those used by bryologists in the tropics. Snell and Keller (2003) collected slime molds from bark at 3-m increments to the tops of five different tree species in the Great Smoky Mountains National Park, USA. They identified 84 species from their 418 cultures, representing 25 trees. They found similar slime mold community composition among the five tree species, but occurrence and abundance differed and were related to differences in bark *p*H. No height differences were apparent, nor did bark moisture seem to make any difference.

Melissa Skrabal found a new myxomycete species (plasmodial slime mold) ***Diachea arboricola*** (Figure 36) in the tree canopy using rope-climbing techniques (Keller & Skrabal 2002). Although these slime molds occur primarily on bark, one collection developed on bark-dwelling bryophytes (Keller et al. 2004). Observations of this species may help to explain the occasional occurrence of some slime molds on bryophytes. The plasmodium (jelly-like slime stage) of ***Diachea arboricola*** moves great distances across the bark surface, but is apparently confined to the tree canopy. In order to traverse the canopy, the plasmodium often encounters bryophytes living there. This behavior was also observed in a Petri dish, where a large plasmodium covered the moss in a moist chamber. Thus, when cultures of slime molds include bryophytes, mosses and liverworts, they serve as a substratum to renew the myxomycete life cycle and develop sporangia. A possible explanation for the bryophyte occurrence of ***Diachea arboricola*** sporangia, and that of other occasional slime mold species on bryophytes, is that the bryophyte dries while the slime mold is on it, and on a sunny day, may trigger fruiting body formation.

Figure 41. ***Diachea arboricola*** sporangium, a bark species that migrates on the tree as a plasmodium. Photo by Kenny Snell, courtesy of Harold W. Keller, from Keller & Skrabal 2002; Keller & Barfield 2017; Keller 2019.

## Liverwort vs Moss Associations

In humid forests, the epiphytic liverworts often serve as substrates for slime molds (Ing 1994). Coincidentally, they also serve as substrates for myxobacteria, providing a food source for the slime molds and permitting their development. Schuster (1957) reported fruiting bodies of ***Lamproderma columbinum*** (Figure 42), ***Collaria arcyrionema*** (Figure 43), ***Physarum flavidum*** (Figure 44), and ***Cribraria violacea*** (Figure 45) on both stems and leaves of leafy liverworts. Ing (1994) considered the epiphytic liverworts to be frequent developmental substrates for slime molds. ***Hemitrichia minor*** is typically associated with ***Metzgeria furcata*** (Figure 46) and ***Radula complanata*** (Figure 47). Isabelle Mazaud photographed ***Diacheopsis synspora*** (Figure 48-Figure 49) from ***Metzgeria furcata*** on the bark of ***Quercus robur*** (Figure 50). ***Licea bryophila*** (Figure 51) seems to be confined to bark-dwelling liverworts, and ***L. gloeoderma*** is found only on the epiphytic leafy liverwort ***Frullania*** (Figure 52) species in Bavaria (Döbbeler & Nannenga-Bremekamp 1979).

Figure 42. ***Lamproderma columbinum*** on moss. Photo from Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 43. ***Collaria arcyrionema***, a species that fruits on leafy liverworts. Photo by Taibif.tw, through Creative Commons.

Figure 44. ***Physarum flavidum*** sporangia, a species that can occur on stems and leaves of leafy liverworts. Photo by Sarah Lloyd, with permission.

Figure 45. ***Cribraria violacea***, a species that can occur on stems and leaves of leafy liverworts. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 46. ***Metzgeria furcata***, a species that is a typical substrate for ***Hemitrichia minor***. Photo from <www.aphotofauna.com>), with permission.

Figure 47. ***Radula complanata***, a species that is a typical substrate for ***Hemitrichia minor***. Photo by Hermann Schachner, through Creative Commons.

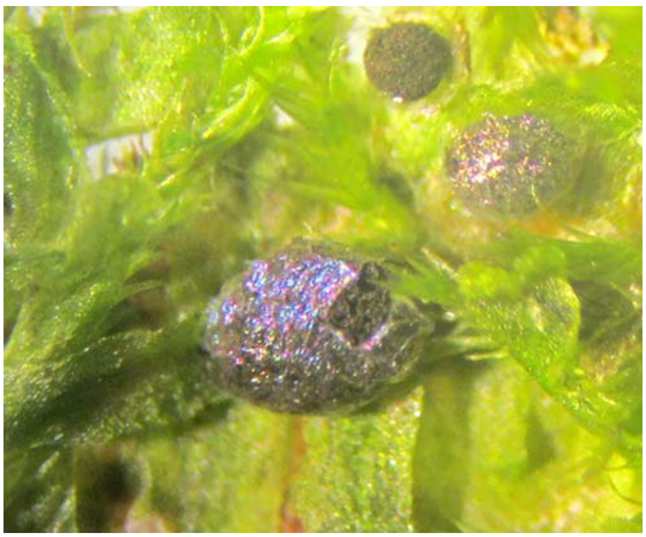

Figure 48. ***Diacheopsis synspora*** on ***Metzgeria furcata*** on ***Quercus robur***. Photo courtesy of Isabelle Mazaud.

Figure 49. ***Diacheopsis synspora*** from ***Metzgeria furcata*** on bark of ***Quercus robur***. Photo courtesy of Isabelle Mazaud.

Figure 50. ***Quercus robur*** with bryophytes on bark, home for ***Diacheopsis synspora*** on the liverwort ***Metzgeria furcata***. Photo by Robert Vidéki, through Creative Commons.

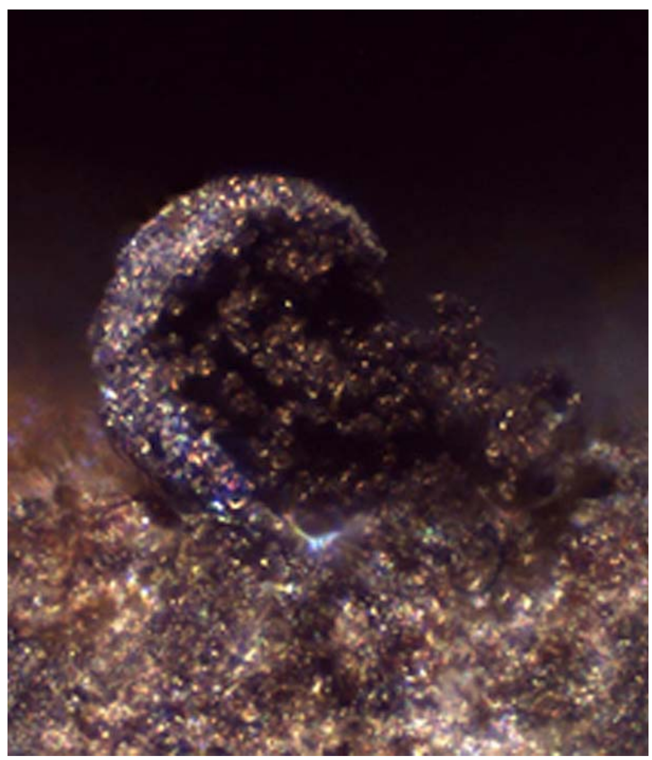

Figure 51. ***Licea bryophila*** sporangia, a species that seems to be confined to liverworts on bark. Photo by Thomas Laxton, through Creative Commons.

Figure 52. ***Frullania*** sp.; ***Licea gloeoderma*** is found exclusively on this genus of leafy liverworts. Photo by Felipe Osorio-Zúñiga, with permission.

The slime mold ***Diacheopsis mitchellii*** grows on epiphytic bryophytes in Flanders, Belgium (de Haan 2017). De Haan included an image of it growing on ***Lophocolea heterophylla***.

***Diderma chondrioderma*** (Figure 13) is commonly associated with the moss ***Hypnum andoi*** (Figure 53; syn.=***Hypnum mammillatum***) and the slime mold ***Macbrideola cornea*** (Figure 54) occurs with several acrocarpous moss species (Ing 1994). ***Macbrideola cornea*** forms a single plasmodium that can migrate to the tips of moss leaves and form stalked sporangia (Harold Keller, pers. comm. 22 April 2019). Unlike most of the known moss dwellers, the common ***Licea parasitica*** (Figure 55) is not confined to mosses in fructification, but its **microcysts** (resistant dormant stage) can become conspicuous on the moss leaves.

Figure 53. ***Hypnum andoi***, a common substrate for ***Diderma chondrioderma***. Photo by Michael Lüth, with permission.

Figure 54. ***Macbrideola cornea*** sporangia, a species that associates with several acrocarpous moss species. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

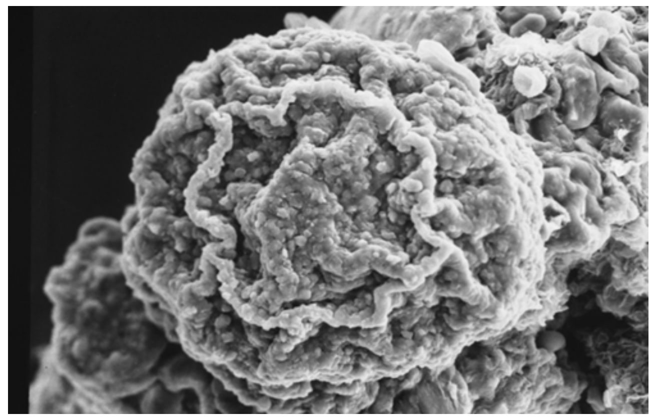

Figure 55. SEM of ***Licea parasitica*** sporangium, a species that forms conspicuous coverings on moss leaves in its microcyst stage. The Eumycetozoan Project, DiscoverLife.org, with online permission.

It is likely that slime mold preferences for mosses vs liverworts relate to moisture or other bark preferences of these two groups of bryophytes. There has been no experimental work to attempt to find the determining factors.

## Limiting Factors

Studlar (1982) examined host specificity of epiphytic bryophytes, reporting on 54 moss and 18 liverwort species on 120 trees comprised of 6 species. She found that among those bryophytes with a frequency of 20% or more on tree trunks up to 1.8 m, only three species were restricted to just one host, with another 21 exhibiting a strong single-host preference. She found that the bryophyte species richness and frequency decreased with decreasing bark *p*H, with water absorption capacity of the bark having a lesser effect. It would be interesting to see if slime molds associated with bryophytes have the same gradients on these trees.

Everhart *et al*. (2009) evaluated the bark characteristics and canopy epiphytes (mosses, lichens, and algae) associated with corticolous slime molds in three temperate forests in the southeastern USA. They used rope-climbing techniques to sample trees and grapevines up to 15 m above the ground. They used five 2 x 2 cm quadrats, resulting in 187 sample sites, for determining percent

cover. They found no association between epiphytic percent cover and slime molds. Rather, like Studlar (1982), they found that bark *p*H was the major factor apparently influencing the presence of the corticolous slime mold species. They considered the patchy distribution to be the result of the small plasmodium typical of most of the corticolous species. They concluded that rather than improving the growing conditions for the slime molds, bryophytes had a negative correlation with them, albeit not a significant one.

Härkönen (1977) actually measured *p*H at the locations of slime molds living on bryophytes. Overall, the bark-dwelling slime molds occurred on a wide range of *p*H from 2 to 9. Specifically, ***Perichaena chrysosperma*** (Figure 30) occurred on *Populus tremula* (Figure 56) with a *p*H of 5.5; ***Stemonitis pallida*** (Figure 57) occurred on *Juniperus communis* (Figure 58) with a *p*H of 4.5.

Figure 57. ***Stemonitis pallida*** sporangia, a species that occurs on *Juniperus communis* with a bark *p*H of 4.5. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 56. ***Populus tremula***, home for ***Perichaena chrysosperma***, with a bark *p*H of 5.5. Photo by J. R. Crellin, through Creative Commons.

Figure 58. ***Juniperus communis***, a species with a bark *p*H of 4.5. Photo by Chris Cant, through Creative Commons.

Härkönen *et al*. (2004) found that slime mold species richness on bark of forests in Hunan, China, was highest when the bark was relatively acidic and had a high water-retention capacity. The bryophytes, on the other hand, had a higher diversity on less acidic, relatively smooth bark. It is assumed that smooth bark holds less water.

Härkönen (1977) inferred that the mosses trapped the spores of the slime molds. To test this hypothesis, he cultured bark from living trees at three localities in Finland. In these moist chambers, 19 species of slime molds appeared on the pieces of bark. He found that ***Comatricha nigra*** (Figure 59) preferred an acid substrate, whereas others like ***Arcyria cinerea*** (Figure 32-Figure 33) preferred a less acid one. Fructification in the cultures varied from a few days to more than 40 days. Source of origin affected the species diversity, with the urban locality samples producing only six species. Interestingly, the virgin forest samples exhibited more species, but fewer fructifications. *Salix caprea* and *Alnus incana* have very few epiphytic mosses, presumably greatly reducing the capture of slime mold spores.

Figure 59. ***Comatricha nigra*** young sporangia, a species that prefers an acid substrate. Photo by Bjorlil, through Creative Commons.

Interestingly, Ing (1994) found that temperature was the only significant factor limiting tropical, subtropical, Mediterranean, and alpine species. Nevertheless, water is of prime importance, with water-retaining substrates being essential. They considered only "a few species" to be particularly associated with terrestrial bryophytes. The slime molds tended to prefer either coniferous or angiospermous wood.

Unlike bryophyte diversity, slime mold diversity and abundance decrease with elevation and associated higher moisture levels in the tropical Costa Rica (Gradstein *et al.* 1989; Wolf 1993; Schnittler & Stephenson 2000). Furthermore, it is in two seasonally dry forests where 90% of the slime mold diversity occurs. The negative correlation between slime molds and bryophytes suggests that the bryophytes may actually out-compete the slime molds in the more moist, bryophyte-dominant ecosystems at higher elevations. Nevertheless, higher species diversity seems to be correlated with higher substrate *p*H. On the other hand, litter-inhabiting slime molds with robust phaneroplasmodia increase with increasing elevation. It also appears that the continuously moist forests at higher elevations are not favorable for slime mold growth and development. These factors all contribute to the fact that biodiversity of slime molds does not reach its highest levels in tropical forests.

Schnittler and Stephenson (2000) found ***Ceratiomyxa fruticulosa*** (Figure 36) twice on mossy bark in the wet Costa Rican forest. All the species found on bark at higher elevations occurred not only on bark, but also on lush epiphytic moss and liverwort mats on the bark. These were ***Arcyria cinerea*** (Figure 32-Figure 33), ***Physarum*** *cf.* ***roseum*** (Figure 34-Figure 35), ***Ceratiomyxa fruticulosa***, ***Cribraria oregana*** (Figure 37), and ***Didymium iridis*** (Figure 38). The culture studies made it "obvious" that a closed cover of epiphytes hampers growth of slime molds. Nevertheless, many cultures prepared with bark having low cover of epiphytes likewise produced no slime molds. In any case, the number of slime mold records, based on cultures, clearly decreased with increasing elevation. Schnittler and Stephenson suggested that the abundant bryophytes use the bark nutrients, hence making them unavailable for bacterial growth, thus making less bacterial food available for the slime molds. But they pointed out that slime molds were often absent at low elevations where bryophytes were likewise rare.

In addition to bark-dwellers, some slime molds find substrates of liverworts growing on leaves to provide a suitable substrate (Schnittler *et al*. 2006). In the tropical forest, these habitats typically have a poor species richness of slime molds (Schnittler *et al*. 2006), but an assemblage dominated by members of the **Physarales** (Figure 19-Figure 22) is common (Schnittler 2001).

## Log and Stump Associations

The most common habitat for slime molds seems to be that of logs (see, for example, Stephenson & Studlar 1985). These include a variety of stages of decay, and the logs often have a dense cover of bryophytes. Stumps offer similar habitats, but may differ in having exposed wood before decay sets in.

Doidge (1950), in her African report, included more detail on substrate than many of the early studies. She reported ***Cribraria cancellata*** (Figure 60) on dead wood and moss. ***Trichia affinis*** (Figure 61) occurred on decayed wood and moss. While it is likely that some of these slime molds grew from a primary substrate onto the mosses, that cannot be discerned from the report.

Figure 60. ***Cribraria cancellata*** sporangia on bryophytes. Photo by George Barron, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 61. ***Trichia affinis*** sporangia. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

A number of species are common on rotten wood, where they are able to provide food for a number of invertebrate organisms (Ing 1967). These slime molds include ***Arcyria denudata*** (Figure 62-Figure 63), ***Stemonitopsis typhina*** (Figure 64), ***Cribraria piriformis*** (Figure 65), ***Didymium iridis*** (Figure 38), ***Fuligo septica*** (Figure 1, Figure 66), ***Lycogala epidendrum*** (Figure 67), ***Reticularia lycoperdon*** (Figure 68), ***Stemonitis fusca*** (Figure 69), ***Symphytocarpus flaccidus*** (Figure 70-Figure 71), ***Trichia varia*** (Figure 72), ***Tubifera ferruginosa*** (Figure 73-Figure 74). All of these slime mold species occur on the same substrata preferred by a number of bryophyte species and are known to occasionally occur on the bryophytes.

Figure 62. ***Arcyria denudata*** plasmodium, a common species on rotten wood. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 63. ***Arcyria denudata*** sporangia in their dispersal stage, with mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 64. ***Stemonitopsis typhina*** mature sporangia. Photo by George Barron, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 65. ***Cribraria piriformis*** sporangia, a slime mold that provides food for log-dwelling organisms. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 66. ***Fuligo septica*** plasmodium, a slime mold that provides food for log-dwelling organisms. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 67. ***Lycogala epidendrum*** sporangia, a species that provides food for invertebrates on logs, on the moss ***Thuidium***. Photo by Andrew Khitsun, with online permission.

Figure 68. ***Reticularia lycoperdon*** on log with moss, a slime mold that provides invertebrates with food. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 69. ***Stemonitis fusca*** sclerotium and sporangia; ***S. fusca*** provides food for invertebrates on logs. Photo by Deryni, through Creative Commons.

Figure 70. ***Symphytocarpus flaccidus*** sporangia, a slime mold that provides invertebrates with food. Photo Sarah Lloyd, with permission.

Figure 71. ***Symphytocarpus flaccidus*** sporangia. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 72. ***Trichia varia*** sporangia on mosses, a slime mold that provides food for invertebrates on logs. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 73. ***Tubifera ferruginosa*** sporangia on mosses on a log, a species that provides food for invertebrates. Photo by Dohduhdah, through Creative Commons.

