

CHAPTER 12-1

TERRESTRIAL INSECTS: HABITAT AND ADAPTATIONS

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CHAPTER 12-1

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Figure 1. This tiny moving moss on the back of an insect is among the many unknown wonders awaiting us among the bryophyte-insect interactions. Photo courtesy of Aline Horvath.

Mosses are useful to the insect tribe, countless numbers of which find homes among their branches, and roam about in their shades as in mighty forests, looking with their thousand eyes upon the wonders of their leaves, and sunning their wings of purple and of gold, and burnishing their shining armour upon the polished columns of their urns. Frances Tripp, *British Mosses*, 1888.

Bryophytes can be so unique as to be the source of as yet undescribed species (Figure 1) and even genera of insects, as will be seen in the many orders of insects discussed in the following subchapters. They harbor numerous kinds of insects as well as other arthropods (*e.g.* Takaki 1957). And they provide habitat to protect insects all over the world (Schwarz *et al.* 1993) and in all kinds of habitats (Merrifield 1994).

Bryophytes as Habitat

Bryophytes not only provide a direct habitat for insects, but they alter the soil habitat beneath them. Gerson (1969) suggested that abundance of arthropods in the Antarctic is dependent on this soil alteration. Presence of moss can moderate the soil temperature and moisture and may in some cases discourage digging by would-be predators on soil organisms.

The bryophyte habitat is subject to the climatic and microclimatic differences dictated by elevation, distance from sea, topography, and latitude, resulting in arthropod community differences (Andrew *et al.* 2003). These differences extend to such limited habitats as that of epiphyllous liverworts (Lücking & Lücking 1998). Andrew and Rodgers (1999) found that in the Tasmanian Mountains, site scale variation (2 km or less) is the major contributor to the bryophyte faunal diversity, seemingly more important than altitude.

Drozd *et al.* (2008, 2009) found that even higher taxonomic levels formed associations that indicate interactions between the presence of bryophytes and other microhabitat features. Sampling only seven bryophyte species in the Czech Republic, they obtained more than 55,000 specimens of arthropods. They show that the presence of bryophytes, the species of bryophytes, and the moisture levels are very important determinants of arthropod abundance. Nevertheless, abundance of arthropods was greater in the litter than in the moss cushions. Since many of the arthropods are searching for prey, the density of the moss cushions limits the size and requires agility to permit the arthropods to navigate to capture prey. Instead, the bryophytes serve as a refuge for prey organisms that can find their food there. These require only limited movement, making them relatively invisible to predators. This limited movement also leads to trap bias in the pitfall traps as these insects typically do not leave the safety of the bryophyte cushions. Weikel and Hayes (1999) pointed out that while the abundance of arthropods as potential food for birds may correlate positively with bryophyte cover, the bryophytes may act as hiding places, thus rendering most of them unavailable to the birds.

Drozd *et al.* (2007) found that about 25% of the insect species in forest floor communities (litter and mosses) are present only among the mosses. Moisture was the primary factor accounting for their distribution.

But, as Drozd *et al.* (2007) pointed out, our knowledge of the mosses as a food source is all but unknown. One of the means of identifying whether bryophytes are eaten is to recognize bryophyte fragments in the faeces or frass. Matthaias Nuss (pers. comm. 16 January 2008) provided me with an image of *Tortula truncata* with chewed leaves and what appeared to be frass on the plant (Figure 2). But then, how often can we identify the producer of the frass?



Figure 2. Possible insect frass on *Tortula truncata*. Matthaias Nuss of the Museum für Tierkunde / Museum of Zoology, Dresden, Germany (pers. comm. 16 January 2008) suggests that these may be sclerified head or mandible parts that have an interesting attachment to the sporophytes of these mosses. There appear to be no silk threads, ruling out moth larvae, but *Byrrhidae* (Coleoptera) or some *Mecoptera* are good candidates. Photo courtesy of Robin Stevenson.

Drozdová *et al.* (2009) considered mosses to be unique habitats that could provide safe sites against predators. To

test this hypothesis, they used living bait in a vertical gradient (surface level, moss cushions, bushes, tree trunks). The bait was living larvae of the blowfly *Calliphora vicina*, a common prey item. The locations included leaves of blueberries (*Vaccinium myrtillus*), mosses [*Polytrichastrum formosum* (Figure 3), *Polytrichum commune* (Figure 4), and *Dicranella* sp. (Figure 4)], and spruce (*Picea abies*) trunks. After 30 minutes of exposure the researchers counted the attacked and missing larvae and noted the presence of predators. The dominant predators were ants and spiders, the same as the forest floor in general (Drozdová *et al.* 2009). The predation rate inside the moss cushions was about the same as that in the litter, but the taxonomic groupings of the predators differed. Millipedes were the dominant predators in cushions of *Dicranella* sp and *Polytrichum commune*, with spiders and beetles (*Carabidae* and *Staphylinidae*) following. Centipedes also occurred on the ground in areas of moss cushions under the *Vaccinium myrtilloides*. The highest predation occurred inside the *Polytrichum* cushions, with the same rate on the terminal parts of the plants as on the tree trunks. It appears that the structure of the moss cushion – the growth form – might be an important determinant of predation risk.



Figure 3. *Polytrichastrum formosum*, a forest moss that houses a moderate number of insects. Photo by David T. Holyoak, with permission.



Figure 4. *Polytrichum commune*. *Polytrichum* cushions can be home to numerous beetle species. Photo by A. J. Silverside, with permission.



Figure 5, *Dicranella heteromalla* with capsules, a species that is home to millipede predators. Photo by Michael Becker, through Creative Commons.

We aren't always sure why or how bryophytes contribute to the habitat needs of insects, but there is certainly evidence that they make a difference. Pavel *et al.* (2007) used pitfall traps in the Czech Republic to compare the beetles (**Coleoptera**) in forest communities with and without a moss layer. With the caveat that there is not necessarily a cause and effect relationship, an accumulation of such studies do indicate that it is worth exploring the role of the bryophytes. In this case, two traps were placed in *Polytrichum* (Figure 4) cushions and two were at least 10 m away from the nearest cushions at each of three sites. In their collections, beetles reached the highest numbers among the insects, with 56 species and the greatest abundance. Overall, they found a higher insect species richness in the moss communities, with ~25% of the insect species only occurring among the mosses. Not surprisingly, moisture was the most important environmental character affecting habitat preference, but presence of a moss layer was not significant. Only one of the species was **bryophagous** (bryophyte consuming), a member of the beetle family **Byrrhidae** (Figure 6). Especially in drier regions, the insects tended to inhabit the moss cushions, behaving as **bryobionts**.

In the Spitsbergen coastal tundra, Bengston *et al.* (1974) found 268,000 insects on the wet moss tundra, compared to 518,000 on grassland. The abundance of major insect groups were similar between the Spitsbergen tundra and high alpine areas of southern Norway.

In the Czech Republic, Božanić *et al.* (2013) used heat extraction from bryophytes to determine the effects of species of bryophytes and environmental factors on the animals present. In these samples they found 45 species of invertebrates among the 15 bryophyte species examined. Surprisingly, few were insects, all in the **Formicidae** (4

species of ants). Rather, there were 9 species of centipedes, 7 of millipedes, 4 of pseudoscorpions, 6 of isopods, 4 of harvestmen, 6 of earthworms, and 5 of spiders. *Brachythecium oedipodium* (Figure 7) had the richest assemblages of invertebrates. These numbers are probably minimal as some bryophyte dwellers do little moving and may die before escaping the heat within the bryophyte clump in the funnel and heat separation apparatus. The ones found are all able to move rather quickly, so this may explain the absence of bugs, beetles, and other insect groups. The type of substrate and height above ground proved to be the most important factors affecting the invertebrate distribution.



Figure 6. *Cytilus sericeus* (Byrrhidae) adult on mosses. Photo by S. Rae, through Creative Commons.



Figure 7. *Brachythecium oedipodium*, home to a rich assemblage of invertebrates. Photo by Michael Lüth, with permission.

At McKenzie Table Mountain Preserve in California, USA, Bettis (2008) found that the moss fauna on two species of **Grimmia** (Figure 8) were mostly tardigrades, mites, springtails, and midge larvae. Studies of bryophyte fauna commonly indicate that spiders (**Araneae**), springtails (**Collembola**), and mites (**Acari**) are the most common fauna (von der Dunk & von der Dunk 1979; Kinchin 1990). Even on Signy Island in the maritime

Antarctic, the mites and springtails predominate (Usher & Booth 1984). The upper, green moss communities differed from the lower, dead moss communities. The same species tended to occur in both layers, but the proportions differed.



Figure 8. *Grimmia pulvinata* with capsules, home to tardigrades, mites, springtails, and midge larvae in California, USA and elsewhere. Photo by Javier Martin, through Creative Commons.