Figure 74. ***Tubifera ferruginosa*** immature sporangia among mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Rojas and Stephenson (2007) examined **Myxomycetes** at high elevations in Costa Rica. They determined that ***Didymium squamulosum*** (Figure 75), ***Lycogala epidendrum*** (Figure 67), and ***Metatrichia floriformis*** (Figure 76) seem to group together at high *p*H levels and lower substrate heights. The sometimes-moss-dwellers ***Cribraria mirabilis*** (Figure 77) and ***Trichia botrytis*** (Figure 25) prefer more acidic substrates and higher substrates. They concluded that while bryophytes are important on the ground there, but not on logs, the bryophytes are not the reason for the presence of these slime molds at greater heights. As seen elsewhere, ***Lamproderma columbinum*** (Figure 42) is strongly associated with bryophytes. ***Cribraria piriformis*** (Figure 65), ***Ceratiomyxa fruticulosa*** (Figure 36) (on stumps overgrown with mosses – see also Stojanowska & Panek 2004), ***Cribraria mirabilis***, and ***Cribraria vulgaris*** (Figure 78) exhibited most of their fruitings on logs, twigs, and bryophytes. Rojas and Stephenson concluded that most of these slime molds were generalists that are able to survive changing microenvironmental conditions.

Figure 75. ***Didymium squamulosum*** on moss. Photo by James K. Lindsey, with permission.

Figure 76. ***Metatrichia floriformis*** sporangia, a species that occurred together with ***Trichia varia*** on a moss-covered aspen log. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 77. ***Cribraria mirabilis*** sporangia, a species that prefers acidic substrates and sometimes occurs on mosses. Photo by Rod Nelson, The Eumycetozoa Project, DiscoverLife.org, with online permission.

Figure 78. ***Cribraria vulgaris*** sporangia, a species occurring on moss-covered stumps and logs. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 80. ***Barbeyella minutissima*** sporangia on leafy liverwort. Photo by Randy Darrah, The Eumycetozoan Project, DiscoverLife.org, with online permission.

The slime mold ***Hemitrichia minor*** is relatively common on logs covered with the leafy liverwort ***Lophocolea heterophylla*** (Figure 79). As shown in many studies cited herein, ***Barbeyella minutissima*** (Figure 80) occurs on such small liverworts as ***Lepidozia reptans*** (Figure 81) and ***Nowellia curvifolia*** (Figure 82) on montane forest logs in such distant locations as Japan, Europe, and North America (Kowalski & Hinchee 1972; Stephenson & Studlar 1985), with a similar relationship shown by the rare ***Licea hepatica*** (Kowalski 1972). ***Lepidoderma tigrinum*** (Figure 83) forms a strong association with both lichens and liverworts, the latter including ***Anastrophyllum michauxii*** (Figure 84), on damp coniferous logs. The frequent association of ***Perichaena corticalis*** (Figure 85) and ***P. depressa*** (Figure 86) with species of ***Hypnum*** (Figure 4) on ash (***Fraxinus***; Figure 87) fallen trunks that haven't "quite reached the ground" is notable (Ing 1982, 1994). I have already noted that ***Cribraria rufa*** (Figure 88) actually seems to damage the moss ***Orthodontium lineare*** (Figure 89) where both grow on conifer logs (Coker 1966).

Figure 81. ***Lepidozia reptans***, one of the preferred substrates for ***Barbeyella minutissima***. Photo by David T. Holyoak, with permission.

Figure 79. ***Lophocolea heterophylla***, apparently overgrowing old slime molds. Photo by Sture Hermansson, with online permission.

Figure 82. ***Nowellia curvifolia***, a leafy liverwort that is an indicator for the presence of ***Barbeyella minutissima*** in that habitat. Photo by Hermann Schachner, through Creative Commons.

Figure 83. ***Lepidoderma tigrinum*** with sporangia on moss, a slime mold found on conifer logs with a thick cover of mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 84. ***Anastrophyllum michauxii***, a common leafy liverwort substrate for ***Barbeyella minutissima***. Photo by Michael Lüth, with permission.

Figure 85. ***Perichaena corticalis*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 86. ***Perichaena depressa***, a slime mold species frequently associated with the moss genus ***Hypnum***. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 87. ***Fraxinus americana*** bark. ***Perichaena corticalis*** and ***P. depressa*** often occur with ***Hypnum*** species on fallen trunks of ***Fraxinus***. Photo by Keith Kanoti, through Creative Commons.

Figure 88. ***Cribraria rufa*** sporangia, a species that seems to damage the moss ***Orthodontium lineare***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 89. ***Orthodontium lineare*** with capsules, a moss that seems to be damaged by the slime mold ***Cribraria rufa***. Photo by David T. Holyoak, with permission.

Clissmann *et al*. (2015) considered the diversity of slime molds on decaying beech (***Fagus sylvatica***; Figure 90) logs. They found that the conspicuous slime molds with large fruiting bodies displayed a strong preference for well-decayed, moist wood. These included ***Fuligo septica*** (Figure 1, Figure 66), ***Lycogala epidendrum*** (Figure 67), and ***Reticularia lycoperdon*** (Figure 68), all of which are known from mosses. DNA identifications revealed that the majority of representatives were in the genera ***Arcyria*** (Figure 32; Figure 62-Figure 63), ***Trichia*** (Figure 72, Figure 92), and ***Lycogala*** (Figure 67). The most common species on these logs were ***Arcyria cinerea*** (Figure 32-Figure 33), ***Hemitrichia clavata*** (Figure 91), ***Trichia scabra*** (Figure 92), and ***T. varia*** (Figure 72). It is notable that all the species named here by Clissmann and coworkers are also known from bryophytes on logs.

Figure 90. ***Fagus sylvatica***; well-decayed logs of this species host large slime molds. Photo by Roger Culos, through Creative Commons.

Figure 91. ***Hemitrichia clavata*** sporangia on log, one of the most common species on ***Fagus sylvatica*** logs. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 92. ***Trichia scabra*** sporangia on mosses, one of the most common slime mold species on ***Fagus sylvatica*** logs. Photo by Fotky, through Creative Commons.

There are even new species to be found in this common Myxomycetes habitat. Sarah Lloyd collected a new species, ***Alwisia lloydiae*** (Figure 93-Figure 94) (Leontyev *et al*. 2014). This species grows on logs, stumps, and mossy logs in New South Wales and Tasmania in Australia.

Figure 93. ***Alwisia lloydiae*** sporangia on mosses. Photo by Sarah Lloyd, with permission.

Figure 94. ***Alwisia lloydiae*** dehiscing capsules with mosses. Photo by Sarah Lloyd, with permission.

Figure 95. ***Tubifera*** cf. ***applanata*** with bryophytes on decaying wood. Photo by Sarah Lloyd, with permission.

It is with this background of the strong relationship between slime molds and logs, and with the most common taxa occurring with bryophytes, that we must evaluate the relationship, if any, of slime molds with the bryophytes that grow on the logs. Are they simply benefitted by the same growing conditions? Or is the relationship **commensalism**, wherein one benefits and one is neither benefitted nor harmed? The slime molds could benefit from the moisture-holding capacity of the bryophytes, or the food organisms they house. It is harder to imagine any benefit to the bryophyte. Or do the slime molds provide food for invertebrates that in turn disperse the bryophyte spores?

## Comparison of Checklists

Many researchers have reported slime molds growing on or over bryophytes on logs. Greene (1929) reported ***Tubifera ferruginosa*** (Figure 73) on mossy logs. Hagelstein (1941), using specimens added to the ***Tubifera applanata*** (Figure 95-Figure 96) similarly grows on decaying logs (Yatsiu, *et al*. 2018) and can grow on the bryophytes there (Figure 95). Herbarium of the New York Botanical Garden, reported a number of species from logs, noting those of conifer logs with a thick cover of mosses, lichens, and liverworts. These bryophyte associates included ***Colloderma oculatum*** (Figure 27), ***Lepidoderma tigrinum*** (Figure 83), ***Diderma roanense***, and ***Lamproderma columbinum*** (Figure 42). Others only indicated mossy logs, including ***Diderma roanense*** and ***Lepidoderma tigrinum***. Thus the short-comings of collections in herbaria deprive us of detailed information from which to draw inferences regarding specificity of the substrate, moisture and light levels, and *p*H. Hagelstein further pointed out that even in the sporangial stage, mosses can conceal the slime molds, so at best the ecology of slime molds associated with bryophytes is poorly represented.

Figure 96. ***Tubifera applanata*** dispersing spores onto bryophytes. Photo by Sarah Lloyd, with permission.

Critchfield and Demaree (1991) reported ***Badhamia nitens*** (Figure 97-Figure 98) from dead wood and bark, but sometimes on mosses (and lichens) in California. Singer *et al*. (2005) reported ***Diderma montanum*** (Figure 99; syn.=*Chondrioderma montana*) and ***Diderma asteroides*** (Figure 100) on mosses on decayed wood. Robbrecht (1974) noted that ***Arcyria*** (Figure 101) occurs on diverse substrates, but mostly on dead wood (including alder, poplar, beech, oak, spruce, willow) at various stages of decay, but also on mosses, presumably on decaying wood. Ing (1982) reported ***Physarum psittacinum*** (Figure 102-Figure 103) on mossy rotten logs and ***Trichia affinis*** (Figure 104) on moss and rotten wood. Nissan (1997) found ***Physarum decipiens*** (Figure 105) on dead branches in association with mosses. Johannesen (1984) found ***Didymium ochroideum*** on mosses on dead wood of the Norway spruce (***Picea abies***; Figure 106). Stephenson

(1985) found ***Licea pusilla*** on the moss ***Hypnum imponens*** (common on logs; Figure 4) and on decaying coniferous wood.

Figure 97. ***Badhamia nitens*** sporangia, a species of dead wood and bark, but that sometimes occurs on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 98. ***Badhamia nitens*** sporangia on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 99. ***Diderma montanum*** sporangia, a slime mold species of dead wood and bark, but also sometimes on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 100. ***Diderma asteroides*** sporangia, a slime mold species of dead wood and bark, but also sometimes on mosses. Photo from Myxotropic, through Creative Commons.

Figure 101. ***Arcyria nutans*** with capsules on decaying wood with mosses. Photo by Lairich Rig, through Creative Commons.

Figure 102. ***Physarum psittacinum*** plasmodium, a species known to occur on mossy rotten logs. Photo by Helen Ginger, through Creative Commons.

Figure 103. ***Physarum psittacinum*** sporangia on moss. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 104. ***Trichia affinis*** sporangia, a species known to occur on mossy rotten logs. Photo by Malcolm Storey, through Creative Commons.

Figure 105. ***Physarum decipiens*** on bryophytes, a species that also occurs on dead branches with mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 106. ***Picea abies***; the slime mold ***Didymium ochroideum*** occurs on mosses on logs of this species. Photo by Qgroom, through Creative Commons.

As we entered the 21st Century, new records continued. Adamonyte (2000) found ***Cribraria argillacea*** (Figure 107) and ***Trichia favoginea*** (Figure 108-Figure 109) on very rotten, moss-covered logs, ***Hemitrichia clavata*** (Figure 91) and ***H. serpula*** (Figure 110) together on a moss-covered deciduous log, ***Metatrichia floriformis*** (Figure 76) with ***Trichia varia*** (Figure 72) on a moss-covered aspen log, ***Stemonitis axifera*** (Figure 23) on a moss-covered log in Estonia. Ukkala *et al*. (2001) reported several ***Physarum album*** (Figure 21) on decayed wood covered with mosses in China. Similarly, Castillo *et al*. (2009) reported ***Physarum leucophaeum*** (Figure 111) "in" moss on wood of the oak ***Quercus pyrenaica*** (Figure 112) in Cabañeros National Park, Spain. Working on Pantelleria, a volcanic island located 110 km southwest of the island of Sicily, Italy, Compagno *et al*. (2016) found ***Trichia persimilis*** (Figure 113-Figure 114) on rotten stumps and mosses.

Figure 107. ***Cribraria argillacea*** among mosses on log; this species is known from well-rotted, moss-covered logs. Photo by Malcolm Storey, through Creative Commons.

Figure 108. ***Trichia favoginea*** with mosses. Photo from Denver Botanical Garden, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 109. ***Trichia flavoginea***, an occasional bryophyte-dweller. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 110. ***Hemitrichia serpula*** producing spores, a species known to occur on a moss-covered deciduous log. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 111. ***Physarum leucophaeum*** expelling its spores. This slime mold species occurs among mosses on wood of the oak ***Quercus pyrenaica***. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 112. ***Quercus pyrenaica*** bark, substrate for the slime mold ***Physarum leucophaeum***. Photo by Xemenendura, through Creative Commons.

Figure 113. ***Trichia persimilis*** with mosses. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 114. ***Trichia persimilis*** fruiting. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

The interesting thing in these lists of slime molds reported by various researchers in diverse parts of the world is that in my limited perusal of various checklists, searching for bryophyte associations, a species has rarely been listed on bryophytes in more than one list. While this perusal is far from extensive, it nevertheless suggests to me that the slime molds on the bryophytes are not unique to that substrate. A more thorough study of the published records, backed up by field studies, will be necessary to support that hypothesis.

A more extensive study of slime molds and their substrates is that of Schnittler and Novozhilov (1996) in the boreal forests of northern Karelia in Russia. Some of these weren't picky about the type of wood, but others seemed to be more specific. Many occurred insufficiently to generalize. For example, ***Badhamia foliicola*** (Figure 115) occurred only once, in that case on a strongly decayed deciduous, moss-covered, decorticated log lying on the forest floor of a spruce-birch-aspen forest. ***Physarum globuliferum*** (Figure 116) produced only two records, both from moderately decayed coniferous wood that was partially covered with mosses. ***Physarum leucophaeum*** (Figure 117) was likewise not very common, but was always on dead wood, mostly aspen (***Populus***; Figure 56), but less commonly on spruce, and was often associated with mosses; lab cultures came from mossy living or dead bark of aspen.

Figure 115. ***Badhamia foliicola*** sporangia, a species known from a strongly decayed deciduous, moss-covered, decorticated log. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 116. ***Physarum** cf. **globuliferum***, a species in Russia from moderately decayed coniferous wood that was partially covered with mosses. Photo by George Shepherd, through Creative Commons.



Figure 117. ***Physarum leucophaeum***, a species that in Russia was not common, occurred on dead aspen wood, but occasionally occurred on bryophytes. Photo by Jerry Cooper, through Creative Commons.

On the other hand, the common ***Physarum album*** (Figure 21) and ***Stemonitis fusca*** (Figure 69) occurred on all kinds of well-decayed wood, but despite records of these species on bryophytes elsewhere, none were mentioned in this Karelian study (Schnittler & Novozhilov 1996). ***Physarum viride*** (Figure 118) likewise occurred on decayed wood, mostly of conifers, but occasionally on deciduous trees; there was no mention of bryophytes, although it has been associated with them in other studies. ***Comatricha laxa*** (Figure 119) was very frequent, and displayed a strong preference for coniferous wood, usually on small branches that had lost their bark and were lying on wet mosses. Might these have spent their plasmodial stage among the mosses, crawling up onto the branches to produce their sporangia?

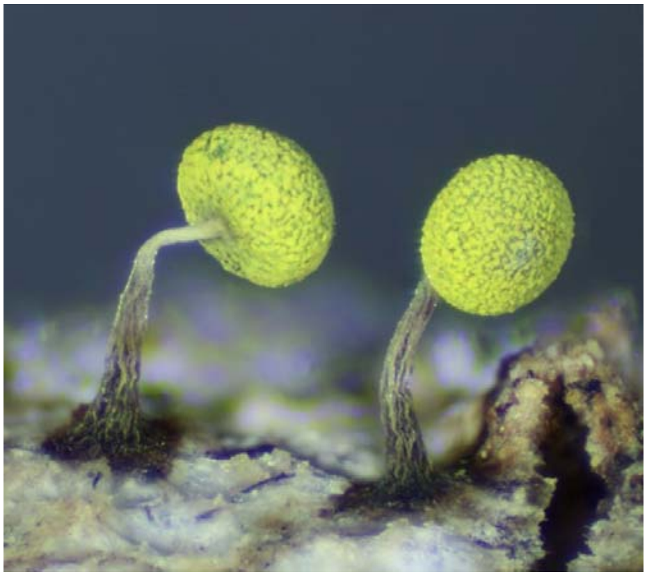

Figure 118. ***Physarum viride*** sporangia, a species of decaying wood, especially conifers. Photo by Sarah Lloyd, with permission.

Figure 119. ***Comatricha laxa*** sporangia on decaying log, a slime mold that also occurs on logs lying on wet moss. Photo by Clive Shirley, The Hidden Forest, with permission.

Schnittler and Novozhilov (1998) conducted another extensive study on slime molds on those fruiting in the late autumn in the Northern Ammergauer Alps on the Bavarian-Tyrolean border. Some of these indicated successional stages, as discussed below. Others related to bryophytes include ***Lamproderma columbinum*** (Figure 42) on thick moss beds of fallen logs (see also Ing 1982) and rocks. The ***Licea pygmaea*** (Figure 120) group, mostly rare, prefer strongly decayed (37% of records), moss-overgrown (31%), or algae-covered wood (22%). But some [***Hemitrichia clavata*** (Figure 91), ***H serpula*** (Figure 110), ***Collaria arcyrionema*** (Figure 43; syn.=*Lamproderma arcyrionema*), ***Lamproderma** cf.* ***sauteri*** (Figure 121), ***Lepidoderma tigrinum*** (Figure 83), ***Trichia varia*** (Figure 72)] occurred on wood without bryophytes, despite all of these being known elsewhere from bryophytes as well. For example, Ing (1982) reported ***Lepidoderma tigrinum*** from mossy wood.

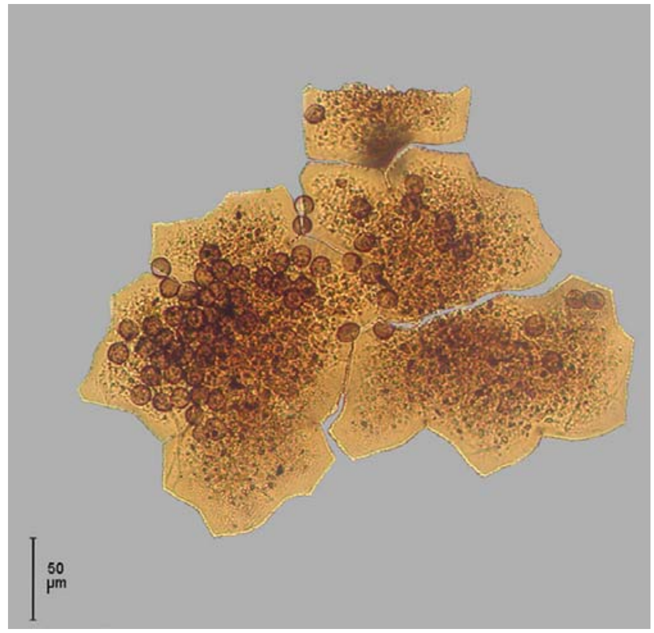


Figure 120. ***Licea pygmaea*** peridium with sporangia, a species with a moderate frequency with mosses. Photo from The Eumycetozoan Project, DiscoerLife.org, with online permission.

Figure 121. ***Lamproderma sauteri*** sporangia. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

A number of biologists have considered ***Barbeyella minutissima*** (Figure 80) to be restricted to bryophytes. Kowalski and Hinchee (1972) found it in relatively good abundance on the slopes of Mount Baker and Mount Rainier, Washington, USA. There it formed associations with the leafy liverworts ***Anastrophyllum michauxii*** (Figure 84), ***Blepharostoma trichophyllum*** (Figure 122), ***Cephalozia bicuspidata*** (Figure 123), ***Plagiochila asplenioides*** (Figure 124), and ***Scapania bolanderi*** (Figure 125). The small size of this slime mold makes it easy to overlook, especially with its very restrictive habitat. Kowalski and Hinchee hypothesized that it is usually overlooked, and that it is likely to occur in any montane area. They suggested searching for it among the leafy liverworts, using a hand lens or dissecting microscope.

Figure 122. ***Blepharostoma trichophyllum***, a common leafy liverwort substrate for ***Barbeyella minutissima***. Photo by Hermann Schachner, through Creative Commons.

Figure 123. ***Cephalozia bicuspidata***, a common leafy liverwort substrate for ***Barbeyella minutissima***. Photo from Botany Website, UBC, with permission.

Figure 124. ***Plagiochila asplenioides***, a common leafy liverwort substrate for ***Barbeyella minutissima***. Photo by Hermann Schachner, through Creative Commons.

Figure 125. ***Scapania bolanderi***, a common leafy liverwort substrate for ***Barbeyella minutissima***. Photo from Botany Website, UBC, with permission.

***Barbeyella minutissima*** (Figure 80) seems to be distributed primarily in montane spruce-fir forests (Schnittler *et al*. 2000). It typically is associated with three other slime molds, ***Colloderma oculatum*** (Figure 27), ***Lamproderma columbinum*** (Figure 42), and ***Lepidoderma tigrinum*** (Figure 83). The leafy liverwort ***Nowellia curvifolia*** (Figure 82) is such a common substrate for it that the liverwort can serve as an indicator species for its presence.

Working in India, Ranade *et al*. (2012) added a different group of species. On living mosses and bark of stumps they found ***Badhamia capsulifera*** (Figure 126), whereas ***B. utricularis*** (Figure 127-Figure 129) seemed to prefer dead wood and mosses; ***Trichia affinis*** (Figure 104) likewise occurred on wood of a stump and live mosses growing on it. Similarly, ***Hemitrichia serpula*** (Figure 110) occurred on both mosses and dead wood, but the researchers specifically stated that ***Arcyria stipata*** (as *Hemitrichia stipitata*; Figure 130) and ***Stemonitis axifera*** (Figure 24) occurred on dead wood and living mosses. ***Trichia botrytis*** (Figure 25) occurs on the bark of trees and mosses growing on it, on dead coniferous wood, and on living mosses. ***Diderma cor-rubrum*** and ***Lamproderma columbinum*** (Figure 42) occurred on a moss-covered stump. ***Physarum stellatum*** (Figure 131), instead, occurred on dead wood, mosses, and an oak stump. As might be expected, ***Barbeyella minutissima*** (Figure 80) was associated with mosses and liverworts on decaying logs. ***Stemonaria nannengae***, ***Stemonitis farrensis***, and ***Trichia favoginea*** (Figure 132) were seemingly more particular about the wood, occurring on decaying gymnosperm wood covered with mosses, whereas ***Diderma alexopouli*** and ***D. indicum*** occurred on a moss-covered conifer stump, with the latter also occurring on mosses. ***Physarum flavidum*** (Figure 44, Figure 133) was found in coniferous forests, where it occurred on decorticated logs and mosses. ***Fuligo aurea*** (Figure 134) was even more specific (or maybe the collectors were able to be more specific), growing on moss covering the decaying wood of the fir, ***Abies pindrow*** (Figure 135-Figure 136). ***Cribraria rubiginosa*** (Figure 137) occurred on mosses on a log.

Figure 126. ***Badhamia capsulifera***, a species that occurs on living mosses and stumps. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 127. Young fruiting bodies of ***Badhamia utricularis*** invading shelf fungi. Are those moss protonemata? Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 128. Mature fruiting bodies of ***Badhamia utricularis*** invading shelf fungi. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 129. Plasmodium stage of ***Badhamia utricularis*** invading shelf fungi. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 130. ***Arcyria stipata*** with sporangia on wood and mosses. Photo from The Eumycetozoan Project, DiscoverLife.com, through online permission.

Figure 131. ***Physarum stellatum*** sporangia ready to disperse spores, a species of dead wood and mosses. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 132. ***Trichia favoginea*** on log with liverworts. Photo by Jerry Cooper, through Creative Commons.

Figure 133. ***Physarum flavidum*** sporangia on log, a species also known from mosses. Photo by Sarah Lloyd, with permission.

Figure 134. ***Fuligo aurea*** plasmodium on wood. Photo through Creative Commons.

Figure 135. ***Abies pindrow*** in Manali, India. The slime mold ***Erionema aureum*** grows on the decaying wood of this species. Photo by Vyacheslav Argenberg, through Creative Commons.

Figure 136. ***Abies pindrow*** in India. Photo by Gaurav Verma, through Creative Commons.

Figure 137. ***Cribraria rubiginosa***, a species known from mosses on a log. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Joshaghani *et al.* (2013) added to our knowledge of both slime mold geography and their substrate uses by studying the slime mold flora of Iran. He named ***Arcyria cinerea*** (Figure 32-Figure 33), ***A. incarnata*** (Figure 138), ***Fuligo septica*** (Figure 1, Figure 66), ***Hemitrichia clavata*** (Figure 91), ***H. serpula*** (Figure 110), ***Lycogala epidendrum*** (Figure 67), ***Lycogala exiguum*** (Figure 139-Figure 140), ***Metatrichia vesparia*** (Figure 141), ***Physarum didermoides*** (Figure 142), ***Stemonitis axifera*** (Figure 24), ***S. fusca*** (Figure 69), ***S. splendens*** (Figure 143), ***Stemonitopsis typhina*** (Figure 144), ***Trichia decipiens*** (Figure 145-Figure 146), ***T. favoginea*** (Figure 132), and ***T. scabra*** (Figure 92) as occurring on rotten wood and mosses.

Figure 138. ***Arcyria incarnata*** mature sporangia, a slime mold of rotten wood and mosses. Photo by Stu's Images, through Creative Commons.

Figure 139. ***Lycogala exiguum*** developing sporangia, a species that occurs on rotten wood and mosses. Photo by Katja Schulz, through Creative Commons.

Figure 140. ***Lycogala exiguum*** mature sporangia. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 141. ***Metatrichia vesparia*** sporangia, a species that occurs on rotten wood and mosses. Photo by George Barron, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 142. ***Physarum didermoides*** on mosses, a species that occurs on rotten wood and mosses. Photo by Andrew Khitsun, with online permission.

Figure 143. ***Stemonitis splendens***, a species that occurs on rotten wood and mosses. Photo by Jennifer Linde, through Creative Commons.

Figure 144. ***Stemonitopsis typhina*** sporangia, a species that occurs on rotten wood and mosses. Photo by Sarah Lloyd, with permission.

Figure 145. ***Trichia decipiens*** developing sporangia on decaying wood, a species that occurs on rotten wood and mosses. Photo by Jerzy Opiola, through Creative Commons.

Figure 146. ***Trichia decipiens*** mature sporangia, a species that occurs on rotten wood and mosses. Photo by Fungi07, through public domain.

Stephenson *et al*. (1993) carried out the unusual comparison between slime molds of the two locations in the middle Appalachian Mountains in eastern USA with those of two regions in India. Using 3788 collections, covering 1954-1990, they compared slime molds from tropical-subtropical southern India and three temperate sites. As one might expect, the tropical-subtropical site had the least similarity to the other three sites. The **Physarales** (Figure 19-Figure 22) formed a greater proportion of the southern India collections (63%), whereas the **Liceales** (Figure 51, Figure 55, Figure 120) were much better represented in the three more northern sites. Furthermore, the typical substrata differed, with more than 63% of the southern collections coming from leaf litter and other non-woody debris. On the other hand, more than 80% of the temperate collections were from woody substrates. These differences in slime mold species groups and substrate preferences may help to explain differences seen in their associations with bryophytes. With 80% of the northern species occurring on woody substrates, and the common presence of bryophytes on such substrates, we should expect them to be associated frequently. It is the nature of that association that remains to be defined.

## Where Bryophyte and Slime Mold Meet

Stephenson and Studlar (1985) attempted to determine if the association of slime molds with bryophytes, particularly on logs and stumps, was a preference or just a coincidence. They included only those plasmodial slime molds for which bryophytes served as the primary substrate for fruiting. They concluded that most of the 52 slime mold species occurring on 55 bryophyte species that they were able to sample in North America were coincidental. Only ***Barbeyella minutissima*** (Figure 80) and ***Lepidoderma tigrinum*** (Figure 83) exhibited a preference for leafy liverworts on rotten conifer logs. In fact, ***B. minutissima*** occurred only on the leafy liverworts ***Nowellia curvifolia*** (Figure 82), ***Lepidozia reptans*** (Figure 81), and ***Cephalozia lunulifolia*** (Figure 147) on decorticated logs of ***Picea rubens*** (red spruce; Figure 148). This is a tiny slime mold and was not even seen until collections were examined in the lab with a microscope. ***Lepidoderma tigrinum*** was usually associated with leafy liverworts, especially ***Nowellia curvifolia*** and ***Lepidozia reptans***, but also occasionally with the mosses ***Dicranum montanum*** (Figure 149) and ***Dicranodontium denudatum*** (Figure 150). This species also was fruiting on parts of the logs that were devoid of bryophytes. Kowalski (1971) likewise reported ***L. tigrinum*** on badly decayed coniferous wood growing over and among the mosses and liverworts.

Figure 147. ***Cephalozia lunulifolia***, one of the preferred substrates for ***Barbeyella minutissima***. Photo by Štěpán Koval, with permission.

Figure 148. ***Picea rubens*** (red spruce); liverwort-covered logs of this species are preferred habitats of ***Barbeyella minutissima***. Photo by Keith Kanoti, through Creative Commons.

Figure 149. ***Dicranum montanum***, a moss that is an occasional substrate for ***Lepidoderma tigrinum***. Photo by Bob Klips, with permission.

Figure 150. ***Dicranodontium denudatum***, a moss that is an occasional substrate for ***Lepidoderma tigrinum***. Photo by David T. Holyoak, with permission.

Dudka and Romanenko (2006) considered the relationships between the slime molds and bryophytes to be spatial when they occur together on woody substrata, not trophic. Rather, they may be regulated by their specific microclimatic conditions within the bryophyte colonies. Nevertheless, they considered most of the slime mold associations with bryophytes to be accidental. They seem to develop more extensively and occur more frequently on fallen decaying logs overgrown with bryophytes because of the high humidity that both thrive in (Stojanowska & Panek 2004).

## What Do These Associations Offer?

### Life Cycle Relationships

It appears that bryophytes might play a role in the life cycle of slime molds. Stephenson and Studlar (1985) found a number of slime molds fruiting on bryophytes in temperate North American forests. They considered that 52 of the slime mold species occurring with the 55 bryophytes species were "coincidental." However, the slime molds ***Barbeyella minutissima*** (Figure 80) and ***Lepidoderma tigrinum*** (Figure 83) appear to be truly bryophilous, particularly on leafy liverworts on rotten conifer logs. ***Barbeyella minutissima***, ***Colloderma oculatum*** (Figure 27), and ***Lepidoderma tigrinum*** are not only truly bryophilous, but ***Barbeyella minutissima*** is especially associated with ***Nowellia curvifolia*** (Figure 82) and members of ***Cephalozia*** (Figure 147) (Dudka & Romanenko 2006), species that can completely cover a decaying coniferous log (Schnittler & Novozhilov 1998; Schnittler *et al.* 2000; Novozhilov 2005). Stephenson and Studlar (1985) suggested that in most cases the bryophytes provide exposed surfaces that are convenient for slime mold spore production. On the other hand, the plasmodial stages might reside there without being noticed. ***Barbeyella minutissima*** and ***Lepidoderma tigrinum*** are often associated with the bryophytes aligned with algal layers on decorticated wood (Stephenson & Studlar 1985; Schnittler 2001; Smith & Stephenson 2007; Rollins & Stephenson 2011).

Stephenson and Studlar (1985) were unable to determine if the bryophytes provided a sustainable food source by harboring microorganisms useful for the feeding stages (swarm cells, myxamoebae, plasmodia) of the life cycle. They did consider the bryophytes to be obvious exposed surfaces "convenient for sporulation." Their conclusion was that plasmodia do not avoid bryophytes, but that their sampling was inadequate to determine exclusivity or preference for bryophytes.

### Algae and Cyanobacteria

Algae and **Cyanobacteria** (Figure 152-Figure 153), in addition to bryophytes, are common on decorticated logs. In their investigation of decaying red spruce (***Picea rubens***; Figure 148) logs with both leafy liverworts and slime molds, Smith and Stephenson (2007) found nine **Cyanobacteria** species, two **Chlorophyta** (Figure 154, Figure 156, Figure 157) species, and one **Bacillariophyta** (diatom; Figure 151) species. Of these, two **Cyanobacteria** [***Chroococcus tenax*** (Figure 152) and ***Aphanothece saxicola*** (Figure 153)] and one green alga (***Chlorococcum humicola***; Figure 154) dominated. In addition to potential nitrogen addition through N-fixation, these **Cyanobacteria** and algae could provide a food source for the slime molds.

Figure 151. Mixed diatoms (**Bacillariophyta**). Photo by Janice Glime.

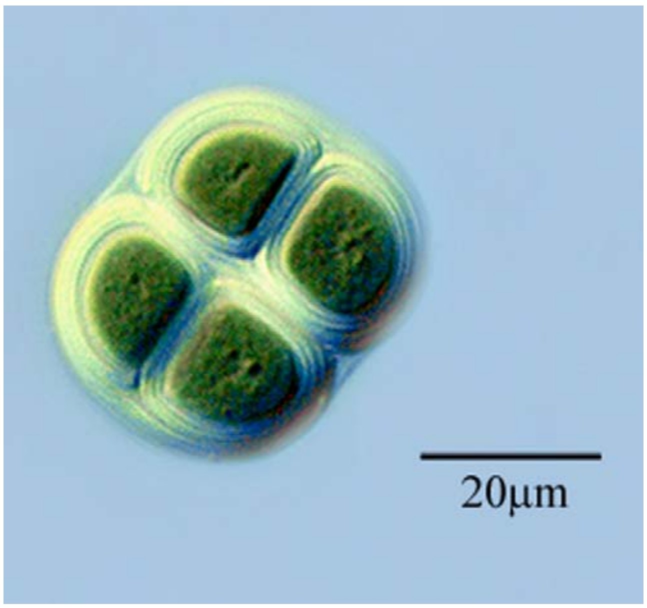


Figure 152. ***Chroococcus tenax***, a species that accompanies both leafy liverworts and slime molds on decaying logs. Photo from Proyecto Agua, through Creative Commons.

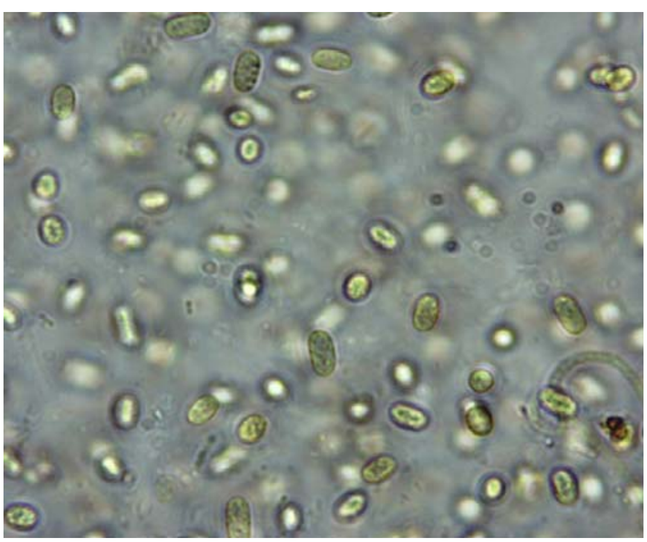

Figure 153. ***Aphanothece*** sp.; ***A. saxicola*** accompanies both leafy liverworts and slime molds on decaying logs. Photo by Karolina Fucikova, through Creative Commons.

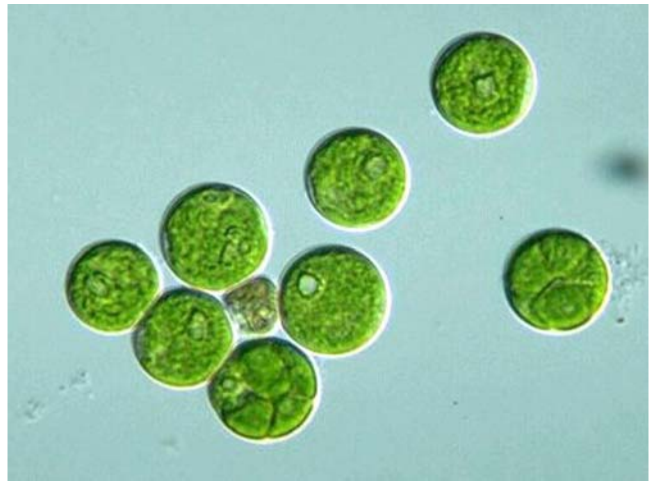

Figure 154. ***Chlorococcum*** sp.; ***C. humicola*** accompanies both leafy liverworts and slime molds on decaying logs. Photo by Yuuji Tsukii, with permission.