Von der Dunk and von der Dunk (1979) listed the arthropods in clumps of five species of mosses in March to May, including counts (Table 1). In addition to unidentified larvae, they listed the *Collembola Sminthurinus* (Figure 9), *Xenylla* (Figure 10), and *Tomocerus* (Figure 11-Figure 12) as well as thrips.



Figure 9. *Sminthurinus aureus* f. *ochropus* on mosses, member of a springtail genus that is common among mosses in spring. Photo by Andy Murray, through Creative Commons.



Figure 10. *Xenylla* sp. among mosses. Photo by Andy Murray, through Creative Commons.



Figure 11. *Tomocerus* sp. juvenile on mosses. Photo by Andy Murray, through Creative Commons.



Figure 12. *Tomocerus minor*, member of a genus that is common among mosses. Photo by Andy Murray, through Creative Commons.

Table 1. Number of insects found in moss polsters in Germany in March to May. From von der Dunk & von der Dunk 1979.

	<i>Rhytidiadelphus</i>	<i>Scleropodium</i>	<i>Hypnum</i>	<i>Plagiothecium</i>	<i>Brachythecium</i>
<i>Sminthurinus</i>	46	52	-	-	-
<i>Xenylla</i>	4	2	7	106	-
<i>Tomocerus</i>	-	-	1	-	4
thrips	+	+	+		+

Nutrients in the ecosystem affect the types of plants that will grow there, and bryophytes seem to have an aversion to high nutrients. Richardson *et al.* (2002) experimented with nutrients and their effects on plant communities and their insect herbivores in a Scandinavian

sub-Arctic dwarf shrub heath. After nine years of nutrient enrichment, the subordinate plant functional groups (grasses and mosses) experienced greater effects than did the dominant dwarf shrubs. The insect herbivores showed evident changes in abundance. The biomass changes in the

grasses and mosses contributed more to these insect changes in biomass and species composition than did the shrubs. One moss-eating species of **Heteroptera** in the fertilized plots dropped to as little as 6% that of the control plots. The abundance of grass specialists in **Homoptera** in fertilized plots, on the other hand, reached 400% that of controls. This study emphasized the importance of the subdominant plant species in driving the insect species composition of the habitat.

Temperature Relations

Because of their construction with lots of air spaces, bryophytes can act like a fluffy winter quilt. They are able to buffer temperatures with these trapped air spaces (Soudzilovskaia *et al.* 2013). In some instances, they may remain warmer from reradiated heat from rocks or soil. In other cases their capillary water may cool them by evaporative cooling. Differences between bryophyte species comply with physical laws and can be explained by differences in mat thickness and moisture content. There are, however, few data sets to evaluate the extent of this role in a variety of ecosystems. Some of these differences are provided in Chapter 10-1 on Temperature in Volume 1.

Of course food is a problem in winter, but some insects are able to feed on alternate food sources. *Diamesa* sp. (**Diptera: Chironomidae**; Figure 13) is a cold-tolerant insect that lives on a glacier in the Nepal Himalayas (Kohshima 1984). This flightless insect is able to walk on the surface and in small cavities beneath the glacier. The larvae feed on Cyanobacteria and other bacteria, permitting this species to spend its entire life in the glacier. And it is still active at -16°C . While this is not a bryophyte dweller, it illustrates the ability of insects to survive in cold habitats, such as those in the Arctic and Antarctic, and to subsist on foods like bacteria and Cyanobacteria that are available among the bryophytes.



Figure 13. *Diamesa bohemani* larva, member of a genus in which at least one species is able to survive on glaciers and feed on Cyanobacteria and bacteria. Photo from NTNU Museum of Natural History & Archaeology, through Creative Commons.

Preparation for Winter

As we noted in the aquatic insect chapter, insects can avoid freezing damage in two ways (Duman *et al.* 1991). The most flexible means is to obtain freeze tolerance, permitting the insect to survive formation of ice on the outside of the body. The second mechanism is to avoid

freezing. The latter can be subdivided into physiological mechanisms that prevent the insect from freezing by altering the freezing point of the organism or preventing ice nucleation through manufacture of antifreeze proteins (Duman *et al.* 2004). The other is a behavioral adaptation that places the insect in a place where it is protected from freezing (Duman *et al.* 1991).

Bryophytes are often a winter refuge or site of hibernation for insects. The bryophyte offers insulation against the wind and cold. Under the snow, the dark color of most bryophytes absorbs heat from the light that is able to penetrate the snow. Nevertheless, bryophytes may be exposed to severe cold before the snow arrives or after it melts in spring. Hence, their inhabitants still require some sort of protection from the cold.

Storey and Storey (1992) listed two stresses that can prevent winter survival in terrestrial insects. The obvious one in many places is lack of food, but some insect larvae are able to feed on the bryophytes. Others may survive as eggs or pupae, stages in which there is no feeding. Some insects compensate for the lack of food by accumulating large lipid and carbohydrate reserves in the body fat in preparation for winter (Storey & Storey 1992). Others enter into a state of reduced metabolic rate (**quiescence**) or arrested development (**diapause**) in which they can rely on limited food reserves.

The second winter stress is tissue damage at low temperatures, especially freezing (Storey & Storey 1992). Insects have two options to survive in areas that attain sub-freezing temperatures: **freeze avoidance** and **freeze tolerance** (Bale 2002). Freeze avoidance includes life cycle adaptations that do not require the insect to be present during the cold period. For some, this is through migration. For others, it is finding warmer locations such as deep soil, in the water, or even among deep mosses. But insects also can have physiological means of freeze avoidance while existing in locations with sub-zero temperatures.

Protein ice nucleators (PINs) limit supercooling and induce freezing (Duman 2001). When the nucleating proteins are internal, a small size can help to prevent the formation of large crystals. In insects, freeze-tolerant species produce PINs in the hemolymph. These allow freezing in the hemolymph at temperatures just below freezing and inhibit freezing within the cells. In some cases, these PINs are "removed" in the winter, promoting supercooling. **Antifreeze proteins** (AFPs) prevent freezing. One beetle has AFPs in the hemolymph and gut that inhibit the ice nucleators in winter.

One theory of freeze avoidance in insects is that of **heterogeneous nucleation**. However Zachariassen *et al.* (2004) provide evidence that it is water volume that determines the nucleation temperatures in freeze-avoiding insects. The relationship between the aqueous solutions and the particular freeze avoidance displayed behaves more like that of homogeneous nucleated samples.

One of the strategies to survive winter is the ability to **supercool** (Holmstrup *et al.* 2002). This ability seems to have evolved at the same time as the ability for insects to retain body water in dry environments. But soil invertebrates are far less resistant to desiccation than the above ground insects. It is likely that bryophyte dwellers are more like the soil invertebrates but in some cases may find greater moisture among bryophytes. Soil invertebrates

dehydrate in frozen soil; only a few degrees of supercooling causes substantial water loss which continues until the vapor pressure of body fluids equals the vapor pressure of the surrounding ice. At this point, tissue ice formation is eliminated and the invertebrate can survive subzero temperatures. But the Arctic soil invertebrates do not base their winter survival on this method of supercooling. Rather, they dehydrate to equilibrate their body-fluid melting point to that of the ambient temperature. This method works even in the extreme cooling rates of the polar soils.

For those insects that are sensitive to freezing, but still exhibit cold hardiness, their survival is typically achieved through **supercooling**, with some exhibiting supercooling points to below -25°C (Zachariassen & Husby 1982). These low non-freezing temperatures are accomplished through polyols and proteinaceous thermal hysteresis antifreeze agents that reputedly prevent the growth of ice crystals down to approximately -10°C . This prevention is increased dramatically when the crystal size is diminished. This added ability to prevent crystal formation permits them to live through temperatures as low as -30°C . In such cases, the insects can survive even in exposed areas where the snow does not accumulate.

Freeze tolerance in terrestrial insects occurs primarily among the **Coleoptera** (beetles), **Lepidoptera** (moths & butterflies), **Diptera** (flies), and **Hymenoptera** (bees & ants) (Storey & Storey 1992), whereas only the **Diptera** seem to have any tolerance to freezing in the aquatic stage (Moore & Lee 1991). Freeze tolerance may require preparation or it may be present year-round.

Freeze tolerance is energetically expensive and carries risks of ice crystal damage or other physical damage. The insect furthermore must survive osmotic stresses when water and solutes are rapidly redistributed across cell membranes during freezing and thawing periods. And part of this strategy is extracellular freezing that can damage membranes, not to mention the obstruction of oxygen flow to the body.