The slime mold ***Clastoderma debaryanum*** (Figure 155) occurs on Norway spruce (***Picea abies***; Figure 106) logs in Lithuania (Adamonytė 2007). These logs are covered with algae and some mosses. In other cases, slime molds occur on dead wood covered with a scanty growth of liverworts and algae, or with only algae. This slime mold species is unusual in its ability to grow on substrates with a wide *p*H range of 3.8 to 7.5 (Rosing *et al*. 2007).

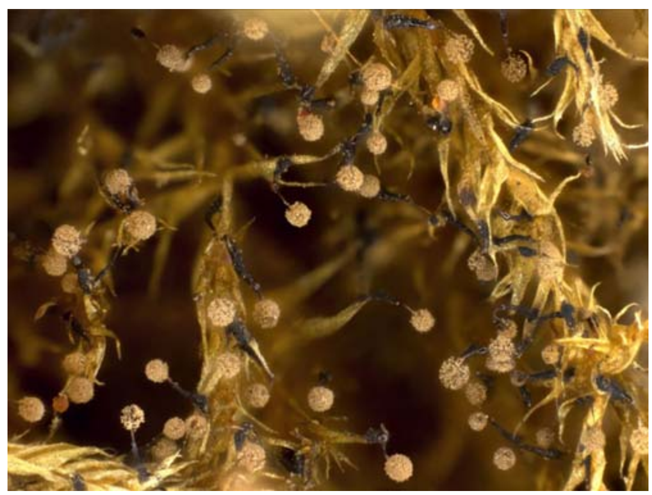

Figure 155. ***Clastoderma debaryanum*** on mosses. Photo from Myxotropic, with online permission.

Interestingly, ***Barbeyella minutissima*** (Figure 80) grows on leaf tips that protrude above the water film (Schnittler & Novozhilov 1998). Association with algae was "obvious" in 70% of the collections and in 60% of the collections of ***Colloderma oculatum*** (Figure 27). The late season fruiting insures cool nights that provide extended dewfall, keeping the logs moist enough for algal/Cyanobacterial growth for weeks. On the other hand, ***Barbeyella minutissima*** and ***Licea pygmaea*** (Figure 120), accompanied by scattered sporocarps of ***Colloderma*** and ***Lepidoderma*** (Figure 83), occur primarily on the lower sides of logs directed towards the rivulet but preserved from rainfall itself.

Slime molds are known to feed on algae (Zabka & Lazo 1962). In fact, Lazo demonstrated that the slime

mold ***Physarum didermoides*** (Figure 142) can incorporate cells of the green alga ***Chlorella*** (Figure 156), a common symbiont in lichens and even *Hydra*, into its plasmodium, causing the plasmodium to be green. In addition to these examples, the plasmodium of occasional moss dweller ***Didymium iridis*** (Figure 38) is known to contain the green alga ***Trebouxia*** (Figure 157) (Keller & Braun 1999), a common lichen symbiont. But who benefits in this relationship with slime molds, and how?


Figure 156. ***Chlorella***, an apparent symbiont in the plasmodium of ***Physarum didermoides***. Photo by Barry H. Rosen, through Creative Commons.


Figure 157. ***Trebouxia***, an apparent symbiont in the plasmodium of ***Didymium iridis***. Photo by Alan J. Silverside, with permission.

## Decay Stages

As noted by Leontyev (2010), most slime molds tend to be limited to a particular type of substrate. Some become more specific, occupying only a particular stage of wood decay. For example, ***Arcyria incarnata*** (Figure 138) and ***Comatricha nigra*** (Figure 158-Figure 159) prefer the second stage, one of firm, decorticated wood. ***Trichia favoginea*** (Figure 132) and ***T. scabra*** (Figure 92) prefer the third stage in which the wood has an average degree of decomposition, but is still not colonized by mosses. In the fourth stage, the wood is fully decomposed and covered by mosses, a stage preferred by the slime molds ***Metatrichia vesparia*** (Figure 141) and ***Tubifera ferruginosa*** (Figure 160).

Figure 158. ***Comatricha nigra*** young sporangia. Photo by Bjorlil, through Creative Commons.

Figure 159. ***Comatricha nigra*** sporangia on firm, decorticated wood. Photo by Helen Ginger, through Creative Commons.

Figure 160. ***Tubifera ferruginea*** on bryophytes, a slime mold that prefers fully decomposed wood covered with mosses. Photo by Amadej Trnkoczy, through Creative Commons.

As wood decays, its structure and moisture content change. Initially, the logs have the species that were present on the living trunk. However, as the log changes,

the bark falls off, and the species of mosses, liverworts, lichens, and algae go through a successional process that results in very different assemblages from those on the living tree (Ing 1994).

Schnittler and Novozhilov (1998) describe the decay stages of the wood from decorticated logs, thicker than 15 cm, that are slightly to moderately decayed. These come from very moist (water-saturated air) and shady places and are covered by a thin, slimy layer of algae and liverworts. The moist wood stage is mostly decorticated, with a moderate to strong decay, and are covered with a thicker cover (>1 cm thick) of mosses, frequently ***Paraleucobryum*** sp. (Figure 161) and sometimes species of the leafy liverwort ***Mylia*** (Figure 162). This association is typically enriched with detritus. Differing from ***Barbeyella minutissima*** (Figure 80) and ***Colloderma oculatum*** (Figure 27) that occur almost entirely on the decorticated spruce and fir logs that have coverings of slimy algae and **Cyanobacteria**, ***Cribraria cancellata*** (Figure 163) and ***Diderma montanum*** (Figure 164) tend to occur in the cooler valley bottoms, where they produce sporangia on moderately decayed wood of spruce and beech, often on logs with mossy, loose bark.

Figure 161. ***Paraleucobryum longifolium***, a moss of the moist wood stage of mostly decorticated logs. Photo by Hermann Schachner, through Creative Commons.

Figure 162. ***Mylia taylorii***; the genus ***Mylia*** often occurs on the moist wood stage of the mostly decorticated logs. Photo by David T. Holyoak, with permission.

Figure 163. ***Cribraria cancellata*** sporangia, a species that occurs on moderately decayed wood of spruce and beech, often on logs with mossy, loose bark. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 164. ***Diderma montanum*** sporangia, a species that occurs on moderately decayed wood of spruce and beech, often on logs with mossy, loose bark. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Stephenson and Studlar (1985) concluded that ***Barbeyella minutissima*** (Figure 80) and ***Lepidoderma tigrinum*** (Figure 83) are bryophilous, being almost invariably associated with bryophytes, and in particular with leafy liverworts. Schnittler *et al*. (2000) examined collections from 27 localities in the Northern Hemisphere. They concluded that these two species are restricted to decorticated coniferous wood covered by 40-100% leafy liverworts, based on 41 collections. They furthermore noted the importance of a "thin, slimy layer" of algae.

Stojanowska and Panek (2004) reported a number of bryophyte-slime mold-log associations from a nature reserve in southwest Poland. ***Cribraria vulgaris*** (Figure 78) and ***Lycogala epidendrum*** (Figure 67) occur there on moss-covered stumps and logs. ***Fuligo septica*** (Figure 1, Figure 66), ***Lycogala exiguum*** (Figure 139-Figure 140), ***Metatrichia vesparia*** (Figure 141), ***Stemonitis fusca*** (Figure 69), ***S. pallida*** (Figure 57), ***Trichia botrytis*** (Figure 25), ***T. persimilis*** (Figure 113-Figure 114), ***T. varia*** (Figure 72), and ***Tubifera ferruginosa*** (Figure 73) occur on bryophyte-covered stumps. ***Diderma radiatum*** (Figure 165-Figure 166) occurs on stumps overgrown with the moss ***Brachythecium rutabulum*** (Figure 167). ***Arcyria cinerea*** (Figure 32-Figure 33), ***A. denudata*** (Figure 62-Figure 63), ***Physarum compressum*** (Figure 168-Figure 169), ***Physarum gyrosum*** (Figure 170-Figure 171), ***Stemonitis axifera*** (Figure 24), and ***Trichia scabra*** (Figure 92) occur on bryophyte-covered logs. ***Lepidoderma tigrinum*** (Figure 83) occurs on decaying logs densely

overgrown with ***Dicranum montanum*** (Figure 149) (see also Neubert *et al.* 1993), whereas ***Badhamia panicea*** (Figure 172-Figure 173) occurs on bark of a recent log with ***Brachythecium rutabulum***. ***Reticularia lobata*** (syn.=***Enteridium lobatum***; Figure 174) occurs on bryophyte-covered conifer wood. They also mentioned that ***Lamproderma columbinum*** (Figure 42) occurs on ***Tetraphis pellucida*** (Figure 175), a moss species most typical of decaying stumps, but that also occurs on rocks. The co-occurrence of particular slime molds with specific mosses may reflect a preference of both for the same microclimate.

Figure 165. ***Diderma radiatum*** sporangia on log with mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 166. ***Diderma radiatum*** sporangia, ready for dispersal. Photo from Myxotropic, through Creative Commons.

Figure 167. ***Brachythecium rutabulum***, a common substrate for ***Diderma radiatum***. Photo by Arnoldius, through Creative Commons.

Figure 168. ***Physarum compressum*** on bryophytes. Photo courtesy of Sarah Lloyd.

Figure 169. ***Physarum compressum*** fruiting. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 170. ***Physarum gyrosum*** fruiting; this slime mold can be found on logs covered with bryophytes. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

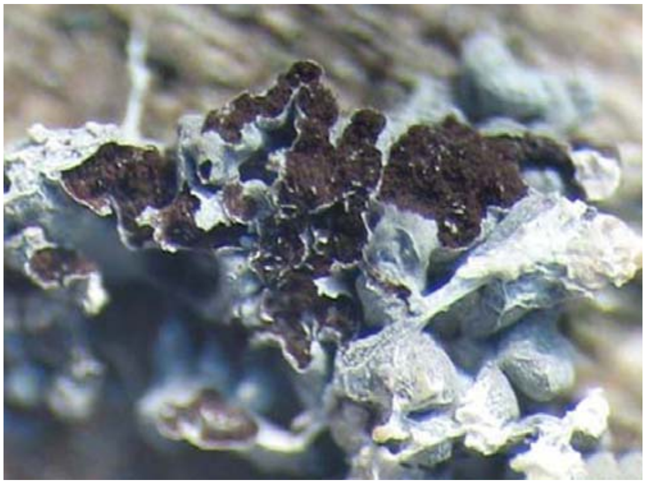

Figure 171. ***Physarum gyrosum*** fruiting and dispersing spores. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 172. ***Badhamia panicea*** sporangia, a species that occurs on bark of a recent log with the moss ***Brachythecium rutabulum***. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 173. ***Badhamia panicea*** sporangia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.


Figure 174. ***Reticularia lobata***, a species of bryophyte-covered conifer wood. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 175. ***Tetraphis pellucida***, a moss that is sometimes a substrate for the slime mold ***Lamproderma columbinum***. Photo by Hermann Schachner, through Creative Commons.

## Spore Traps

We know from studies on dwarf males that some bryophyte spores successfully germinate on leaves of the same species. This raises the questions of what other kinds of propagules are successful there, and how widespread are these relationships with other kinds of organisms.

Stephenson and Rojas (2020) raised this question regarding slime molds associated with bryophytes. Most spores are dispersed by wind; some are dispersed by animals. The wind dispersal appears to be very efficient within distances of at least 50 meters (Schnittler *et al.* 2006; Schnittler & Tesmer 2008). The spores seem able to travel until they meet a physical surface where they can rest (Stephenson & Rojas 2020). Since mosses can provide such surfaces, Stephenson and Rojas used nylon bags containing sterilized mosses from the tropics in Costa Rica (predominantly ***Pilotrichella flexilis*** – Figure 176) and the temperate deciduous forest of northwest Arkansas, USA (predominantly ***Thuidium delicatulum*** – Figure 3). The mosses in the bags were collected after more than four months and cultured. Of the 40 moist chamber cultures from the tropics, 95% showed growth of **Myxomycetes** and 90% of these produced fruiting bodies. However, the temperate cultures produced **Myxomycetes** growth in only 70% of the cultures, with only 18% producing fruiting

bodies. The Costa Rica cultures similarly had 91 specimens appearing; the Arkansas cultures had only three species, representing three different genera. ***Diderma effusum*** (Figure 177) was the only species present in cultures from both locations. From Arkansas, only ***Diderma effusum*** (3 records) and ***Cribraria microcarpa*** (2 records; Figure 178) were present in at least two cultures. Interestingly, the most abundant species in Costa Rican cultures were ***Diderma effusum*** (16 records) and ***Cribraria violacea*** (16 records; Figure 45, Figure 179), as well as ***Perichaena dictyonema*** (16 records; Figure 180) and ***Gulielmina vermicularis*** (15 records; Figure 181-Figure 182). Furthermore, 44% of the 91 Costa Rican specimens were members of the genus ***Perichaena***/***Gulielmina***. However, many of these species occurred only once. Those cultures from Costa Rica had a mean of 2.3 specimens per culture; those from Arkansas had only 0.2 per culture.

Figure 176. ***Pilotrichella flexilis***, a spore trap for slime molds in Costa Rica. Photo by Claudio Delgadillo Moya, with permission.

Figure 177. ***Diderma effusum*** on rotting wood. Photo by Clive Shirley, Hidden Forest (hiddenforest.co.nz), with permission.

Figure 178. ***Cribraria microcarpa*** on log with mosses. Photo by Tyson Ehlers, through Creative Commons.

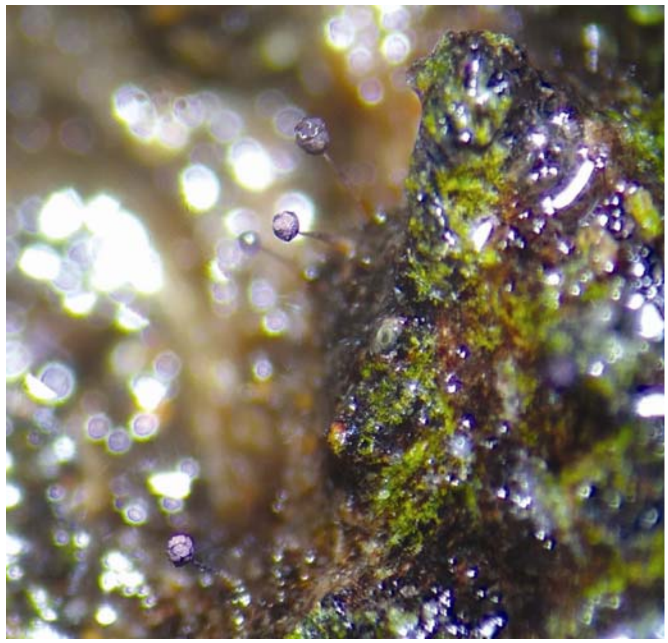

Figure 179. ***Cribraria violacea*** with mosses. Photo by Peta McDonald, through Creative Commons.

Figure 180. ***Perichaena dictyonema*** on rotting wood. Photo by Allison K. Pollack, through Creative Commons.

Figure 181. ***Gulielmina vermicularis*** transforming to its sporangial phase. Photo by Merlu, through Creative Commons.

Figure 182. ***Gulielmina vermicularis*** on rotting wood. Photo by Alejandro Huereca, through Creative Commons.

Differences in environmental factors may be responsible for the differences in species abundance between the two sites (Stephenson & Rojas 2020). The Arkansas site had a lower mean *p*H and was drier during the study period. Sporangia of **Myxomycetes** are more common in moist periods. There are insufficient data from the two regions to make a comparison of number of species present in the area. This study demonstrates the potential role of mosses as spore traps that increase the diversity of slime molds and remind us of the moss potential to serve a similar role for other kinds of organisms with small propagules.


## Summary

Bark and logs are the two most common substrata for slime molds. And both of these substrates frequently have bryophytes on them. The motile slime molds therefore encounter bryophytes as they move about and may traverse them or stay and form sporangia. On logs in particular, leafy liverworts are common, and these seem to be suitable substrates for a number of slime molds. In some cases, the underlying algae might contribute to this association, providing fixed nitrogen or food.

Slime molds that move upward and into the light to produce sporangia may gain some advantage on the slightly elevated bryophytes. This positioning can provide greater access to dispersal agents, including wind and invertebrates. Nevertheless, the bryophytes used are of low stature, with **smooth mats** being the most frequent.

***Diderma corrugatum*** seems to be restricted to moss-covered bark, whereas ***D. chondrioderma*** seems only to prefer it. Some of the slime molds seem to be confined to liverworts, including ***Barbeyella minutissima*** on logs, ***Licea bryophila*** on bark, and ***Licea gloederma*** on bark. ***Licea parasitica*** seems to prefer mosses in its **microcyst** stage. ***Colloderma oculatum***, ***Lamproderma columbinum***, and ***Lepidoderma tigrinum*** are common only associated with ***Barbeyella minutissima*** on bryophyte-covered logs, especially with the liverwort ***Nowellia curvifolia***. On the other hand, most of the bryophyte dwellers seem to be accidentals – generalists that tolerate the substrate with no preference for it. Others occur on mossy logs or bark, but not directly on the bryophytes.

In some cases, the slime mold seems to start on bark and invade the bryophyte. In other cases, it germinates on the bryophyte and moves onto the bark or wood. In the latter case, the bryophyte might benefit from the greater moisture in the bryophyte mat, in addition to the ability of the bryophyte to trap the spores.

Both of bark and logs have periods of drying out, especially tree boles. The slime molds and mosses are both tolerant of these events, but mosses are able to slow the drying process due to their capillary spaces. In addition to moisture, *p*H seems to be important in separating substrata among slime mold species. Decay stages are likewise important, with different stages providing different moisture levels, but also typically having more bryophytes as they decay more. Slime molds on logs with bryophytes are often also associated with algae and Cyanobacteria, especially ***Chroococcus tenax***, ***Aphanothece saxicola***, and ***Chlorococcum humicola***.

Bryophytes are important as spore traps for slime molds, but many questions remain regarding the importance of this relationship.



## Acknowledgments

Marianne Meyer and Isabelle Charissou were very helpful in providing me with pictures of slime molds on mosses and Marianne helped me with identification of some images contributed by others. Harold W. Keller provided additional information and images to support the story on ***Diachea arboricola***. Steve Stephenson provided me with the paper on spore traps and helped me sort out the nomenclature.

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# CHAPTER 3-4
# SLIME MOLDS: ECOLOGY AND HABITATS – LESSER HABITATS

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# CHAPTER 3-4 SLIME MOLDS: ECOLOGY AND HABITATS – LESSER HABITATS

Figure 1. ***Lophocolea heterophylla*** with slime molds. Photo by Sture Hermansson, with online permission.

## Epiphyllous Leafy Liverwort Associations

In the tropics, **epiphyllous** (growing on leaves) liverworts (Figure 2) are common, typically associated with lichens, fungi, algae, and bacteria. Mosses are rare in this association. But some associations also include slime molds.

Schnittler (2001) found eleven species of slime molds associated with epiphyllous liverworts (Figure 2) in Ecuador, Costa Rica, and Puerto Rico. He found 11 species, with 97% of the 131 cultures producing growths of slime molds. One of his finds, ***Arcyria afroalpina*** (Figure 3-Figure 4), was a new find for the Neotropics (Schnittler *et al*. 2002). When samples of 15 leaf pieces were cultured in moist chambers, the most frequent slime mold species (59-66%) were ***Arcyria cinerea*** (Figure 5), ***Didymium iridis*** (Figure 6), and ***D. squamulosum*** (Figure 7). These most likely occur with the epiphylls as myxamoebae. Lowland rainforests that have a high annual rainfall provide the greatest numbers of slime molds. However, the habitat appears to be less than ideal, as evidenced by the atypically small sporocarps.

Figure 2. ***Leptolejeunea epiphylla*** on leaf. Photo by Tom Thekathyil, with permission.

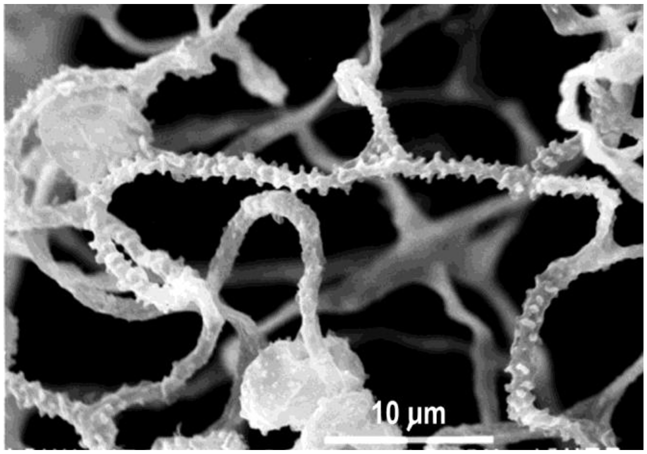


Figure 3. ***Arcyria afroalpina*** spores and capillitia. Photo by Yuri Novozhilov, Eumycetozoan Project, DiscoverLife.org, with online permission.

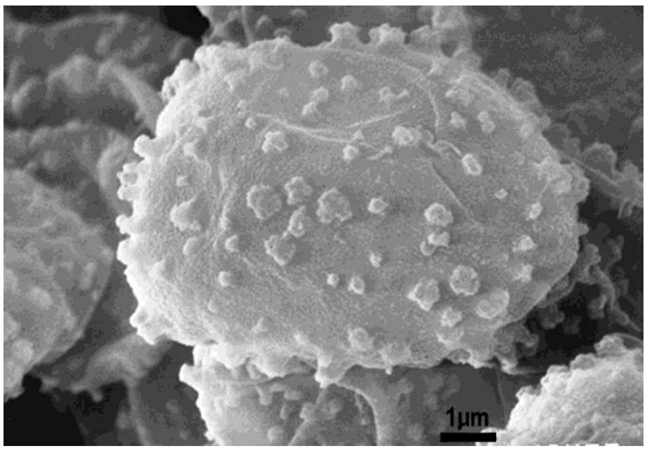


Figure 4. ***Arcyria afroalpina*** spore, SEM. Photo by Yuri Novozhilov, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 5. ***Arcyria cinerea***, one of the most frequent epiphyllous species of slime molds cultured from leaves with epiphyllous liverworts. Photo by Kim Fleming, through Creative Commons.

On the other hand, all six sites clearly share an assemblage of common species (Fig. 2) (Schnittler 2001). The average frequency of the three most common species on epiphyllous liverwort covers was surprisingly high, with 0.59 for ***Arcyria cinerea*** (Figure 5) and 0.66 for both ***Didymium iridis*** (Figure 6) and ***D. squamulosum*** (Figure 7). At least the three most common species of slime molds (***Arcyria cinerea***, ***Didymium iridis***, and ***D. squamulosum***) are very probably regular inhabitants of liverwort-covered leaves. Several lines of evidence seem to support this. First, all three species were found with very scattered and often solitary sporocarps considerably smaller than typical for fructifications of these species in other microhabitats. In addition, tiny **phaneroplasmodia** (conspicuous plasmodia, as in the **Physarales**; Figure 8), 1-3 mm in extent were frequently observed in the first two weeks of culture. Plasmodia migrating from the litter layer to fruit on living plants are much larger.

Figure 6. ***Didymium iridis*** sporangia, one of the most frequent epiphyllous species of slime molds cultured from leaves with epiphyllous liverworts. Photo through Creative Commons.

Figure 7. ***Didymium squamulosum***. Photo by John Shadwick, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 8. Phaneroplasmodium. Photo by Sarah Lloyd, with permission.

There is a potential for direct leaf-to-leaf dispersal of myxamoebae as well as their dormant stages (**microcysts**) by rainwater or leaf-dwelling insects (Schnittler 2001). Occasional cultures produce growths of ***Diderma effusum*** (Figure 9), ***D. hemisphaericum*** (Figure 10), ***Lamproderma scintillans*** (Figure 11), and ***Physarum compressum*** (Figure 12); all other recorded slime molds are rare. None of the slime molds found in this study seems to be specialized for living leaves as a microhabitat. The leaf microflora most likely supplies ample food for successful colonization. However, some differ sufficiently from non-epiphyllous populations that they might be separate races.

Figure 11. ***Lamproderma scintillans*** sporangia, a slime mold that occasionally occurs with epiphyllous liverworts. Photo by Ray Simons, The Eumycetozoa Project, DiscoverLive.com, with online permission.

Figure 9. ***Diderma effusum*** on moss, a slime mold that occasionally occurs with epiphyllous liverworts. Photo by Ray Simons, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 12. ***Physarum compressum***, a slime mold that occasionally occurs with epiphyllous liverworts. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Camino *et al*. (2008) reported on the slime molds in the mountains of central Cuba. There they found two species associated with epiphyllous liverworts: ***Arcyria afroalpina*** (Figure 4-Figure 3) and ***Comatricha laxa*** (Figure 13).

Figure 10. ***Diderma hemisphaericum***, a slime mold that occasionally occurs with epiphyllous liverworts. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 13. ***Comatricha laxa*** sporangia on decaying log, a species known to also associate with epiphyllous leafy liverworts. Photo by Clive Shirley, The Hidden Forest, with permission.

## Non-Epiphyllous Liverwort Associations

Stephenson and Studlar (1985) reported ***Arcyria cinerea*** (Figure 5), ***Physarum viride*** (Figure 14), ***Stemonitis axifera*** (Figure 15-Figure 16), ***Trichia decipiens*** (Figure 17), and ***T. favoginea*** (Figure 18) associated with non-epiphyllous leafy liverworts, but they were not restricted to this substrate. As already noted, ***Barbeyella minutissima*** (Figure 19) and ***Lepidoderma tigrinum*** (Figure 20) exhibited a preference for leafy liverworts on rotten conifer logs. In fact, the rare ***B. minutissima*** is mostly known from the leafy liverworts ***Nowellia curvifolia*** (Figure 19, Figure 21), ***Lepidozia reptans*** (Figure 22), and ***Cephalozia lunulifolia*** (Figure 23-Figure 24).

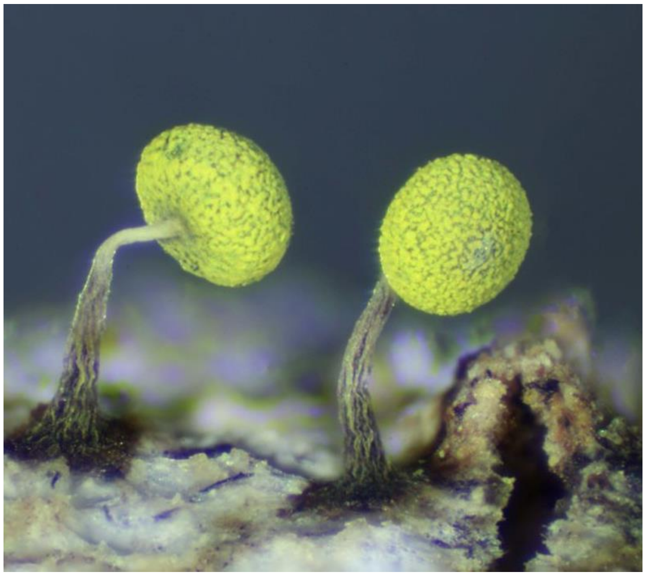

Figure 14. ***Physarum viride*** sporangia, a species that can be associated with leafy liverworts on logs and elsewhere. Photo by Sarah Lloyd, with permission.

Figure 15. ***Stemonitis axifera*** plasmodium starting to produce sporophytes, a species that can be associated with leafy liverworts on logs and elsewhere. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 16. ***Stemonitis axifera*** with liverworts, a species that can be associated with leafy liverworts on logs and elsewhere. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 17. ***Trichia decipiens*** sporangia, a species that can be associated with leafy liverworts on logs and elsewhere. Photo by Fungi07, through public domain.

Figure 18. ***Trichia favoginea*** on log with liverworts. Photo by Jerry Cooper, through Creative Commons.

Figure 19. ***Barbeyella minutissima*** sporangia on the leafy liverwort ***Nowellia curvifolia***. Photo by Randy Darrah, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 20. ***Lepidoderma tigrinum*** with sporangia on moss, a species that is more common on leafy liverworts. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 21. ***Nowellia curvifolia*** on log, a suitable substrate for a number of species of slime molds. Photo by Bernd Haynold, through Creative Commons.

Figure 22. The liverwort ***Lepidozia reptans***. Photo by Michael Lüth, with permission.

Figure 23. ***Cephalozia lunulifolia***, a suitable substrate for a number of species of slime molds. Photo by Michael Lüth, with permission.

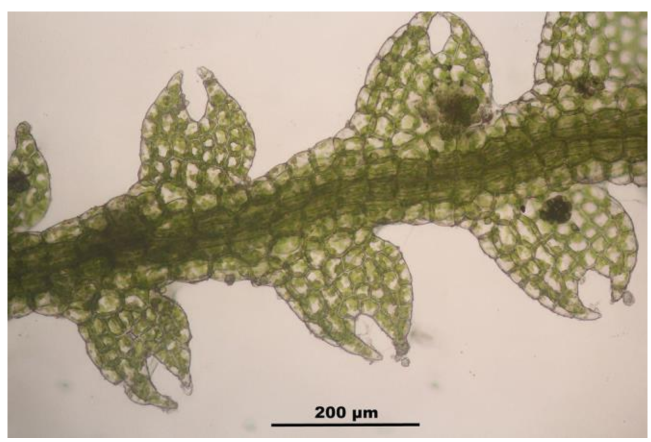


Figure 24. ***Cephalozia lunulifolia***, a suitable substrate for a number of species of slime molds. Photo by Hermann Schachner, through Creative Commons.

***Nowellia curvifolia*** (Figure 19, Figure 21) is the most common slime mold associate (Stephenson & Studlar 1985); it is a liverwort found almost exclusively on rotten logs (Schuster 1957). Hence, the preference in the rotting log habitat for leafy liverworts may simply be that leafy

liverworts are common on rotting logs. The mosses ***Tetraphis pellucida*** (Figure 25) and ***Dicranum montanum*** (Figure 26-Figure 27) are also common associates of slime molds, and likewise are characteristic of rotting wood (Stephenson & Studlar 1985). It is likely that the slime molds are opportunists or simply have broad enough habitat requirements to permit their survival **on** the potentially competing bryophytes.

Figure 25. ***Tetraphis pellucida*** with gemmae, a common rotten wood moss. Photo by Hermann Schachner through Creative Commons.

Figure 26. ***Dicranum montanum***, a suitable substrate for some slime molds, on rotting log. Photo by Janice Glime.

Figure 27. ***Dicranum montanum*** showing the curly leaves when dry. Photo by Janice Glime.

## Leaf Litter

Some moss dwellers are also litter slime molds. Compagno *et al*. (2016) reported ***Didymium melanospermum*** (Figure 28) on mosses or litter. Moreno *et al*. (2018) found ***Didymium nigripes*** (Figure 29) on moss debris in Spain. Doidge (1950) reported ***Diderma subdictyospermum*** on moss and dead leaves. Similarly, Ranade *et al.* (2012) reported ***Diderma alpinospumarioides*** on dead leaves and twigs, but sometimes on living moss in India. Renade and coworkers found that ***Physarum melleum*** (Figure 30) occurs on dead leaves as well as among living mosses. Sarah Lodge photographed ***Collaria*** *aff.* ***rubens*** (Figure 31) on mosses; this is a species that typically is associated on deciduous leaf litter (Takahashi 2015).

Figure 28. ***Didymium melanospermum*** on leaves of a soil moss (**Mniaceae**). Photo by Armand Turpel, through Creative Commons.

Figure 29. ***Didymium nigripes*** sporangia, a species known from moss debris. Photo by Christophe Quintin, with online permission.

Figure 30. ***Physarum melleum*** sporangia, a species of dead leaves and living mosses. Photo by Clive Shirley, The Hidden Forest, with permission.

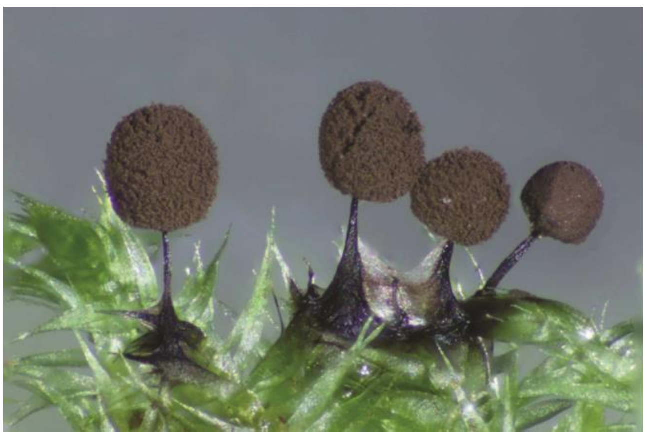

Figure 31. ***Collaria*** *aff.* ***rubens*** on mosses, a species associated with leaf litter. Photo by Sarah Lloyd, with permission.

## Soil Associations

Soil associations between bryophytes and slime molds seem to be much less common than associations in other habitats. In temperate forests, mosses of **Polytrichaceae** (Figure 32, Figure 36), **Dicranaceae** (Figure 33-Figure 34), and **Hypnaceae** (Figure 35) are common, with the slime molds ***Fuligo muscorum*** (Figure 36), ***Physarum citrinum***, ***P. confertum*** (Figure 37), and ***P. virescens*** (Figure 38-Figure 39) occasionally occurring on them (Ing 1994). One very rare slime mold (***Elaeomyxa cerifera*** – Figure 40-Figure 41) is known from the soil-dwelling thallose liverwort ***Pellia epiphylla*** (Figure 42) (Hadden 1921; Ing 1994) and from decaying wood, usually in association with bryophytes (Steven Stephenson, pers. comm. 1 June 2019).

Figure 32. ***Polytrichum*** sp. on the forest floor, habitat for ***Fuligo muscorum*** and several species of ***Physarum***. Photo by Janice Glime.

Figure 33. ***Dicranum scoparium*** on the forest floor, habitat for ***Fuligo muscorum*** and several species of ***Physarum***. Photo by Janice Glime.

Figure 34. ***Dicranum scoparium***, habitat for ***Fuligo muscorum*** and several species of ***Physarum***. Photo by Janice Glime.

Figure 35. ***Hypnum curvifolium***, a species of the forest floor and logs and a common substrate for moss-dwelling slime molds. Photo by Bob Klips, through Creative Commons.

Figure 36. ***Fuligo muscorum*** on **Polytrichaceae**. Photo by James K. Lindsey, with permission.

Figure 37. ***Physarum confertum***, a slime mold species that occurs on forest mosses in the families **Polytrichaceae**, **Dicranaceae**, and **Hypnaceae**. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 38. ***Physarum virescens*** in early fruiting stage on moss. Photo by Alexey Sergeev, with permission.

Figure 39. ***Physarum virescens*** on the moss ***Dicranum***. Photo by Alexey Sergeev, with permission.

Figure 40. ***Elaeomyxa cerifera*** with sporangia on mosses. Photo by Sarah Lloyd, with permission.

Figure 41. ***Elaeomyxa cerifera*** sporangium beginning to dehisce. Photo from Myxotropic.org, through Creative Commons.

Figure 42. ***Pellia epiphylla*** with capsules, substrate for ***Elaeomyxa cerifera***. Photo by Li Zhang, with permission.

Pant and Tewari (1982) described the growth of ***Fuligo intermedia*** (Figure 43) on mosses in Nainital in the Himalayan region of India. These slime molds occurred on the mosses ***Atrichum obtusulum***, ***Pogonatum aloides*** (Figure 44), ***Barbula*** sp. (Figure 45), and ***Leucodon secundus***. Only the green tips of the mosses appeared above the yellowish-white of the ***Fuligo intermedia*** (Figure 43). They suspected that the growth of the mosses was retarded. A related species, ***Fuligo cinerea*** (Figure 46-Figure 47) occurs on dead leaves, yeast, and rotten cloth pieces, as well as on mosses and lichens.

Figure 43. ***Fuligo intermedia*** on ***Polytrichum***. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 44. ***Pogonatum aloides*** (**Polytrichaceae**), one of the substrates for the slime mold ***Fuligo intermedia***. Photo by Hermann Schachner, through Creative Commons.