Freeze avoidance is the less expensive strategy and permits insects to be active under the snow where the snow provides suitable insulation (Storey & Storey 1992). Insects in cold environments further avoid freezing by the presence of hairs and dark body colors (Danks 2004), the former to insulate and the latter to absorb heat on sunny days. The insects complement these physical adaptations by behavioral adaptations – being active on sunny days and going to protected locations when it is getting cold (Danks 2004, 2005). Danks (2007) discusses their responses, including dispersal, habitat selection, habitat modification, resistance to cold, dryness, and food limitation, recognition of environmental signals, diapause, modifications to developmental rate, life cycle patterns that include multiple alternatives within the species, variation in phenology and development, and tradeoffs among these.

The behavioral escape of freezing could be to burrow into the ground below the frost line, go into decomposing material that generates heat, or find some other protected location locally. But for a few insects, this escape is a migration to a warmer climate, as is well known for the Monarch butterfly.

Bryophytes may come into the picture for some of the insects that are able to eat them. Cold induces changes in

membranes and protein structure in insects due to phase changes in the molecules, changes in electrolyte concentrations and other solutes in body fluids, and changes in metabolism (Ramløv 2000). In some cases, animals switch diets prior to winter, some of which may include bryophytes (Prins 1982). This usefulness of such a behavior among insects remains unknown.

We know that bryophytes are rich in **arachidonic acids** that help to keep membranes pliable (Hansen & Rossi 1991). Insects produce little or no arachidonic acid (McPartland *et al.* 2001). Nevertheless, ladybird beetles (*Coleomegilla maculata*; Figure 14-Figure 15) have their highest proportion of arachidonic acid in the coldest part of winter (Zar 1968). Thus, a winter switch to bryophytes by some insects seems to be a reasonable hypothesis, and a potential source of arachidonic acid.



Figure 14. *Coleomegilla maculata* larva, a species with its highest concentrations of arachidonic acid in the coldest part of winter. Photo by Tom Murray, through Creative Commons.



Figure 15. *Coleomegilla maculata* adult, a species with its highest concentrations of arachidonic acid in the coldest part of winter. Photo by Tom Murray, through Creative Commons.

Whether arachidonic acids help in cold resistance for insects or not, they may help to keep membranes pliable for movement. Although Prins (1982) demonstrated a relationship with bryophytes in the diet of vertebrates, arachidonic acid, and winter survival, and we know that insects typically have quantities of the acid in their tissues (Dadd & Kleinjan 1979; Stanley-Samuelson & Dadd 1983), there does not yet seem to be research to demonstrate this relationship between arachidonic acid, winter tolerance, and insects. The closest evidence is that arachidonic acid enables the mosquito *Culex pipiens* to fly when it emerges as an adult (Dadd & Kleinjan 1979).

Arachidonic acid may not be the only chemical change in preparation for winter. Low temperatures not only affect the insects and cause different cell and membrane chemicals to initiate, the bryophytes also produce different chemicals or different concentrations when the temperatures drop. In *Rhytidiadelphus squarrosus* (Figure 16) and *Eurhynchium striatum* (Figure 17) there is a switch from 30% arachidonic acid (AA) and 5% eicosapentaenoic acid (EPA) to higher percentages of EPA, α -linolenic acid, and dihomogamma-linolenic acid, accompanied by a slight decrease in AA and linoleic acid (Hansen & Rossi 1991). This particular study does not support the hypothesis that AA increases in bryophytes in preparation for winter, but it is likely that the bryophytes still have higher concentrations of arachidonic acids than tracheophytes at those temperatures or any time (Herbert & Prins 1982; Hartmann *et al.* 1986; Groenewald & Van der Westhuizen 1997; Kajikawa *et al.* 2008).



Figure 16. *Rhytidiadelphus squarrosus*, a species that decreases in arachidonic acid in winter. Photo by Michael Lüth, with permission.



Figure 17. *Eurhynchium striatum* with a capsule, a species that decreases in arachidonic acid in winter. Photo by J. C. Schou, with permission.

Field biologists often consider winter to be a "down" season when insects are inactive, and therefore it is not a useful season for field work. But insects must find some way to survive winter and pass their genes to the next generation. Many do this as eggs or pupae. And bryophytes seem to be an ideal place for both, at least for some insects. They provide protection against easily damaged tissues of pupae when larger animals walk or climb about, they hide them from predators, they decrease the threat of desiccation, and they provide insulation. And for active insects, they may provide food directly or through other organisms that live among the bryophytes. Surely many species spend their winters there in this bryophytic safe site.

But little literature exists on the bryophyte as an overwintering home. Not only is this season less conducive to field study, but even those who do collect are faced with a daunting task of identification. Pupae and eggs must be matched with adults to avoid the danger of creating new species for what is simply a different life cycle stage. That requires rearing to maturity, a special challenge for eggs. And someone needs to have done that already if there are to be any keys or descriptions to aid identification. Hence, even those collections that are made rarely see publication due to the lengthy process of putting names to the organisms.

Most taxonomic treatments on insects give only general habitats for the insects, and often I wonder if there wasn't a moss involved, as food or shelter, but unnoticed, or at least unreported, by the collector. Treatments of forest floor insects often compare soil and litter organisms, and even those on rocks, but no mention is made of mosses, although they are often lumped with litter.

The use of bryophytes on a phenological calendar is demonstrated by The Entomologist's Calendar (Samouelle 1819). Those arthropods living on or under mosses in January were *Philosia muscorum* (Isopoda; Figure 18), *Cylindroiulus londinensis* (Diplopoda), *Cylindroiulus punctatus* (Figure 19), *Geophilus acuminatus* (Chilopoda; see Figure 20), *Siro rubens* (Opiliones; see Figure 21), *Neobisium carcinoides* (Pseudoscorpiones; Figure 22), *Cychnus caraboides* (Coleoptera; Figure 23), *Acropagus glabricollis* (name no longer in use); in February *Bryaxis haematica* (Coleoptera; species name no longer in use; see Figure 24), *Staphylinus morio* (Coleoptera; see Figure 25); in March *Gyrophynus punctulatus* (Coleoptera; Figure 26), *Chlaenius prasinus* (Figure 27), *Tachinus analis* (Coleoptera), *Tachyporus analis* (Coleoptera), *Choleva oblonga* (Coleoptera), *Catops sericeus* (Coleoptera; species name no longer in use; see Figure 28); in April *Staphylinus aenoecephalus* (Coleoptera; species name no longer in use), *Staphylinus decorus*; species name no longer in use; in May *Dasytes ater* (Coleoptera; species name no longer in use; see Figure 29); in June – November no moss records; in December *Tachyporus chrysomelinus* (Coleoptera; Figure 30). This change from winter to summer suggests that the bryophytes offer these insects something in winter, whether it is only shelter, or there is also a food source.



Figure 18. *Philoscia muscorum*, an isopod that can be found under mosses in January in Europe. Photo by Africa Gomez <abugblog.blogspot.com>, through Creative Commons.



Figure 21. *Siro* sp. on moss; *Siro rubens* occurs under mosses in January in Europe. Photo by Marshal Hedin, through Creative Commons.



Figure 19. *Cylindroiulus punctatus*, a millipede that can be found under mosses in January in Europe. Photo by G. Drange <Biopix>, through Creative Commons.



Figure 22. *Neobisium carcinoides*, a pseudoscorpion species that spends January under mosses in Europe. Photo by Trevor and Dilys Pendleton <www.eakingbirds.com>, with permission.



Figure 20. *Geophilus flavus* (centipede) on moss protonemata. *Geophilus acuminatus* can be found under mosses in Europe in January. Photo by Anthony Barber, through Creative Commons.



Figure 23. *Cychrus caraboides* adult, a species that occurs under mosses in January in Europe. Photo by Siga, through Creative Commons.



Figure 24. *Bryaxis bulbifer* adult; *Bryaxis haematica* occurs under mosses in February in Europe. Photo by Christoph Benisch <kerbtier.de>, with permission.



Figure 27. *Chlaenius prasinus* adult, a species that occurs among mosses in March. Photo by Mike Quinn, through Creative Commons.



Figure 25. *Staphylinus* sp. adult; *Staphylinus morio* occurs under mosses in February in Europe. Photo by Alvesgaspar, through Creative Commons.



Figure 28. *Catops tristis* adult; *Catops sericeus* occurs under mosses in March in Europe. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 26. *Gyrohypnus punctulatus* adult, a species that occurs among mosses in March in Europe. Photo from Naturalis, Biodiversity Centre, through Creative Commons.



Figure 29. *Dasytes plumbeus* adult. "*Dasytes ater*" is associated with mosses in May. Photo by Sarefo, through Creative Commons.



Figure 30. *Tachyporus chrysomelinus* adult on bryophytes. Photo by Malcolm Storey, through Creative Commons.

Water Relations

Water is often the limiting factor for terrestrial insects (Tauber *et al.* 1998; Hayward *et al.* 2004). It can account for the importance of other variables such as elevation (Lee & La Roi 1979). Tauber *et al.* (1998) suggested that moisture was important in determining insect seasonality, stimulating diapause, modulating development and reproductive rates, and providing a cue for seasonal events. Bryophyte species are also limited by moisture, thus creating different moisture regimes available to the ground-dwelling and arboreal insects (Whittaker & Niering 1975; Slack 1977; Lee & La Roi 1979; Vitt 1991; During 1992; Wolf 1994; Li & Vitt 1995; Vitt & Belland 1997).

Fragmentation and Corridors

One of the causes of declines in species is the inability to disperse due to unfavorable habitat between suitable locations. Gonzalez *et al.* (1998) found that when patches of suitable habitat were connected by habitat corridors, they provided a rescue effect. Both abundance and distribution improved when habitats were connected. For many kinds of insects, bryophytes can provide such corridors, providing moisture and shelter even when they are unsuitable as food.

Starzomski and Srivastava (2007) experimented with landscape geometry and found that reducing the size of patches had little effect on community resilience. However, habitat loss caused complete loss of connectivity between patches. In their experiments with the microarthropod community (mostly mites and springtails) of mosses (*Polytrichum* and *Bryum*) on a granitic outcrop in BC, Canada, repeated disturbance caused rapid declines in species richness and abundance, altering community structure. These two arthropod groups were highly abundant, reaching 200 or more morphospecies in areas of only 20 m².

Insect Adaptations to Bryophytes

Insects often modify their environment to make it suitable for their homes. These include excavations in soil and other substrates, construction of feeding or resting shelters, inducing plant responses such as galls, forming aggregations, building colonial nests, and using parental care (Danks 2002). These alterations can buffer temperatures, increase moisture, and avoid flooding.

Moisture needs (Danks 2004) may drive them to bryophytes, especially during summer dry spells. The excavations and shelters protect primarily against physical factors (Danks 2002). On the other hand, aggregations, colonies, and parental actions usually influence the ability to acquire resources.

Perhaps the most important characteristic of a bryophyte inhabitant is the ability to navigate within the small spaces available. This means the insects must be small, and it means their appendages must not get in the way. Hence, large insects like butterflies and moths cannot navigate as adults, and many are likewise too large as larvae to move within the mat.

Another adaptation is the ability to utilize the moss. If it is unable to use the bryophyte as a food source, it might not be worth the energy to enter the moss community.

But food is not the only reason to enter a bryophyte clump. As seen in other invertebrates, insects can seek out the moss as a safe site from the dangers of desiccation. However, they lack the ability to encyst that is beneficial to several invertebrate groups. Instead, their life cycles permit them to be inactive during the winter season, and their mobility permits them to leave when the going gets rough. Thus, pupae of insects with a **holometabolic** (having eggs, larvae, pupae, and adults) life cycle and eggs of all insects provide life cycle options to permit residency during dry or cold periods. And most likely they, like many other invertebrates, migrate vertically as moisture or temperature within the bryophyte community changes (Markkula 1981).

The bryophyte can provide camouflage. In addition to having the bryophyte create a plethora of light and dark areas with small spaces and overlying leaves and branches, the insect may itself exhibit camouflage (Lacrampe 2003), permitting it even greater protection against predators. For example, the crane fly *Triogma* (Figure 31) has a green and black pattern that makes it resemble a moss branch, sporting projections that resemble leaves (Figure 31). Species in this genus exist in both aquatic and terrestrial habitats, exhibiting a camouflage that suggests it evolved to survive in its mossy habitat (Alexander 1920).



Figure 31. This larva of the crane fly *Triogma* has green and black patterns that make it resemble the moss branches where it lives. Photo by Janice Glime.

Abundance

Invertebrates, and particularly arthropods, can be especially abundant among mosses. Peck and Moldenke (1999) found 125 morphospecies, comprising 18 orders and

5 functional groups, in their study of vine-maple (*Acer circinatum*; Figure 32) in the Willamette National Forest (Oregon, USA). The bases of shrubs exhibited the highest species richness and abundance. The composition likewise differed between the bases and tips of the shrubs. The most abundant insect was *Sminthurus* (Figure 33), a springtail (*Collembola*). Such abundance raises serious concerns about the harvest and export of mosses, especially in the first half meter above the ground.



Figure 32. *Acer circinatum* (vine maple), a species with a rich bryophyte fauna. Photo by El Grafo, through Creative Commons.



Figure 33. *Sminthurus* sp. with spermatophore, the most abundant species among bryophytes on the vine maple. Photo by Petter Bøckman, through Creative Commons.

The high abundance of insects in some moss communities requires special extraction techniques. Andrew and Rodgers (1999) suggest using kerosene to float the insects because it attaches to the cuticle of the insects. The moss-insect community must first be preserved in 95% ethanol for two weeks. This preserved mix is shaken vigorously after topping off with kerosene. The insects settle to the bottom, then float at the interface between the ethanol and kerosene. The kerosene can be pipetted off and insects collected from the interface layer. I have not actually tried this method, but it would appear to work only on relatively small insects and things without legs to get caught. Further discussion of sampling methods appears later in this chapter.

Food Sources

Many researchers have considered bryophytes to be inedible for insects and other invertebrates (Haines & Renwick 2009). Others have commented on how rare bryophagy seems to be (Longton 1984). Even on Bryonet, people familiar with bryophytes marvelled at how little we know about bryophyte herbivory. Nevertheless, Paul Johnson reported studying several groups of insects that feed on mosses or liverworts, many of which are strict **bryophages** (organisms that feed on bryophytes). Kathy Merrifield reported finding much evidence of grazing on mosses that grow in the cracks of tree bark. Several members have provided images that evidence the bryophage damage, as will be seen in succeeding subchapters of terrestrial insect interactions. It is likely that the presence of bryophagy has been largely overlooked.

Nevertheless, some of the oddities among growth forms seem to be the result of **bryophagy** (see Ghullam & Stevenson 2013; Figure 35). Since a dense cluster of apical filaments is an oddity among members of *Zygodon rupestris* (Figure 34), those clusters (Figure 35) observed by Robin Stevenson (pers. comm. 2 June 2016) seem to be produced in response to herbivory. The herbivore is unknown. Normal gemmae (Figure 36) of this species were present along the stem, but these terminal filaments (Figure 37-Figure 38) seemed to be the result of damage to the terminal bud (pers. comm., Robin Stevenson 2 June 2016). *Fontinalis* produces similar filaments (protonemata) when the apex of the stem is removed (Figure 39). And could it be that the herbivore deposits a hormone such as that used to produce galls in tracheophytes? Stevenson suggested that the normal axillary gemmae may be dispersed by hares and deer that brush against the tree trunks where the moss lives. It is possible that these terminal filaments might likewise be dispersed and serve as propagules. Anomalies such as these should provide an interesting area for research on development and evolution.



Figure 34. *Zygodon rupestris* growing normally with no terminal clusters of filaments. Photo by David T. Holyoak, with permission..



Figure 35. Chewed *Zygodon rupestris*. Note that several of the apices lack the gemmae clusters. Photo courtesy of Robin Stevenson.

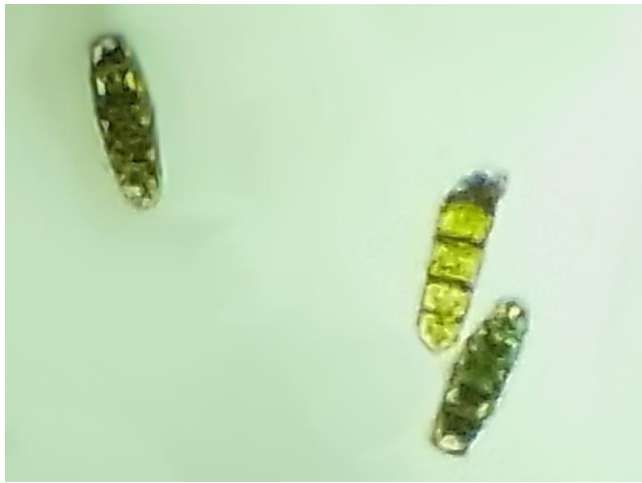


Figure 36. *Zygodon rupestris* normal axillary gemmae. Photo courtesy of Robin Stevenson.