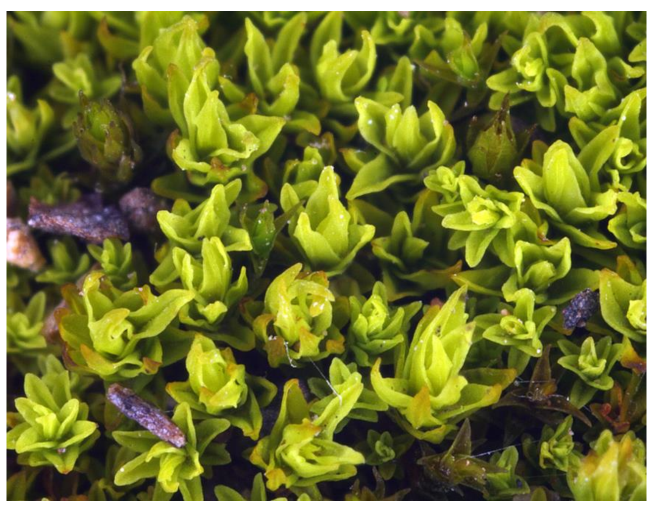

Figure 45. ***Barbula convoluta***; the genus ***Barbula*** is one of the substrates for the slime mold ***Fuligo intermedia***. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

Figure 46. ***Fuligo cinerea*** on lichens and leafy liverworts on bark. Photo by Alexey Sergeev, with permission.

Figure 47. ***Fuligo cinerea*** on a mossy forest floor. Photo by Ramsés Pérez, through Creative Commons.

It is not unusual to find that species cannot be put into their proper substrate heading when using the descriptions. This is not necessarily the fault of the author. Information is often based on herbarium labels and material present with the specimen, but not seen in the field by the author(s). ***Physarum citrinum*** occurs on terrestrial mosses in woodlands, but were the mosses on soil (Ing 1982)? Later, Ing (1994) reported this species from soil. Ing (1982) was able to be more specific in reporting ***Physarum virescens*** (Figure 38-Figure 39) as mostly on terrestrial mosses in woodlands and characteristic of sessile oakwoods, a species that elsewhere is also almost always associated with bryophytes (Steven Stephenson, pers. comm, 1 June 2019). In Spain, ***Physarum bivalve*** (Figure 49) occurs on mosses (Castillo *et al*. 2009), but in what habitat?

Figure 48. ***Typhula lutescens*** with sporangia on mosses. Photo by Tomasz Pachlewski, with permission.

Figure 49. ***Physarum bivalve***, a species known from mosses in Spain. Photo by Rod Nelson, DiscoverLife.org, with online permission.

Schnittler and Novozhilov (1996) described several slime mold-bryophyte associations that appear to be on soil in their study of the northern Karelia of Russia. One they noted as a very scanty collection of ***Physarum*** *cf.* ***carneum*** on mosses. They were more specific in noting ***Physarum virescens*** (Figure 38-Figure 39) as preferring big moss tussocks on the ground, especially ***Dicranum*** (Figure 103). ***Stemonitis fusca*** (Figure 50) was represented by a single collection on moss tussocks in a spruce-birch-aspen woodland. ***Didymium melanospermum*** (Figure 28) typically occurs on thick moss tussocks on soil, but it also occurs at the base of rocks, or even more rarely on litter.

Similarly, ***Leocarpus fragilis*** (Figure 51-Figure 52) can grow on the ground, on mosses, and on litter, but it can only be located in autumn.

Figure 50. ***Stemonitis fusca*** with sclerotia and sporangia on mosses. Photo by Deryni, through Creative Commons.

Figure 51. ***Leocarpus fragilis*** on moss. Photo by Matt Goff, Sitka Nature, with permission.

Figure 52. ***Leocarpus fragilis*** on a soil moss in the **Polytrichaceae**. Photo by Boris Loboda, with permission.

Ranade *et al*. (2012) reported several species that are likely to be associated with soil or litter. ***Cribraria intricata*** (Figure 53; syn.=*C. dictydioides*) occurs not only on rotten wood, but also on roots and dead mosses. ***Cribraria languescens*** (Figure 54-Figure 55) occurs on rotten stems and mosses, presumably on the ground. They reported that ***Physarum didermoides*** (Figure 56; syn.=*Diderma spumarioides*) occurs on living moss, presumably on soil mosses. ***Collaria arcyrionema*** (Figure 57; syn.=*Lamproderma arcyrionema*) occurs not only on wood, but also on dead leaves and mosses. ***Lamproderma echinulatum*** (Figure 58) and ***Metatrichia floriformis*** (Figure 59; syn.=*Trichia floriformis*) likewise occur on mosses, presumably on the forest floor. ***Physarum brunneolum*** (Figure 60) occurs not only on mosses, but also on lichens and decaying wood; again, the substrate of the mosses and lichens is not provided. The most unusual substrate is that of ***Stemonitis flavogenita*** (Figure 61) on a dead archegoniophore of the thallose liverwort ***Marchantia*** sp. (Figure 62), presumably with the latter growing on soil.

Figure 53. ***Cribraria intricata*** sporangia on bark with a few mosses. Photo by Fluff Berger, through Creative Commons.

Figure 54. ***Cribraria languescens***, a species that occurs on rotten wood, roots, and dead mosses. Photo from Myxotropic, through Creative Commons.

Figure 55. ***Cribraria languescens*** sporangium. Photo from Myxotropic, through Creative Commons.

Figure 56. ***Physarum didermoides*** on mosses. Photo by Andrew Khitsun, with online permission.

Figure 57. ***Collaria arcyrionema***, a species that occurs on dead wood and mosses. Photo by Taibif.tw, through Creative Commons.

Figure 58. ***Lamproderma echinulatum*** sporangia on bryophytes. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 59. ***Metatrichia floriformis*** with mosses on bank. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 60. ***Physarum brunneolum***, a species of mosses, lichens, and decaying wood. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 61. ***Stemonitis flavogenita***, a species that has been found on a dead archegoniophore of ***Marchantia***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 62. ***Marchantia polymorpha*** archegoniophores, one of the substrates for ***Stemonitis flavogenita***. Photo by Janice Glime.

Joshaghani *et al*. (2013) reported ***Badhamia ovispora*** as occurring on forest mosses in Iran. This suggests that they grew on soil mosses as the other records were more specific in referring to wood or rotten wood.

Stojanowska and Panek (2004) were specific about a number of species of slime molds that occurred on mosses on logs or stumps, but they reported some simply from mosses. Presumably, these were forest floor mosses, including ***Diachea leucopodia*** (Figure 63), ***Diderma testaceum*** (Figure 64), and ***Physarum virescens*** (Figure 38-Figure 39) (plasmodial stage). They described ***Diderma deplanatum*** (Figure 65) as surrounding mosses. ***Lamproderma columbinum*** (Figure 66) occurred on the moss ***Tetraphis pellucida*** (a species of rocks and decaying wood; Figure 25), but also on the moss ***Dicranum scoparium*** (Figure 33-Figure 34) – a moss that could occur on soil, rocks, logs, or tree bases.

Figure 63. ***Diachea leucopodia*** on leaf litter, a species that also occurs on mosses. Photo by Rosser1954, through Creative Commons.

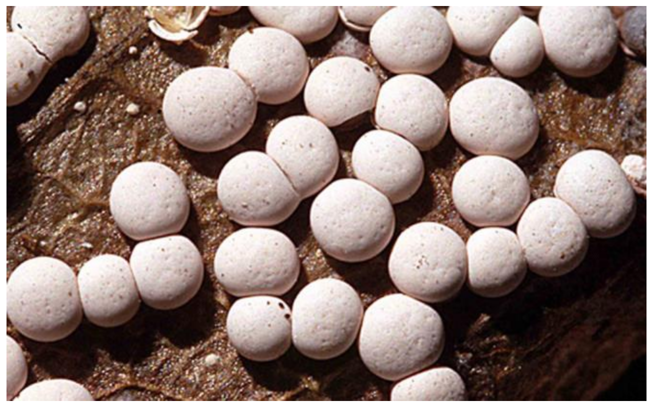

Figure 64. ***Diderma testaceum*** on leaf litter, a species that also occurs on mosses. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.


Figure 65. ***Diderma deplanatum*** on mosses. Photo by The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 66. ***Lamproderma columbinum***, with fruiting bodies of slime mold on bryophytes. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

## Rock Associations

Among the earliest moss-slime mold associations reported is that of Kaiser (1913). Brown capsules of the slime mold ***Leocarpus fragilis*** (Figure 51) occurred on the moss ***Dicranum fulvum*** (Figure 67) in the southern Catskill Mountains of New York. The substrate was not reported, but this moss commonly occurs on sandstone rocks (Seltzer & Wistendahl 1971). The slime mold is not bryophilous, being common on dead leaves (Kaiser 1913).

Figure 67. ***Dicranum fulvum***, sometimes a substrate for the slime mold ***Leocarpus fragilis***. Photo by Bob Klips, with permission.

Schnittler and Novozhilov (1996) reported on a number of slime molds using bryophytes as a substrate in the northern Karelia of Russia. One of the most common species, ***Physarum album*** (Figure 68) appears to be a generalist and includes moss tussocks on rocks among its substrata. ***Physarum viride*** (Figure 14) likewise accepts a number of substrata, including moss and liverwort layers of rocks, where "it prefers medium-wet places between the pure slimy algae layers and the big moss tussocks."

Figure 68. ***Physarum album*** sporangia on decaying wood, a generalist that also occurs on mosses. Photo by George Shepherd, through Creative Commons.

On granite rocks Schnittler and Novozhilov (1996) found two subassociations of slime molds. One prefers the thicker tussocks (> 0.5 cm), especially the mosses ***Sanionia uncinata*** (Figure 69), ***Dicranum fuscescens*** (Figure 70), and ***Cynodontium strumiferum*** (Figure 71). These tussocks have dry leaf tips, but the tussocks have a wet interior and are enriched with small particles of detritus. The slime molds ***Lamproderma columbinum*** (Figure 66), ***L. sauteri*** (Figure 72), and ***Didymium melanospermum*** (Figure 28) fruit here, the latter often at the bases of the rocks. The second sub-association occurs in thin water films and will be discussed below under the Wet Habitat Associations.

Figure 69. ***Sanionia uncinata***, a species forming thick mats with dry tips but moist interiors and collections of detritus. It serves as substrate for the slime molds ***Lamproderma columbinum***, ***L. sauteri***, and ***Didymium melanospermum***. Photo by Hermann Schachner, through Creative Commons.

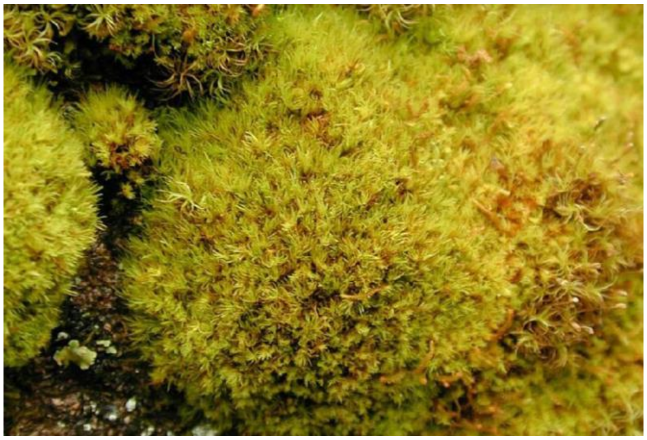

Figure 70. ***Dicranum fuscescens***, a rock-dwelling moss that serves as substrate for the slime molds ***Lamproderma columbinum***, ***L. sauteri***, and ***Didymium melanospermum***. Photo by Michael Lüth, with permission.

Figure 71. ***Cynodontium polycarpon*** with capsules, a rock-dwelling moss that serves as substrate for the slime molds ***Lamproderma columbinum***, ***L. sauteri***, and ***Didymium melanospermum***. Photo by Štěpán Koval, with permission.

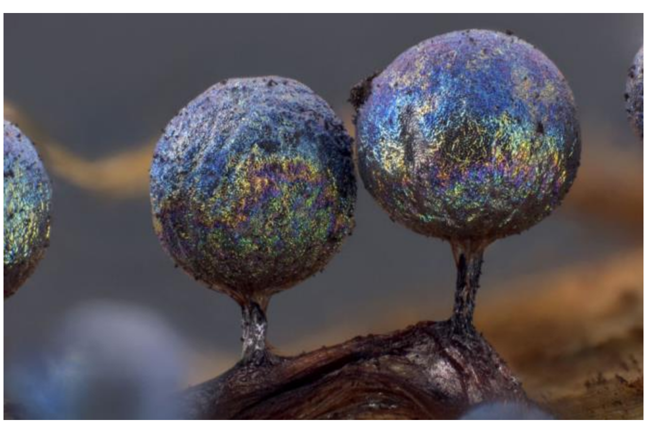

Figure 72. ***Lamproderma sauteri*** sporangia that can occur on moss-covered rocks. Photo by The Eumycetozoan Project, DiscoverLife.org, with online permission.

***Diderma lucidum*** seems to be restricted to mossy rocks (Brooks *et al*. 1977).

Few studies seem to have included the rock habitat. Schnittler and Novozhilov (1996), studying the boreal woodlands of northern Karelia in Russia, have contributed a number of records of slime molds that seemingly are able to live on rocks by using bryophytes as their immediate substrate. ***Lamproderma columbinum*** (Figure 66) occurred almost exclusively on moss-covered rocks, where it was often accompanied by ***L. sauteri*** (Figure 72) and ***Colloderma oculatum*** (Figure 73), but preferring drier and thicker moss tussocks than the substrate preferred by these two slime molds. ***Lamproderma columbinum*** forms large and conspicuous colonies on thick moss beds on rocks (as well as on moss-covered logs). ***Lepidoderma tigrinum*** (Figure 20) fruits in autumn after the first frosts and snowfalls, when it is visible in a rock association of very wet, thin liverwort and algae mats. In summer the plasmodia are visible.

Figure 73. ***Colloderma oculatum*** on bryophytes. Photo by David Mitchell, The Eumycetozoan Project, DiscoverLife.org, with online permission.

## Sand Dunes

Sand dunes are inhospitable habitats for both bryophytes and slime molds. But where there is a niche, some bryophyte will usually fill it. Hence, the slime mold ***Physarum didermoides*** (Figure 56; syn.=*Diderma spumarioides*) is common in sand dunes and often forms "plaques of sporangia up to a square meter" on carpets of the moss ***Syntrichia ruralis*** (Ing 1994).

## Alpine and Polar

When investigating the alpine and Arctic/Antarctic areas, researchers have often been surprised at the low diversity of slime molds. They are both less abundant and exhibit fewer species than in other areas, but some rarer species elsewhere can be present more commonly in the Arctic (Stephenson *et al*. 2000).

Although the cold regions do not appear to be friendly toward slime molds, the most bryophyte-exclusive (perhaps leafy liverwort-exclusive) slime mold, ***Barbeyella minutissima*** (Figure 19) is a common alpine slime mold (Kowalski & Hinchee 1972). Similarly, Kowalski (1972) found that in the mountains of Washington, USA, ***Licea***

***hepatica*** seems to be restricted to leafy liverworts, a species that seems to be unknown from other substrata (Steven Stephenson, pers. comm. 1 June 2019).

This may cause us to be hopeful of special bryophyte associations high in the mountains, but beyond these two limited cases, that does not appear to be the case.

***Elaeomyxa australiensis*** (Figure 74) is known from an alpine snowbank habitat in Australia (Moreno *et al*. 2009; Stephenson & Shadwick 2009). There it grows on litter in association with bryophytes, with only 3 collections out of 300 actually occurring on bryophytes (Stephenson & Shadwick 2009). In these Australian alpine areas, ***Meriderma cribrarioides*** (reported as ***Lamproderma atrosporum***; Figure 75) also occurs on bryophytes.

Figure 74. ***Elaeomyxa*** *cf.* ***australiensis***, an alpine snowbank species that grows with litter in association with bryophytes. Photo by Sarah Lloyd, with permission.

Figure 75. ***Meriderma cribrarioides*** sporangium, a species that sometimes occurs on bryophytes in alpine areas of Australia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Stephenson *et al*. (2000) set out to determine what factors limit slime mold distribution in high-latitude and cold-dominated regions in the Northern Hemisphere. They collected 938 specimens and cultured 1453 substrate samples from 12 study areas in Iceland, northern Russia, Alaska, and Greenland. They identified 150 species, with 33 being widely distributed in at least five study areas. With only 41 species having a frequency greater than 1%, most of the species seemed to have only limited distribution or low frequency. Although the Arctic species seem to have a depauperate representation of species known from the temperate region, as already noted, some species that are considered rare in temperate areas are common in the Arctic, supporting the conclusion that the Arctic slime mold communities are different from those in temperate regions.

Novozhilov *et al*. (1999) reported 56 species of slime molds from the Taimyr Peninsula in north-central Siberia. Among these, only two species apparently were found ever associated with bryophytes. ***Didymium melanospermum*** (Figure 28) typically occurs on mossy coarse woody debris. ***Mucilago crustacea*** (Figure 76) is even less associated, occurring in a moss- and grass-rich, open patch of the forest tundra. It is notable that slime mold species numbers decrease progressively from the northern taiga, northward to the tundra subzone. This study supports the contention that the tundra is represented by an impoverished flora from the northern taiga subzone.

Figure 76. ***Mucilago crustacea***, a species that occurs in moss-rich habitats in the forest tundra. Photo by Alexey Sergeev, with permission.

Stephenson *et al*. (1991) expressed their disappointment at the small number of species they were able to find on the soils of the Alaskan tundra. After collecting from nine different study sites, their cultures yielded only ***Dictyostelium mucoroides*** (Figure 77; **Dictyosteliomycetes**) and ***D. sphaerocephalum*** (Figure 78). The total number of slime mold colonies per gram of wet soil averaged more than 100 for all samples and was more than 200 at three of the four Arctic tundra sites. These values are similar to those they found for forest soils in two spruce study sites of interior Alaska.