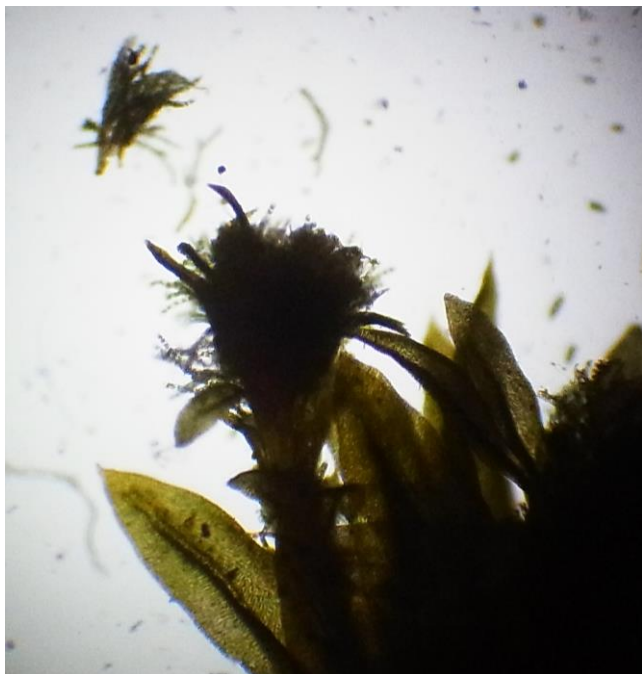


Figure 37. *Zygodon rupestris* with apical threads produced after herbivory. Photo courtesy of Robin Stevenson.



Figure 38. *Zygodon rupestris* apical threads produced after herbivory. Photo courtesy of Robin Stevenson.



Figure 39. *Fontinalis hypnoides* filaments (protonemata) produced after the stem apex was broken. Photo by Janice Glime.

Biologists have considered three classes of mechanisms to provide barriers to bryophagy: chemical defenses, low digestibility, and low nutrient content. But just as in tracheophytes, not all bryophytes are the same. Some are eaten while others just beside them are not, suggesting chemical defenses (Swain 1977). Haines and Renwick (2009) compared four bryophyte species by examining pre- and post-ingestive defenses by the bryophytes, all of which were mosses. Using the generalist caterpillar *Trichoplusia ni* (Figure 40-Figure 41), a generalist caterpillar, they found that mosses were consumed much less than lettuce or wheat germ. Of the four mosses tested [(*Bryum argenteum* (Figure 42), *Climacium americanum* (Figure 43), *Leucobryum glaucum* (Figure 44), and *Sphagnum warnstorffii* (Figure 45)], only *Climacium americanum* was consumed in sufficient quantity to evaluate post-ingestive responses by the caterpillars. Extracts of *Leucobryum glaucum* placed on discs showed that this moss, the least eaten, contained a deterrent. Haines and Renwick suggested that preingestive mechanisms are more important than post-ingestive mechanisms, but much more study is needed before such a generalization is well supported.



Figure 40. *Trichoplusia ni* caterpillar, a species that prefers lettuce over mosses, and avoids mosses even when only mosses are offered as food. Photo by Phil Bendle, with permission.



Figure 41. *Trichoplusia ni* adult, a species whose larvae prefer lettuce over mosses, and avoids mosses even when only mosses are offered as food. Photo by Kurt Kulac, through Creative Commons.



Figure 42. *Bryum argenteum*, a food source that is less preferred by *Trichoplusia ni* than is lettuce. Photo by Michael Becker, through Creative Commons.



Figure 43. *Climacium americanum*, a food source that is less preferred by *Trichoplusia ni* than is lettuce, but it is eaten. Photo by Alan S. Heilman, through Creative Commons.



Figure 44. *Leucobryum glaucum*, a food source that is less preferred by *Trichoplusia ni* than is lettuce. Photo by James K. Lindsey, with permission.



Figure 45. *Sphagnum warnstorffii*, a food source that is less preferred by *Trichoplusia ni* than is lettuce. Photo by Jouko Rikkinen, through Creative Commons.

Longton (1984) reviewed the literature on the role of bryophytes and concluded that the energy content of bryophytes is generally slightly lower than that of

associated plants. Wielgolaski and Kjelson (1975) demonstrated this for Scandinavian tundra Communities. Lewis Smith and Walton (1973) demonstrated it for a sub-Antarctic island and Bliss (1962) for an alpine tundra. But is this true in warmer habitats? Gorham and Sanger (1967) found it likewise to be true in Minnesota, USA, but that is still a relatively cold climate, at least in winter.

There does seem to be an increase in caloric content with latitude (Forman 1968, 1969; Rastorfer 1976), as there is for flowering plants, with a range of 3.7-4.8 Kcal g⁻¹ for bryophytes. Longton (1984) suggests that the lower energy content in bryophytes results from lower concentrations of carbohydrates, proteins, and lipids. This was true at least for proteins and readily soluble carbohydrates in a Norwegian alpine tundra (Skre *et al.* 1975).

Lawrey (1987) challenged the notion that bryophytes had little nutritional value. Some researchers have argued that they are lower in calories than tracheophytes (Forman 1968; Pakarinen & Vitt 1974), but others consider them to fall into the same range as those of tracheophytes (Bliss 1962; Forman 1968; Pakarinen & Vitt 1974; Rastorfer 1976). Davidson *et al.* (1990) compared uneaten gametophytes to edible sporophytes and found that the ash-free caloric values did not differ, further suggesting that caloric values are not a limiting factor. On the other hand, Skre *et al.* (1975) found that both their protein and carbohydrate content is typically low in alpine bryophytes compared to tracheophytes. And levels of potassium and magnesium tend to be lower in mosses than in tracheophytes (Prins 1982).

The sugars in bryophytes are the same as in tracheophytes, although some additional ones occur. Spores are especially high in lipids and may account for consumption by ants (Plitt 1907). Pelser *et al.* (2002) even reported that some mosses [*Catharomnion ciliatum* (Figure 46), *Canalohypopterygium tamariscinum* (Figure 47)] produce oils. They considered that the oil may have an energy storage function, but rather than considering it to be a food source for invertebrates, they suggested that it could serve to repel invertebrates, fungi, or bacteria.



Figure 46. *Catharomnion ciliatum*, a species that produces oils that may be a deterrent to herbivory. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.



Figure 47. *Canalohypopterygium tamariscinum*, a species that produces oils that may be a deterrent to herbivory. Photo by Pieter B. Pelser, with educational permission.

Sveinbörnsson and Oechel (1991) questioned the carbohydrate and lipid changes in tundra mosses as the seasons changed. Using *Polytrichum commune* (Figure 4) and *Polytrichastrum alpinum* (Figure 48), they samples three times per year. On the raised polygon rims, both lipid and carbohydrate concentrations were higher in *Polytrichum commune* than in *Polytrichastrum alpinum*. The green parts of the plants had significantly higher concentrations of lipids than did rhizomes in *Polytrichum alpinum*, but this relationship was not true in *Polytrichastrum alpinum*. Sugar concentrations were higher in green parts in both species, whereas starch concentrations were highest in the rhizomes.

Only *Polytrichum commune* demonstrated seasonal variation in starch and sugar concentrations (Sveinbörnsson & Oechel 1991). There was a significantly strong negative relationship between sugars and starches. On the other hand, there was a significant positive relationship between lipids and starch+sugar. The seasonal relationship of these two *Polytrichaceae* mosses is like that of evergreen tracheophytes.



Figure 48. *Polytrichastrum alpinum*, a polygon rim species in the Arctic. This species has high sugar content in green parts and high starch content in the rhizomes. Photo by David T. Holyoak, with permission.

Chapin *et al.* (1986) found that seasonal fluctuations in carbohydrate concentration varied between moss species in

the Alaskan tundra. Brown parts of *Aulacomnium* spp. exhibited greater seasonal differences than did species of *Polytrichum* and *Pogonatum*. Lipids increased in autumn in brown tissues of mosses and declined in summer. Surprisingly, mosses had the greatest levels of lignin-like substances when compared with tussock graminoids (grasses & sedges), deciduous shrubs, evergreen shrubs, deciduous forbs (non-graminoid herbs), and lichens; *Eriophorum* (cottongrass) and lichens had the least. The preferences of the eight generalist herbivores in the study responded to nutrient levels, preferring higher levels of

nitrogen, phosphorus, and potassium but lower levels of lipid and cellulose in the plants.

Russell (1979) found that the liverworts preferred by *Caurinus dectes* actually had a low nutrient content (Table 2), particularly for nitrogen, an important component of protein. But he pointed out that the *Caurinus* was able to extract the nutrients from the cells without having to eat and digest the cellulose that is so abundant in some bryophyte leaves, thus making the concentrations higher than that indicated in the table.

Table 2. Macronutrient concentrations (% dry weight) in the gametophytes of some bryophytes collected in *Caurinus dectes* habitat at Marys Peak, Oregon, USA. From Russell 1979.

		P	N	Na	K	Ca	Mg
Mosses							
<i>Dicranum fuscescens</i>	Figure 49	.142	.932	.038	.546	.418	.145
<i>Rhizomnium glabrescens</i>	Figure 50	.251	2.083	.043	1.125	.972	.261
<i>Eurhynchium oreganum</i>	Figure 51	.146	.829	.056	.741	.518	.190
<i>Isothecium spiculiferum</i>	Figure 52	.142	.949	.034	.512	.516	.177
<i>Antitrichia curtipendula</i>	Figure 53	.151	.686	.028	.631	.430	.170
<i>Rhytidiadelphus loreus</i>	Figure 54	.164	.727	.072	.770	.440	.171
mean		.166	1.034	.045	.721	.551	.186
Liverworts							
<i>Scapania bolanderi</i>	Figure 55	.072	.748	.035	.659	.275	.111
<i>Porella navicularis</i>	Figure 56	.155	.890	.026	1.040	.426	.156
<i>Frullania tamarisci</i>							
ssp. <i>nisquallensis</i>	Figure 57	.107	.874	.030	.904	.515	.134
mean		.111	.834	.030	.868	.405	.134

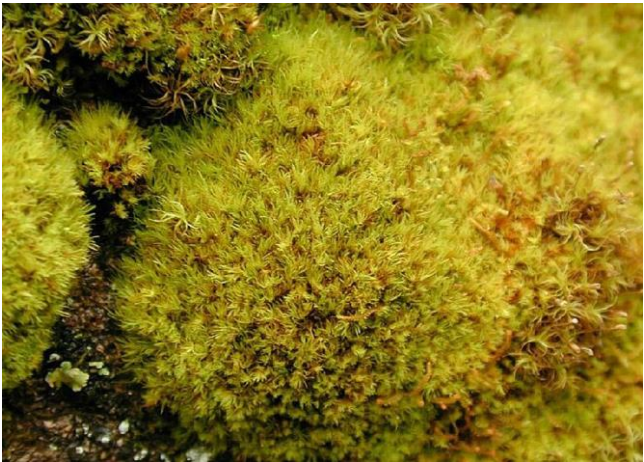


Figure 49. *Dicranum fuscescens*, the species with the lowest concentrations of several macronutrients among the nine bryophytes tested (Table 2). Photo by Michael Lüth, with permission.



Figure 50. *Rhizomnium glabrescens*, the species with the highest concentrations of P, N, K, Ca, and Mg among the nine bryophytes tested (Table 2). Photo by Matt Goff <www.sitkanature.org>, with permission.



Figure 51. *Eurhynchium oregonum*, the species with the highest concentration of Mg of the nine species tested (Table 2). Photo by Matt Goff <www.sitkanature.org>, with permission.



Figure 54. *Rhytidiadelphus loreus*, the species with the highest concentration of Na among the nine species of bryophytes tested (Table 2). Photo by Malcolm Storey <www.discoverlife.org>, with online permission.



Figure 52. *Isohetecium spiculiferum*, the species with the lowest concentrations of P and K among the nine bryophytes tested (Table 2). Photo by Ben Carter, through Creative Commons.



Figure 55. *Scapania bolanderi* with capsules, a species with the lowest concentrations of P, Ca, and Mg among the nine species tested (Table 2). Photo by Chris Wagner, with permission.



Figure 53. *Antitrichia curtipendula*, the species with the lowest concentrations of N and Na among the nine bryophytes tested (Table 2). Photo by Hermann Schachner, through Creative Commons.



Figure 56. *Porella navicularis*, the species with the highest concentration of P and N among the liverworts tested (Table 2). Photo by Rosemary Taylor, with permission.



Figure 57. *Frullania tamarisci*, the species with the highest concentration of Ca among the liverworts tested (Table 2). Photo by Tim Waters, through Creative Commons.

Rather than low nutrients, it seems likely that antiherbivore compounds may contribute to the avoidance of bryophytes by herbivores (Clymo & Hayward 1982; Davidson 1988; Davidson *et al.* 1989; Liao 1993). Lawry (1987) suggests that the same compounds already known for their antibiotic activity (Madsen & Pates 1952; Pates & Madsen 1955; Ramaut 1959; McCleary *et al.* 1960; Wolters 1964a,b; McCleary & Walkington 1966; Gupta & Singh 1971; Banerjee & Sen 1979) may serve also as antiherbivore compounds. For example, phenolic compounds and other related bio-active compounds have been demonstrated multiple times (Markham & Porter 1978, 1983; Asakawa 1981, 1982, 1984, 1990; Wilschke & Rudolph 1988; Harborne 1988; Zinsmeister & Mues 1988; Davidson *et al.* 1989; Xie & Lou 2009).

Ferulic acid in shoots (but not young capsules) of *Mnium hornum* (Figure 58) may account for avoidance of the shoots; ferulic acid, one of the hydroxycinnamic acids, is considered a primitive defense against herbivores in flowering plants (Swain 1977; Fry 1983). These cell wall components would be likely to discourage organisms that chew and grind, but may have no effect on those that pierce and suck, explaining the high incidence of such invertebrates (Longton 1992). In liverworts, it seems that the oil bodies store terpenoids and lipophilic aromatic compounds that have strong antifeedant activity, as shown against the African army worm *Spodoptera exempta* (Lepidoptera; Figure 59-Figure 60) (Asakawa 1990).

Thus far there is no evidence that insects take an **offensive approach** to bryophyte herbivory (Karban & Agrawal 2002). Karban and Agrawal suggest that offensive behavior includes choices for feeding and oviposition, enzymes that make it possible to digest or assimilate certain foods, sequestration of toxins, *etc.*, morphological adaptations, symbionts, induction of plant galls, and induced plant susceptibility. Isopods seem to have such offensive tactics that enable them to eat and assimilate bryophytes (see Chapter 10-3 in this volume). However, special enzymes, bacteria, or other mechanisms permitting insects to digest and assimilate bryophytes seemingly remain to be discovered.



Figure 58. *Mnium hornum*, a species that produces ferulic acid, a known antiherbivore compound. Photo by Tim Waters, through Creative Commons.



Figure 59. *Spodoptera exempta* larva, a species that avoids liverworts with oil bodies that store terpenoids and lipophilic aromatic compounds that have strong antifeedant properties. Photo from the University of Arkansas, through Creative Commons.



Figure 60. *Spodoptera exempta* adult, a species whose larvae avoid liverworts as food. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Both algae (Ceh *et al.* 2005) and tracheophytes have inducible antiherbivore compounds (*e.g.* Fowler & Lawton 1985; Kruidhof *et al.* 2012). The brown alga *Sargassum asperifolium* (Figure 61) and red alga *Hypnea pannosa*

(Figure 62-Figure 63) both exhibited lower grazing levels on individuals that had been grazed previously than on those with no previous grazing, suggesting that these algae produced antiherbivore compounds in response to grazing.



Figure 61. *Sargassum* sp., a brown alga that seems to have inducible antiherbivore compounds. Photo through Creative Commons.



Figure 62. *Hypnea pannosa*, a red alga that seems to have inducible antiherbivore compounds. Photo by Ria Tan, through Creative Commons.

No one has attempted to show whether these secondary compounds are ever induced in bryophytes. Karban and coworkers considered the advantages of inducible antiherbivore compounds (Karban & Baldwin 1997; Karban *et al.* 1997). Whereas most ecologists had argued that the inducible compounds saved costs, empirical data failed to support this argument (Karban *et al.* 1997). Karban and coworkers suggested that instead it was the variability that was important – "maximal levels of defense are constrained, variability will increase the effectiveness of a given level of investment in defense."

Gerson (1969, 1982) reports that some members of **Collembola**, **Diptera**, **Hemiptera**, **Hymenoptera**, **Orthoptera**, **Cryptostigmata**, and **Prostigmata** (Acarina) feed on mosses. But it is likely that the number is far greater than we suppose. Certainly **Lepidoptera** must be added to the list (Chapman 1894; Tillyard 1926). We have found that Isopods can do considerable damage to mosses, but their feeding occurs at night. A number of insects are night active, hence avoiding visibility to birds that feed on them.



Figure 63. *Hypnea pannosa*, a red alga that seems to have inducible antiherbivore compounds. Photo by Cal Photos, through Creative Commons.

Antiherbivore compounds in liverworts have been greatly elaborated by Asakawa (1981, 1982, 1984, 1990). Despite the widespread presence of these compounds, some liverworts are still eaten. For example, Robin Stevenson sent me an image of *Marchantia polymorpha* (Figure 64) with evidence of herbivory on the gemmae cups.



Figure 64. *Marchantia polymorpha* showing gemmae cups where the gemmae have apparently been eaten; the bottom of the cup is eaten through to the soil. Photo courtesy of Robin Stevenson.

A common pattern of bryophyte consumption is for the insect to strip the leaf lamina cells while avoiding the costa and border cells (Wyatt & Stoneburner 1989; Davidson *et al.* 1990). Other insects avoid the cell wall problem by using a straw-like stylet, such as those of aphids and mites, sucking out the contents without the necessity of digesting cell walls.