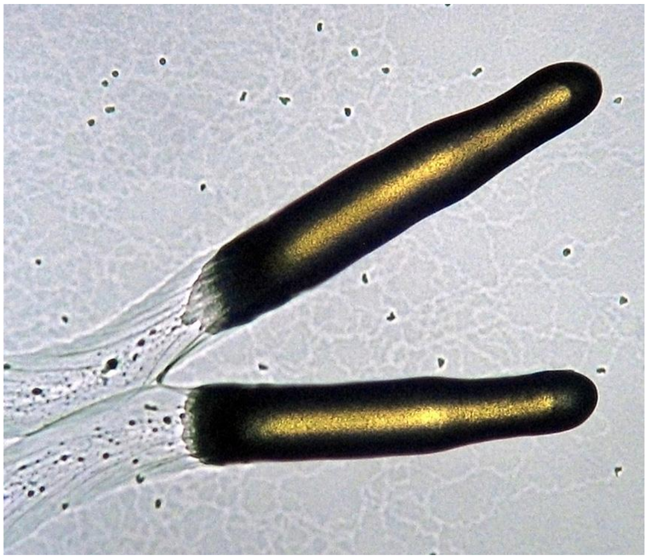

Figure 77. ***Dictyostelium mucoroides*** (**Dictyosteliomycetes**) plasmodial slug, a tundra species. Photo by Dmitry Leontyev, The Eumycetozoan Project, DiscoverLife.org, with online permission.

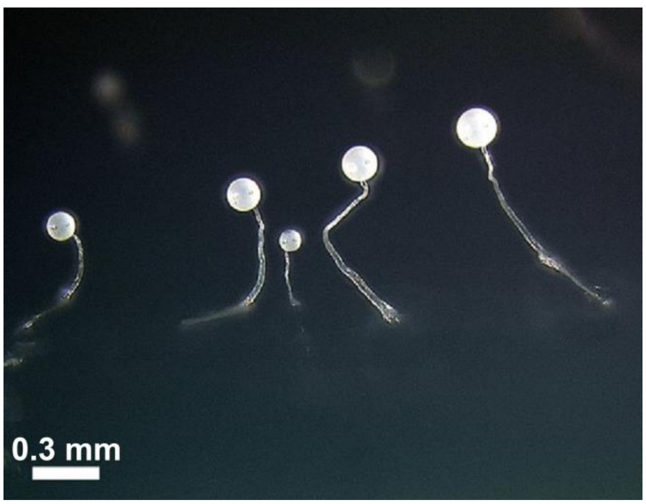


Figure 78. ***Dictyostelium sphaerocephalum*** fruiting body, sometimes the only slime mold present in the Alaskan tundra. Photo by Andy Swanson, with permission, image provided by Steve Stephenson.

The report from Stephenson *et al*. (1991) is similar to that of Benson and Mahoney (1977). But the latter authors considered ***Dictyostelium mucoroides*** (Figure 77) to be conspecific with ***D. sphaerocephalum*** (Figure 78). They found the latter inclusive species to be dominant above 1700 m in Southern California.

Cavender conducted a number of studies in Arctic and high altitude locations. He found a new Alaskan tundra species of ***Dictyostelium***, ***D. septentrionale***, along with ***D. mucoroides*** (Figure 77), ***D. sphaerocephalum*** (Figure 78), and ***D. giganteum*** in that tundra habitat (Cavender 1978). He considered ***D. sphaerocephalum*** and ***D. mucoroides*** to have sufficiently large populations to play a role in tundra ecology. When Cavender (1983) sampled slime molds in the Rocky Mountains, USA, he found that the soil slime molds were 29.5% ***Dictyostelium sphaerocephalum*** and 68% ***D. mucoroides*** when appearing in cultures. Cavender (1980, 1983) concluded that the altitudinal distribution of slime molds is similar to that of latitude. In the Appalachian Mountains, eastern USA, Cavender (1980) found that the dictyostelid slime molds predominate, with 15 species. The greatest ***Dictyostelium*** richness occurred at 590 - 820 m.

Landolt *et al*. (1992) found ***Dictyostelium mucoroides*** (Figure 77) and ***D. sphaerocephalum*** (Figure 78) to be overwhelmingly dominant in the Kantishna Hills of Denali National Park (formerly Mt. McKinley), Alaska, USA, with the number of clones per gram of wet soil ranging 0-1203. Some of these sites were restoration sites; the natural sites had far greater slime mold density. The mean number of clones per gram of wet soil was 259 clones for the 14 study sites, with the seven natural sites having a mean of 430. ***Dictyostelium mucoroides*** was the dominant species (59-98%) in the natural sites. In the restoration sites, ***D. sphaerocephalum*** was dominant (50-100% of all clones) in the six restoration study plots where slime molds were found.

But none of the preceding studies reported any ***Dictyostelium*** species on bryophytes.

Emphasizing the paucity of species in these cold habitats, Kanda and Sato (1982) were unable to find any cellular slime molds in the alpine tundra of Mt. O-Akan, Hokkaido, Japan. Hence, we should not be surprised that most of these polar and alpine studies did not report any slime molds growing on bryophytes.

In the Carpathians of Poland, other species emerge as nivicolous species (Ronikier *et al*. 2008). These include 18 species, of which 10 are reported for the first time in Poland. ***Diderma niveum*** (Figure 79), ***Lepidoderma chailletii*** (Figure 80), and ***Lamproderma ovoideum*** (Figure 81) are very abundant, particularly in the spring in glades and shrub communities. ***Diderma alpinum*** (Figure 82) and ***D. niveum*** occur on mosses.

Figure 79. ***Diderma*** *cf.* ***niveum*** sporangia on mosses. Photo by Tom Thekathyil, with permission.

Figure 80. ***Lepidoderma chailletii*** sporangia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

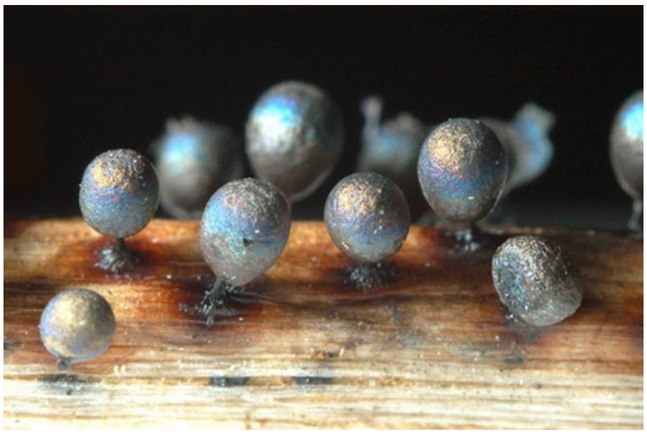

Figure 81. ***Lamproderma ovoideum*** sporangia. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 82. ***Diderma alpinum*** sporangia, a species that occurs on mosses in the Carpathian Mountains. Photo by The Eumycetozoan Project, DiscoverLife.org, with online permission.

Stephenson *et al*. (1992) noted the paucity of reports of slime molds from Antarctica and the subAntarctic islands. Several genera occurring there are known from bryophytes elsewhere, but many of the Antarctic species are different. ***Diderma effusum*** (Figure 9) is known from mosses in the Antarctic (unpublished record from Steven Stephenson, pers. comm. 1 June 2019).

***Lepidoderma crustaceum*** (Figure 83) is among the bryophyte dwellers found on the subAntarctic Macquarie Island in the Antarctic region (Stephenson *et al*. 2007a). ***Lamproderma ovoideum*** (Figure 84) similarly occurs on the leafy liverwort ***Lepidozia*** sp. (Figure 22) on Macquarie Island (Stephenson *et al.* 1992). But most of the species in the Antarctic region are **niveal** (subject to actions of snow and ice) species, and their fruiting is associated with winter snow packs. ***Lamproderma ovoideum*** is typical of such habitats in alpine areas. Whereas only 6 slime mold species were known in 1990 from the Antarctic region, 32 were known from Iceland and 54 from Greenland (Gøtzsche 1989, 1990). In an intensive study, Stephenson *et al*. (2007b) located 22 species on Macquarie Island.

Figure 83. ***Lepidoderma crustaceum*** sporangia, one of the bryophyte dwellers on Macquarie Island. Photo from Myxotropic, through Creative Commons.

Figure 84. ***Lamproderma ovoideum*** sporangia, a late snowmelt species in alpine areas, sometimes occurring on bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Stephenson *et al*. (2007b) reported a more diverse slime mold fauna on Macquarie Island, including several that occurred on bryophytes. These bryophyte dwellers included 6 of 80 collections of ***Trichia verrucosa*** (Figure 85), 1 of 78 of ***Diderma alpinum*** (Figure 86-Figure 87), 2 of 59 of ***Craterium leucocephalum*** (Figure 88), 2 of 48 ***Didymium*** *cf.* ***dubium*** (Figure 89-Figure 90), 7 of 15 ***Lamproderma arcyrioides*** (Figure 91-Figure 92), and 13 of 68 of all other species. ***Diderma radiatum*** (Figure 93-

Figure 94) had a higher ratio, but poor representation, with 1 of the 3 collections being on bryophytes. ***Lamproderma ovoideum*** (Figure 84) is considered **nivicolous** (associated with snow), but the only collection of this species was on bryophytes. ***Lepidoderma crustaceum*** (Figure 84) also was reported from bryophytes. The most common bryophytes serving as slime mold substrates on Macquarie Island are the mosses ***Brachythecium salebrosum*** (Figure 95), ***Achrophyllum dentatum*** (Figure 96-Figure 97), and the leafy liverwort ***Lophocolea bidentata*** (Figure 98).

Figure 85. ***Trichia verrucosa*** mature and dispersing sporangia, a Macquarie Island slime mold that occasionally fruits on bryophytes. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 86. ***Diderma alpinum*** sporangia, a Macquarie Island slime mold that occasionally fruits on bryophytes. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

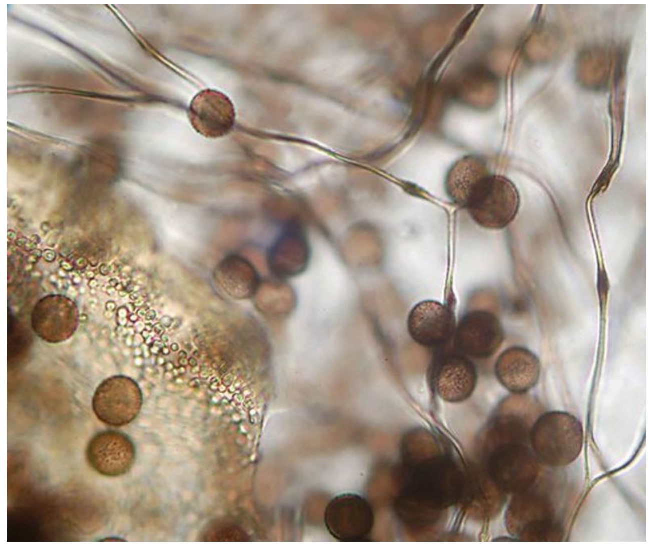

Figure 87. ***Diderma alpinum*** spores and capillitium. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 88. ***Craterium leucocephalum***, a slime mold that occasionally appears on bryophytes on Macquarie Island in the Antarctic. Photo by Clive Shirley, the Hidden Forest, with permission.


Figure 89. ***Didymium dubium*** on leaf litter, a species that can also occur on bryophytes on Macquarie Island. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

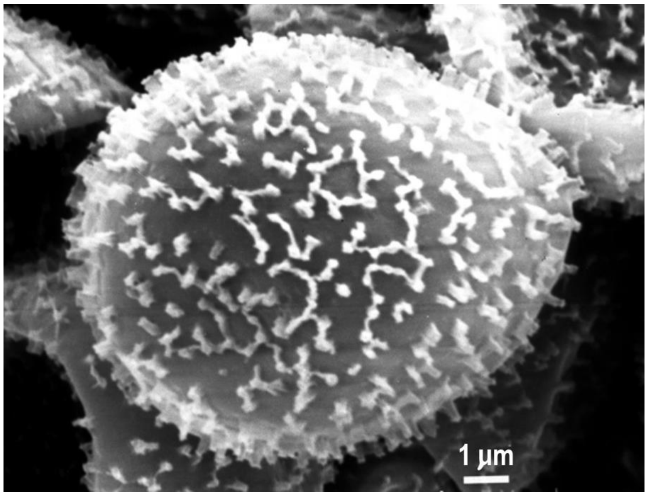


Figure 90. ***Didymium dubium*** spore SEM. Photo from The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 91. ***Lamproderma arcyrioides*** sporangia with moss, sometimes a bryophyte inhabitant on Macquarie Island. Photo by James K. Lindsey, with permission.

Figure 92. ***Lamproderma arcyrioides*** mature sporangia. Photo by Randy Darrah, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 93. ***Diderma radiatum*** sporangia with mosses on decaying wood, a slime mold that occasionally appears on bryophytes on Macquarie Island in the Antarctic. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 94. ***Diderma radiatum*** after the capsules dehisce. Photo by Clive Shirley, The Hidden Forest, with permission.

Figure 95. ***Brachythecium salebrosum***, one of the preferred bryophyte substrates for slime molds on Macquarie Island. Photo by Michael Lüth, with permission.

Figure 96. ***Achrophyllum dentatum***, one of the preferred bryophyte substrates for slime molds on Macquarie Island. Photo by David Tng, through Creative Commons.

Figure 97. ***Achrophyllum dentatum*** with leaf gemmae. Photo by Des Callaghan, through Creative Commons.

Figure 98. ***Lophocolea bidentata***, one of the preferred bryophyte substrates for slime molds on Macquarie Island. Photo by Hermann Schachner, through Creative Commons.

## Wet-Habitat Associations

Lindley *et al*. (2007) remarked on the paucity of information on slime molds in aquatic habitats. They found that the distributions of slime molds above and below the water level were different.

### Ravines

Krziemiewska (1934) reported ***Colloderma oculatum*** (Figure 73; as *C. dubium*) from wet wood covered with mosses and liverworts in her study in the Zarocœlak forest, eastern Carpathians. But studies that concentrate on ravine slime molds are still very limited.

One reason for the lack of study in this interesting habitat is that they can only be identified during their fruiting season. In most habitats, bark and other substrate samples can be taken to the lab and cultured. But Novozhilov *et al*. (2000) lamented the difficulty of culturing the slime molds that prefer the trickling water of humid ravines. This lack of success forces researchers to be in the field when the slime molds are producing sporangia, noting that this is predominately in the late autumn, a time when most slime mold specialists, who are also academicians, are busy with their educational responsibilities. With all this difficulty in being at the right place at the right time, Novozhilov and coworkers estimate that less than 5% of the species occur in such habitats.

Whereas most of the slime molds seem to prefer rotting logs, some prefer more moist or even wet habitats. One reason for this may be the associated algae that can serve as a food source. Ing (1994) noticed that algae were typically abundant in association with the mats of bryophytes that served as substrate for slime mold fruiting bodies in cool, moist ravines of the western British Isles (Ing 1983). In another European study, Schnittler and Novozhilov (1998) reported the slime molds ***Colloderma oculatum*** (Figure 73) fruiting on wet, moss-covered rock surfaces that presented a continuous layer of algae.

***Craterium muscorum*** (Figure 99; syn.=*Badhamia rubiginosa* var. *globosa*) and ***Diderma lucidum*** are rare Atlantic species that can be found on moss-covered rocks in wooded ravines (Ing 1982). ***Lamproderma columbinum*** (Figure 66) and ***Lepidoderma tigrinum*** (Figure 20), both species noted elsewhere from bryophytes, are characteristic of ravines. ***Fuligo muscorum*** (Figure 100) occurs in wet, terrestrial mossy habitats.

Figure 99. ***Craterium muscorum*** sporangia on mosses, a species that occurs in wet, terrestrial mossy habitats. Photo by Janet Graham, through Creative Commons.

Figure 100. ***Fuligo muscorum*** on the moss ***Hypnum***. Photo by Charles Hipkin, with permission from Barry Stewart.

***Lamproderma sauteri*** (Figure 72) occurs on bryophyte layers on rocks and boulders where there is running water (Novozhilov *et al*. 2000). These occurrences seem to be mostly in association with the Arctic-alpine leafy liverwort, ***Gymnomitrion concinnatum*** (Figure 101). ***Colloderma oculatum*** (Figure 73) and ***Lepidoderma tigrinum*** (Figure 20) seem to benefit from living on thin, slimy layers of liverworts under a thick cover of mosses and having a covering of water film.

Figure 101. ***Gymnomitrion concinnatum***, an Arctic-alpine leafy liverwort that serves as substrate for ***Lamproderma sauteri***. Photo by Michael Lüth, with permission.

In his 1983 study of ravines in the UK, Ing found that slime molds were associated with the moist bryophytes near waterfalls and dripping areas that kept the mosses moist. Novozhilov *et al*. (2000) reported a similar relationship on wood and rocks near trickling water in humid ravines. In fact, ***Lamproderma columbinum*** (Figure 66; **Stemonitidaceae**) is an ecotype that is associated with mosses in such habitats. Ing (1983) found that sporangia of slime molds occur most commonly on the mosses ***Cratoneuron commutatum*** (Figure 102), ***Dicranum majus*** (Figure 103), ***D. scoparium*** (Figure 33-Figure 34), ***Hyocomium armoricum*** (Figure 104), ***Hypnum cupressiforme*** (Figure 105), ***Isothecium myosuroides*** (Figure 106), ***Plagiothecium undulatum*** (Figure 107), and ***Rhytidiadelphus loreus*** (Figure 108), and the liverworts ***Bazzania trilobata*** (Figure 109), ***Lepidozia reptans*** (Figure 22), ***Plagiochila asplenioides*** (Figure 110), ***P. spinulosa*** (Figure 111), ***Saccogyna viticulosa*** (Figure 112), and ***Scapania gracilis*** (Figure 113). The most common slime molds that occur on these ravine bryophytes are ***Craterium muscorum*** (Figure 99), ***Diderma lucidum***, ***D. ochraceum*** (Figure 114), ***Lamproderma columbinum*** (Figure 66), and ***Lepidoderma tigrinum*** (Figure 20).

Figure 102. ***Cratoneuron commutatum***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 103. ***Dicranum majus***, a large ***Dicranum*** where slime molds commonly form sporangia. Photo by Michael Lüth, with permission.

Figure 104. ***Hyocomium armoricum***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 105. ***Hypnum cupressiforme***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 106. ***Isothecium myosuroides***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 107. ***Plagiothecium undulatum***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 108. ***Rhytidiadelphus loreus***, one of the more common mosses serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 109. The leafy liverwort ***Bazzania trilobata***, one of the more common liverworts serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 110. ***Plagiochila asplenioides***, one of the more common liverworts serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 111. ***Plagiochila spinulosa***, one of the more common liverworts serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 112. ***Saccogyna viticulosa***, one of the more common liverworts serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 113. ***Scapania gracilis***, one of the more common liverworts serving as substrate for fruiting slime molds. Photo by Michael Lüth, with permission.