Loren Russell (pers. comm.) observed the locations and food habits of insects in western Oregon and Washington, USA, and researched their food habits through

published feeding observations and gut analyses. He found at least 26 species of **bryophagous** insects (those eating bryophytes). Among these, only three species were reported as associated with liverworts. To the list of liverwort consumers, he added **Tipulidae** larvae and ***Lioligus striolatus*** (a member of the bryophyte-dwelling beetle family **Byrrhidae**; Figure 65).



Figure 65. *Lioligus nitidus* adult, a bryophyte dweller and liverwort consumer. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Bryophyte herbivory may have been more extensive among early bryological evolution. As insects and other herbivores became more abundant and diverse, those that survived were more likely to be those protected by antiherbivore compounds, tough tissues, lack of nutrients, or inconspicuous locations. To shed light on early herbivory, Labandeira *et al.* (2014) examined fossil evidence from the late Middle Devonian liverwort ***Metzgeriothallus sharonae*** (Figure 66) from eastern New York state shale fragments. Using microscopic analysis, they detected an "extensive repertoire" of arthropod herbivory. This represented three functional feeding groups and nine types of damage by arthropods. They considered the oil bodies were similar to those of modern liverworts and probably provided chemical defense against the arthropod herbivory on this species. The evidence suggested that these early herbivores were significantly smaller than those of the later Palaeozoic and that they had an important role in early terrestrial ecosystems.

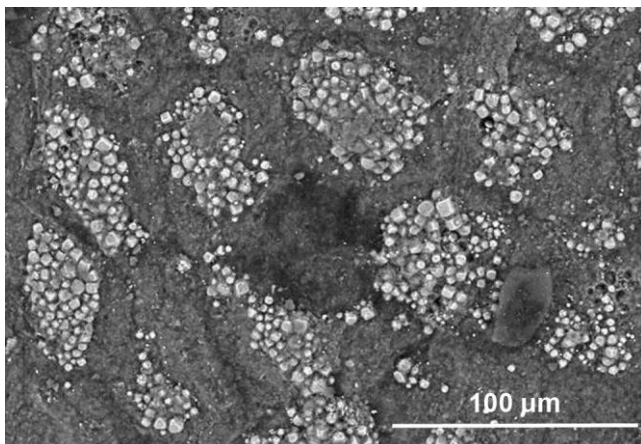


Figure 66. *Metzgeriothallus sharonae* fossil showing cells. This fossil species is known to have provided food for at least three feeding groups. Photo by Susan Tremblay, with permission.

It is now clear that bryophytes are eaten, but that this is not widespread among the members of the animal kingdom. Claudio Delgadillo (pers. comm. 30 March 2016) was surprised when a student discovered bryophyte tissue in a sea urchin gut. One had a liverwort and one had a moss! And most of us have probably seen capsules with holes in their sides, indicating something had been nibbling. Sometimes only the stems remain, and in the image of ***Orthotrichum affine*** (Figure 67) sent to me by Robin Stevenson. It remains a challenge to match the identity of the bryophages with their food organisms.



Figure 67. *Orthotrichum affine* eaten by some sort of terrestrial invertebrate, most likely an insect or isopod. Photo courtesy of C. Robin Stevenson.

Bryophytes as Pesticides

Since many bryophytes have been refused in feeding trials, and many bryologists consider their secondary compounds with antifeedant properties to be important in deterring potential feeders, it should be no surprise that some enterprising bryologists and their colleagues have attempted to use these compounds in pesticides (Singh *et al.* 2015). Singh and coworkers found the enzyme thiaminase from ferns and mosses exhibited insect resistance activity. They were able to patent crude protein extracts of several ferns and mosses that caused 70-100% mortality and reduced growth in caterpillars of the Noctuidae *Spodoptera frugiperda* (fall army worm) and *Helicoverpa zea* (corn earworm), neither of which is known to eat mosses. Such pesticides may be a boon to agriculture by decreasing destruction. Since they are natural compounds, they are probably already avoided by birds. Nevertheless, their safety as a pesticide must be evaluated, particularly in regard to pollinators.

Sampling Methods

Field Collection

A common method of field collection for soil and bryophyte invertebrates is the use of **pitfall traps**. Drozd *et al.* (2009) were surprised to find that the total abundance for arthropods was higher in the litter samples than from the moss cushions. As they point out, conclusions of this sort should be evaluated carefully based on the methods. Bryophyte dwellers may seek refuge there and may be relatively immobile. They also may be species that tend to desiccate easily, hence their retreat into the more moist

bryophyte cushions. Their nighttime movements may be vertical rather than horizontal, hence never going near the pitfall traps. In the daytime they retreat into the protective cushion of bryophytes where it is harder for predators to see them and they are more protected from desiccation. This same protection in a dense moss cushion prevents rapid movement. The arthropod surface activity may be mostly that of predators in search of dinner. Those within the bryophyte clump may be species that feed on bryophytes or the collected detritus and microorganisms, hence having no need to move from the clump at all.

If these problems concern you, then the best method of collection is to sample bryophyte clumps. Andrew and Rodgerson (1999) recommend 2.5 x 2.5 cm clumps. Unfortunately, this method is destructive and should never be done with rare bryophyte species or fragile ecosystems.

One method I have not tried is to use a **sugar flotation** technique with live bryophyte cushions (see Pask & Costa 1971 below). After floating off the insects, clean the cushion well in rainwater or stream water and return it to its original position. If the clump is kept intact, it may survive. But I don't know if it will survive the sugar solution, and the effectiveness of extracting the insects without disturbing the integrity of the moss clump needs to be tested.

Extraction

Heat gradients are common methods for extracting invertebrates from soil and bryophytes. Tuf and Tvardik (2005) used a Tullgren funnel with a heat source (lamp) above the mosses in the funnel. Invertebrates are then captured in a jar of alcohol or other preservative below the funnel. This is biased against slow-moving organisms that desiccate easily.

In mosses as dense as some *Sphagnum* (Figure 45) mats, behavioral extraction (also a heat technique) may be beneficial (Fairchild *et al.* 1987). But Fairchild and coworkers added another gradient – dissolved oxygen. Both the heat and oxygen form a vertical gradient in a column of water with the *Sphagnum* immersed at the top. Mean sorting time was reduced from >16 hr to <2 hr per sample. This method was effective for insects and other invertebrates, but was intended for aquatic invertebrates. Its usefulness for emergent bog species remains to be tested. The method takes advantage of the need for oxygen and the avoidance of warmer temperatures among the aquatic organisms.

Temperature gradients have their problems for extracting insects. Some are slow-moving or might burrow deeper into the bryophytes to avoid the heat. Others may become desiccated by the heat and no longer be able to move.

Preserved samples permit the researchers to do the extractions at their convenience. This is sometimes a necessity for extended field work. Pask and Costa (1971) recommend preserving the samples in 10% formalin, but this is highly carcinogenic and should be avoided. Using 70% ethanol (or 95% for aquatic samples) works well. A few drops of glycerine can protect the organisms if too much alcohol evaporates (pers. experience). Pask and Costa compared preserved vs unpreserved samples using extraction with a sucrose solution of 1.12 sp. gr. They found a mean recovery of 90.8% for persevered samples

compared to 83% from unpreserved samples. Furthermore, the unpreserved samples yielded much greater variability in efficiency of recovery than did the preserved samples. And some groups seemed to be easier to recover in the preserved samples (**Zygoptera**, **Hemiptera**, **Trichoptera**, and **Chironomidae**). No group was under-represented in the preserved samples.

Andrew and Rodgerson (1999) tested two common insect extraction methods: **Tullgren funnels** (e.g. Tuf & Tvardik 2005) and **sugar flotation** (Pask & Costa 1971), and compared these to a new technique using kerosene phase separation. They found that the kerosene extraction recovered significantly more invertebrate individuals than did the sugar extraction and represented similar numbers of orders.

Kerosene phase separation (Andrew & Rodgerson 1999; Andrew *et al.* 2003): Upon collection in the field (2.5 x 2.5 cm samples), the bryophyte-invertebrate samples should be placed in 95% ethanol for 2 weeks before extraction. For densely tufted bryophytes, pre-washing samples in 95% ethanol may be useful because there is more interference by the bryophytes. In the **kerosene phase separation**, the kerosene attaches to the insect cuticle to facilitate flotation:

1. First put the bryophyte-insect mix into 2 large test tubes (2 cm wide X 17 cm long).
2. Then fill the test tube 3/4 full of sample with ethanol and top it off with 1 cm of kerosene.
3. Shake this mix vigorously to fully mix the solutions.
4. After 10-15 minutes of settling, roll each tube to release trapped bubbles from the sides and bottom.
5. When the tubes are then kept upright, a distinct interface will form between the ethanol and kerosene; insects will collect onto the interface layer. Pipette off the kerosene to within 1 mm of the interface layer.
6. Then pipette off remaining kerosene plus interface.
7. Wash the sides of the tube with 95% ethanol to dislodge the kerosene stuck to the sides and repipette and collect.
8. Repeat the whole process to get remaining invertebrates (increases total number by about 16%).
9. Push the invertebrates in the kerosene layer into the ethanol, using a fine brush, to dislodge the kerosene from the cuticle.
10. Examine the interface mix in a Petri dish with a binocular microscope under a fume hood for your own safety. Collect and sort the invertebrates.