Figure 114. ***Diderma ochraceum*** sporangia on moss, a common slime mold on ravine bryophytes. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

A very detailed study of slime molds in ravines and their associated bryophytes, using 127 small-scale relevés, is that of Schnittler *et al*. (2010) in sandstone gorges of Switzerland. They followed the methods developed by Holz (1997) for ravine bryophyte communities. Only five taxa account for 87% of the records, and all of these except ***Lamproderma puncticulatum*** (Figure 115-Figure 116) are reported elsewhere in this chapter from bryophyte associations: ***Colloderma robustum*** (Figure 117), ***Diderma ochraceum*** (Figure 114), ***Lamproderma columbinum*** (Figure 66), ***L. puncticulatum*** agg., and ***Lepidoderma tigrinum*** (Figure 20). They determined that the community is relatively unique, occurring only in the deep, narrow ravines on nearly vertical rocks, mostly on northern exposures. The substrate has a very acidic *p*H with a mean of 3.35. The fruiting season, in the beginning of October, has a very constant microclimate with nearly 100% relative humidity and ~10ºC. Green algae, most commonly ***Coccomyxa confluens*** (Figure 118), were associated with all the slime mold collections. The mosses ***Dicranodontium denudatum*** (Figure 119) (59%) and ***Tetraphis pellucida*** (Figure 25) (50%) and leafy liverworts ***Mylia taylorii*** (Figure 120) (64%) and ***Diplophyllum albicans*** (Figure 121) (40%) had high indicator values for the community. Nevertheless, the five most common slime molds had high niche overlap values, but low niche width values, indicating their high degree of specialization. I have to wonder if these slime molds were cryptospecies because they are relatively well known outside ravines and are among species more frequently cited as associated with bryophytes. For example, Hoffmann (1795) originally described ***Diderma ochraceum*** from mosses. On the other hand, sufficient habitat information is often lacking.

Figure 115. ***Lamproderma puncticulatum*** immature sporangia on bryophytes. Photo by Mireille Lenne, courtesy of Marianne Meyer.

Figure 116. ***Lamproderma puncticulatum*** on the liverwort ***Pellia***. Photo courtesy of Isabelle Mazaud.

Figure 117. ***Colloderma robustum***, a species associated with ravine bryophytes. Photo by Sarah Lloyd, with permission.

Figure 118. ***Coccomyxa confluens*** on mosses. Photo by James K. Lindsey, with permission.

Figure 119. ***Dicranodontium denudatum***, a common substrate for slime molds in ravines. Photo by David T. Holyoak, with permission.

Figure 120. ***Mylia taylorii***, a common ravine substrate for slime molds. Photo by Hermann Schachner, through Creative Commons.

Figure 121. ***Diplophyllum albicans***, a common ravine substrate for slime molds. Photo by David T. Holyoak, with permission.

Ing (1983) described a ravine slime mold community having a preference for bryophytes on rocks in numerous Atlantic locations in the British Isles. But the species differed somewhat from those in Switzerland: ***Craterium muscorum*** (Figure 99), ***Diderma lucidum***, ****D. ochraceum*** (Figure 114), ****Lamproderma columbinum*** (Figure 66), and ****Lepidoderma tigrinum*** (Figure 20), with *species being common in ravines of both countries. Later he (Ing 1994) recognized the ravine slime mold community as a distinct community.

Schnittler *et al*. (2010) did note that even when the inclination was suitable, pure turfs of ***Tetraphis pellucida*** (Figure 25) rarely had slime molds, but also tended to have less trickling water or algae. The leafy liverwort ***Mylia taylorii*** (Figure 120), on the other hand, is a good indicator organism for the presence of ravine slime molds. These researchers concluded that most of the ravine species are rare outside the ravines, citing ***Colloderma robustum*** (Figure 117) and ***Diderma ochraceum*** (Figure 114), two species closely associated with ***Mylia taylorii***. ***Lamproderma puncticulatum*** (Figure 115-Figure 116) agg. was likewise closely associated with ***M. taylorii***. Other common ravine species, specifically ***Lamproderma columbinum*** (Figure 66) and ***Lepidoderma tigrinum*** (Figure 20), occur elsewhere in forests with constantly humid conditions; in the British ravines they are closely associated with ***Tetraphis pellucida*** (Figure 25). As noted earlier in this chapter, they may be true bryophiles. ***Diderma umbilicatum*** (Figure 122) was always "in close neighborhood" with ***Mylia taylorii*** and ***Dicranodontium denudatum*** (Figure 119), suggesting that this slime mold preferred similar conditions to these two bryophytes. The moving plasmodia of ***D. umbilicatum*** were a conspicuous bright yellow. These segregate to form distinct sporangia on the tips of the bryophyte shoots, often forming a doughnut shape around the narrow leaves of ***Dicranodontium***.

Other species preferring ***Tetraphis pellucida*** (Figure 25) in ravines include ***Diderma lucidum*** and ***Lamproderma columbinum*** (Figure 66), the latter occurring there in 73% of the ***Tetraphis*** turf records where green algae were present in Saxonian Switzerland (Schnittler *et al*. 2010). ***Lamproderma puncticulatum*** (Figure 115-Figure 116) prefers thicker bryophyte tufts [64% with ***Mylia taylorii*** (Figure 120), 56% with ***Tetraphis pellucida***]. ***Lepidoderma tigrinum*** (Figure 20) prefers ***Dicranodontium denudatum*** (Figure 119) (74% of all records) and ***Mylia taylorii*** (65%), but occurred several times on ***Sphagnum*** (Figure 128-Figure 129) tufts at the base of large rocks; ***Diderma umbilicatum*** (Figure 122) had a similar preference for these two species. ***Physarum album*** (Figure 123) was less common, with only three records on ***Tetraphis pellucida*** and one on ***Dicranodontium denudatum***. Overall, the slime molds seem to prefer the closed turfs of ***Mylia taylorii*** and ***Dicranodontium denudatum***, but not the common pure short turfs of ***Tetraphis pellucida***.

Figure 122. ***Diderma umbilicatum*** on mosses, a species often near bryophytes in ravines. Photo by Alain Michaud, The Eumycetozoan Project, DiscoverLife.org, with online permission.

Figure 123. ***Physarum album***, a species that occasionally occurs on mosses in ravines. Photo by Sarah Lloyd, with permission.

Schnittler *et al*. (2010) agreed with Ing (1994) that nitrogen-fixing activity of the **Cyanobacteria** may be beneficial in some way to the slime molds, possibly as nutrients for their food source, or directly as a food source. But experimental evidence to support this is lacking. They in fact suggested that bryophilous slime molds may instead be phycophilous.

## Wet Rocks

One of the early reports on slime mold-bryophyte associations in wet habitats is that of Lister (1918) in the UK. He found ***Lamproderma scintillans*** (Figure 11) on stones in a shallow stream. He surmised that they had migrated to these rocks from mosses and leaf litter on the stream bank.

Schnittler and Novozhilov (1996) described a granite rock community that is comprised of ***Colloderma oculatum*** (Figure 73) and ***Lepidoderma tigrinum*** (Figure 20). These two species fruit on very thin (< 0.5 cm), slimy layers of liverworts, covered with a water film. These microhabitat films are found at 1-3 m height on rocks that are provided with trickling water. The large moss tussocks on the upper margins of the rocks can function as a water reservoir. Both slime mold species produce sporangia directly on the water film of the liverworts. The researchers assumed that the plasmodia lived within the bryophyte layers because of their location on the rocks. The huge colonies, especially of ***Colloderma oculatum***, suggest that moss layers are a normal microhabitat. The **Cyanobacteria** (Figure 124-Figure 127) present are a possible food source for the plasmodia. In the northern Ammergauer Alps, Schnittler and Novozhilov (1998) also found ***Colloderma oculatum*** on wet rock surfaces where they were associated with mosses and a continuous layer of algae (probably including **Cyanobacteria**).

One such bryophyte dweller that may really be an algae/**Cyanobacteria** dweller is ***Physarum viride*** (Figure 14). This species occurs on two substrate types, one of which is on the moss and liverwort layers of rocks (Schnittler & Novozhilov 1996). It prefers medium-wet places between the pure slimy algae layers and the big moss tussocks.

One advantage to living on a wet rock is the presence of **Cyanobacteria**. Not only do the rocks present slimy layers of these nitrogen-fixing organisms, but so also do the bryophytes (Ing 1994). In the study by Ing, these encrustations are predominantly ***Nostoc muscorum*** (Figure 124-Figure 125) or ***N. commune*** (Figure 126-Figure 127). For the slime molds, these can be a food source, whereas for the bryophytes, they may improve the nitrogen availability. The beneficial aspects of this association are supported by the frequency with which this assemblage of species coincides with the ***Nostoc*** growths. In this case, the rocks are base-rich, and Ing hypothesized that the nitrogen-fixing activity of the ***Nostoc***, enhanced by a high *p*H, may be beneficial for the slime molds. ***Craterium muscorum*** (Figure 99), ***Lamproderma columbinum*** (Figure 66), and ***Lepidoderma tigrinum*** (Figure 20) typically develop plasmodia that have close contact with the ***Nostoc*** on these wet rocks.

Figure 124. ***Nostoc muscorum*** gelatinous ball, a **Cyanobacterium** frequently associated with wet bryophytes and of likely benefit to slime molds. Photo from Protist Information Server, with permission.

Figure 125. ***Nostoc muscorum*** individual filaments. Photo by Charles Krebs, with online permission.

Figure 126. ***Nostoc commune*** on mosses. Yamamaya, through Creative Commons.


Figure 127. ***Nostoc commune*** individual filaments. Photo by David Wagner, with permission.

## *Sphagnum* and peatland Dwellers

***Sphagnum*** (Figure 128) offers both a habitat modifier that maintains a high moisture level, and a substrate. Carr (1939) provided an early record of ***Didymium iridis*** (Figure 6; as *Didymium nigripes* var. *xanthopus*) growing in abundance on ***Sphagnum***.

Figure 128. ***Sphagnum fallax*** with capsules. Photo by David T. Holyoak, with permission.

Schnittler and Novozhilov (1996) noted species of slime molds that were in some way associated with ***Sphagnum*** (Figure 128) in the northern Karelia of Russia. Nevertheless, they observed that the ***Sphagnum***-rich spruce (***Picea***; Figure 129) woodland, despite its nearly continuously moist environment, served as a poor habitat for slime molds. Only ***Physarum virescens*** (Figure 38-Figure 39) appeared to be adapted sufficiently to live on the large moss tussocks.

Figure 129. ***Sphagnum*** in spruce forest. Photo courtesy of Kim Barton.

In his examination of mosses of wet habitats, Ing (1994) found two slime molds that are mostly restricted to growing on ***Sphagnum*** (Figure 128). These are ***Symphytocarpus trechispora*** (Figure 130) and ***Amaurochaete trechispora***. On the other hand, Salamaga *et al*. (2014) concluded that in Poland ***S. trechispora*** is acidophilic. Whereas it frequently occurs on ***Sphagnum***, it is not restricted to that substrate. They reported it also from ***Polytrichum*** sp. (Figure 131) (growing with ***Sphagnum fallax*** – Figure 128). It is also known from ***Sphagnum*** in Scotland, England, and Germany (Ing 1999; Schnittler *et al.* 2011).

Figure 130. ***Symphytocarpus trechispora*** on moss. Photo by Thomas Laxton, through Creative Commons.

Figure 131. ***Polytrichum commune***, a common substrate for ***Symphytocarpus trechispora***. Photo by Christopher Tracey through Creative Commons.

In the same study, Ing (1994) found that two bryophiles, ***Lamproderma columbinum*** (Figure 66, Figure 132) and ***Lepidoderma tigrinum*** (Figure 20), occur on ***Sphagnum*** (Figure 128) as well as other bryophytes. ***Diderma simplex*** (Figure 133) is a moorland species that includes bog mosses among its substrates. Hagelstein (1941) reported ***Paradiachea caespitosa*** (Figure 134) growing on the tips of ***Sphagnum***. But Ing (1994) concludes that in general, the low *p*H and low oxygen availability make many mires and bogs unsuitable for the growth of slime molds.

Figure 132. ***Lamproderma*** *cf*. ***columbium***, on ***Sphagnum***, Catfield Fen. Photo courtesy of Isabelle Masaud.

Figure 133. ***Diderma simplex***, a species that can grow on bog mosses. Photo by Bruce Watt, University of Maine, Bugwood.org, through Creative Commons.

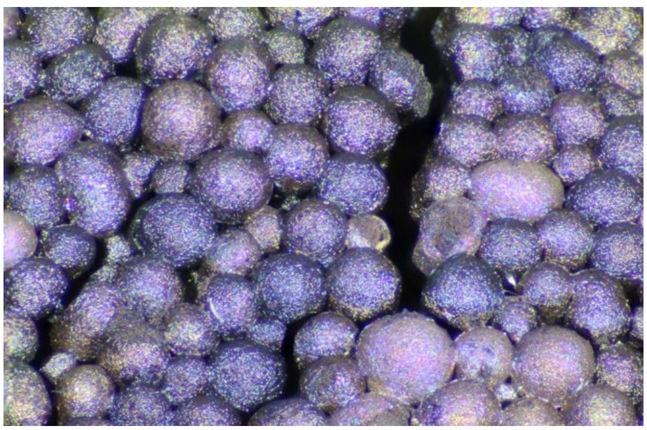

Figure 134. ***Paradiachea caespitosa***, a species that grows at the tip of ***Sphagnum***. Photo by Sarah Lloyd, with permission.

Cavender *et al*. (2005) reported a new species of cellular slime mold, ***Dictyostelium quercibrachium*** (**Dictyosteliomycetes**), from the margin of a small bog in Ohio, USA. Cavender and Vadell (2006) likewise reported the cellular slime mold ***Acytostelium magniphorum*** from the margin of a small bog in Ohio. Landolt *et al*. (2006) suggested that bog margins provide relict habitats that have been under explored for slime molds and therefore may hold more unknown species or range extensions.

In a more recent study in the Ukraine, Yatsiuk *et al*. (2018) found ***Didymium ovoideum*** (Figure 135) on ***Sphagnum*** (Figure 128). ***Didymium melanospermum*** (Figure 28) and ***Stemonitis axifera*** (Figure 136) occurred on species of ***Sphagnum*** and **Polytrichaceae** (Figure 131). ***Didymium melanospermum*** typically occurs on acid substrates, including mosses (Stephenson & Studlar 1985; Nannenga-Bremekamp 1991; Ing 1994). On the other hand, ***Stemonitis axifera*** does not appear to be bryophilous in most locations.

Figure 135. ***Didymium ovoideum*** sporangium on wood, a species that sometimes occurs on ***Sphagnum***. Photo by Thomas Laxton, through Creative Commons.

Figure 136. ***Stemonitis axifera*** sporangia on decorticated log, a species that also occurs on ***Sphagnum*** and **Polytrichaceae**. Photo by Clive Shirley, The Hidden Forest, with permission.

In ***Sphagnum*** (Figure 128) bogs, ***Badhamia lilacina*** (Figure 137-Figure 138) seems to prefer aquatic areas, but their fruiting occurs on moss leaves (Tamayama & Keller 2013). Others, like the ***Leocarpus fragilis*** (Figure 139) in occur in peatlands but seem to avoid the ***Sphagnum***. Only one tiny patch of this one is on the moss.

Figure 137. ***Badhamia lilacina*** plasmodium on ***Sphagnum***. Photo from <www.vestrehus.dk>, with implied permission.

Figure 138. ***Badhamia lilacina*** on ***Sphagnum***. Photo by Janet Graham, through Creative Commons.

Figure 139. ***Leocarpus fragilis*** on ***Sphagnum*** and twigs. Photo by Boris Loboda, with permission.

Ravines provide a unique assemblage of species, and many of these occur on bryophytes, probably in part because bryophytes provide a high cover there. ***Craterium muscorum***, ***Diderma lucidum***, ***D. ochraceum***, ***Lamproderma columbinum***, and ***Lepidoderma tigrinum*** are common on bryophytes there. The presence of ***Mylia taylorii*** is a good indicator organism for the presence of ravine slime molds, and many also occur on the moss ***Dicranodontium denudatum***. The **Cyanobacteria** ***Nostoc muscorum*** and ***N. commune*** are common associates on wet rocks and may provide food for the slime molds. Slime molds occurring in peatlands in association with ***Sphagnum*** may be there because of the low *p*H.

Of the 79 genera of slime molds in the **Mxyomycetes**, **Dictyosteliomycetes**, and **Ceratiomyxomycetes** listed by nomen.eumycetozoa.com as of 5 May 2019, 44 have at least one member that has been found on a bryophyte. I have found no records among the protostelids.

Summarizing this chapter raises more questions than answers. Do either the bryophytes or the slime molds, or both, benefit from their association? If so, how? Do the bryophytes and slime molds simply prefer the same environmental conditions? It seems likely that moisture is a major factor, but experiments are needed on a sponge or other non-biological material to provide moisture with no nutrients. Do some bryophytes inhibit the growth of slime molds? Do some provide food through the microflora and fauna of the bryophyte, and do others fail to provide it because of growing conditions or inhibitors? Are some slime molds inhibited while others are not by the same bryophyte species? Experiments with bryophyte extracts on cultures of slime molds could be illuminating.

## Summary

Habitats for the slime molds are arguably as diverse as those of bryophytes. Some of the "less important" habitats, in terms of number of species, are on epiphyllous leafy liverworts, on liverworts elsewhere, on leaf litter, on soil, on rocks, on sand dunes, in alpine and polar regions, in ravines, on wet rocks, and in peatlands, including on ***Sphagnum***. These habitats contrast with the higher richness and abundance on bark and rotting wood. In all of these habitats, some slime molds exist on bryophytes. Our understanding of this slime mold-bryophyte relationship is almost non-existent. The presence of plasmodia on bryophytes is even less well understood than the presence of sporangia. In contrast to the bryophytes, the species richness and abundance changes of slime molds with increasing elevation mimic those seen for increasing altitude.

Alpine areas seem have some of the bryophiles, such as ***Barbeyella minuta***. Polar regions, on the other hand, are often dominated by **Dictyosteliomycetes**. Records of bryophyte dwellers are rare or non-existent in the polar regions.

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