Habitats

Many practices of humans threaten the bryophytes on the planet Earth. Perhaps the greatest of these in purely terrestrial ecosystems is the management practices of forests. Management for timber threatens the forest floor bryophytes, not to mention those that live on the trees themselves. A major problem is the imposed dispersal limitation to recolonize cut forests, and the larger the cut and isolation, the greater the problem for recolonization (Fenton & Frego 2005). Islands of trees provide refugia where at least some bryophytes may survive long enough to recolonize. Temperature, total daily photosynthetically active radiation, and vapor pressure deficit were significantly different between areas with remnant canopy and those without. If bryophytes are unable to colonize or

survive, the insects that depend on them for moisture, food, and refuge from predators are vulnerable and their mortality increases, often to their local extinction.

Bogs and Wetlands

Data would suggest that bogs and wetlands have the highest populations of insects living among bryophytes. This is at least in part due to the greater biomass of mosses, a ratio of 1.6:1 in a Stordalen mire when compared to tracheophytes (Rosswall *et al.* 1975). Since they are also the habitats with the greatest cover of bryophytes, this high population of insects should probably be expected. Nevertheless, there seems to be little evidence that the bryophytes are used as food. Of nine species of *Nematocera* (midges) larvae, Smirnov (1961) found that only *Psectrocladius* from the *psilopterus* group (Figure 68-Figure 69) had eaten *Sphagnum*, and then it constituted only 16% of the food volume. Rather, algae and detritus among the bryophytes formed the main food for the herbivorous members of the group. The *Collembola* (springtails) eat the fungi that grow on decomposing *Sphagnum*. Thus, the *Sphagnum* provides the substrate needed to make the food available.



Figure 68. *Psectrocladius* sp. larva, a genus that includes one species that eats *Sphagnum*. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 69. *Psectrocladius psilopterus* adult, species group where some larvae eat *Sphagnum*. Photo by NTNU Museum of Natural History and Archaeology, through Creative Commons.

Insects in boreal peat bogs may be more distinctive. Spitzer and Danks (2006) found that these bogs have not only the generalists that seem to be common in many bogs, but also distinct **tyrphobionts** (species restricted to bogs) and **tyrphophiles** (species frequenting bogs but not restricted to them). One reason for the great diversity in some bogs is the topographic diversity of bogs, including hummocks that can become dry and hollows that are underwater, with the opportunity to migrate short distances vertically to find suitable moisture levels. Especially in boreal regions, many bogs may be hundreds and some thousands of years old, preserving relict communities that are well established. The isolation of bogs from each other has permitted them to develop unique insect communities.

Brink and Wingstrand (1949) found that the four species considered typical for bogs (Krogerus 1939, 1947) were also present in the Virihaure area of Swedish Lapland. These were the beetles (*Coleoptera*) *Agonum consimile* (*Carabidae*) and *Elaphrus lapponicus* (*Carabidae*) and the flies (*Diptera*) *Dolichopus fraterculus* (*Dolichopodidae*) and *Delia lineariventris* (*Anthomyiidae*). They also considered *Staphylinidae* beetles *Anthobium lapponicum*, *Stenus hyperboreus*, *S. umbratilis*, the *Linyphiidae* spiders *Erigone capra* and *Bathypantes setiger*. On the other hand, Agrell (1941) was unable to find any *Collembola* that were characteristic bog species.

Forests

Biomass production of bryophytes in forests can be high. In oak woodlands, Rieley *et al.* (1979) reported that bryophytes contributed 90% of the ground vegetation green biomass compared with only 60% of the annual production, providing a standing crop (green + brown) of 200-640 g m⁻² in pine forests and mires.

Garry Oak trees sport a variety of bryophytes, providing habitat for various invertebrates (pers. comm. Wynne Miles 12 January 2008). Miles found tufts of *Orthotrichum* (Figure 70) that were missing their sporophytes and only the broken setae remained. In another case, a collection of epiphytes, including *Tortula* (Figure 71), was grazed while in its collecting bag.

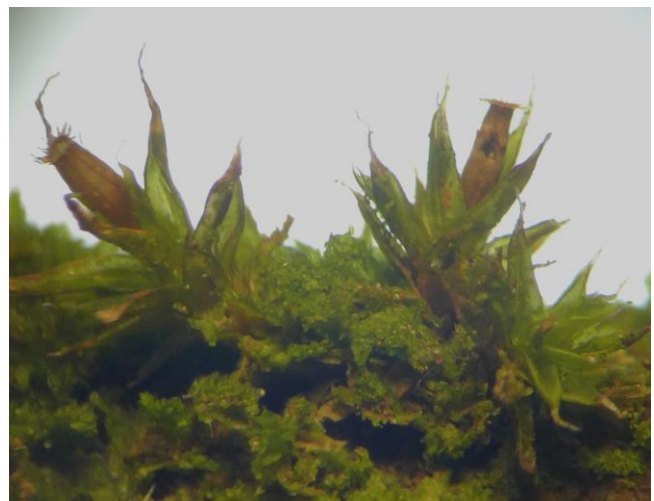


Figure 70. *Orthotrichum diaphanum* with a chewed capsule (on right) similar to that observed by Wynne Miles. Photo courtesy of Robin Stevenson.



Figure 71. Larva (**Lepidoptera**) on *Tortula* sp. This inadvertently collected larva grazed a collection of epiphytic mosses that had been growing on a large Garry Oak. Photo courtesy of Wynne Miles.



Figure 72. *Sphagnum teres*, a forest moss that houses a moderate number of arthropods. Photo by A. Neumann <www.biopix.org>, with online permission.

Forest ecosystems offer a diversity of habitats to insects. Because of their ability to fly as adults, the adult habitat can differ significantly from that of the larvae. The habitats of eggs and pupae – immobile stages – are typically the same as those of the larvae. But once the adult emerges, it is able to move from the food habitat of the larva to the feeding habitat of the adult, or in some cases, the adult does not feed. For many of the adults mating is the first and only priority.

In boreal forests, the bryophytes can often form 100% cover (Oechel & Van Cleve 1986). Although they are a minor part of the biomass, they perform a major portion of the primary productivity and ground cover. Hence, they also provide a major function in determining the invertebrate communities.

Drozd *et al.* (2009) used pitfall traps in a submountain and mountain forest ecosystem of the Czech Republic amid *Polytrichum commune* (Figure 4), *Polytrichastrum formosum* (Figure 3), *Sphagnum teres* (Figure 72), *Sphagnum girgensohnii* (Figure 73), *Sphagnum fallax* (Figure 74), *Bazzania trilobata* (Figure 75), *Pleurozium schreberi* (Figure 76), *Eurhynchium angustirete* (Figure 77), and *Oligotrichum hercynicum* (Figure 78). The traps followed a moisture gradient in moss cushions and in litter with no moss (controls). Drozd and coworkers suggested that the relationship with the mosses seemed to have broader implications than just that of a substrate, *i.e.*, the data indicate interaction between moss presence and other microhabitat features. The great number of insects in these forest floor habitats was indicated by the 55,000 specimens collected (66 traps, 5 locations), averaging 850 individuals per trap. Drozd and coworkers found that moss species, as well as moss presence, was important in determining both total abundance and taxon diversity (Figure 79). But moisture was important as well, perhaps contributing to moss species preference. Nevertheless, trapped arthropod abundance was greater in the litter samples.



Figure 73. *Sphagnum girgensohnii*, a forest moss that houses large numbers of arthropods, including insects. Photo by Mark Melton (Noah Project), with permission.



Figure 74. *Sphagnum fallax*, a forest moss that houses a small number of arthropods. Photo by Michael Lüth, with permission.



Figure 75. *Bazzania trilobata*, a forest liverwort that houses a moderate number of arthropods with few being insects. Photo by Bernd Haynold, through Creative Commons.



Figure 77. *Eurhynchium angustirete*, a forest moss species that houses insects. Photo by Marko Vainu, through Creative Commons.



Figure 76. *Pleurozium schreberi*, a forest moss species with a moderate number of insects. Photo by Sture Hermansson, with online permission.



Figure 78. *Oligotrichum hercynicum*, a forest moss species that houses insects. Photo by Hermann Schachner, through Creative Commons.

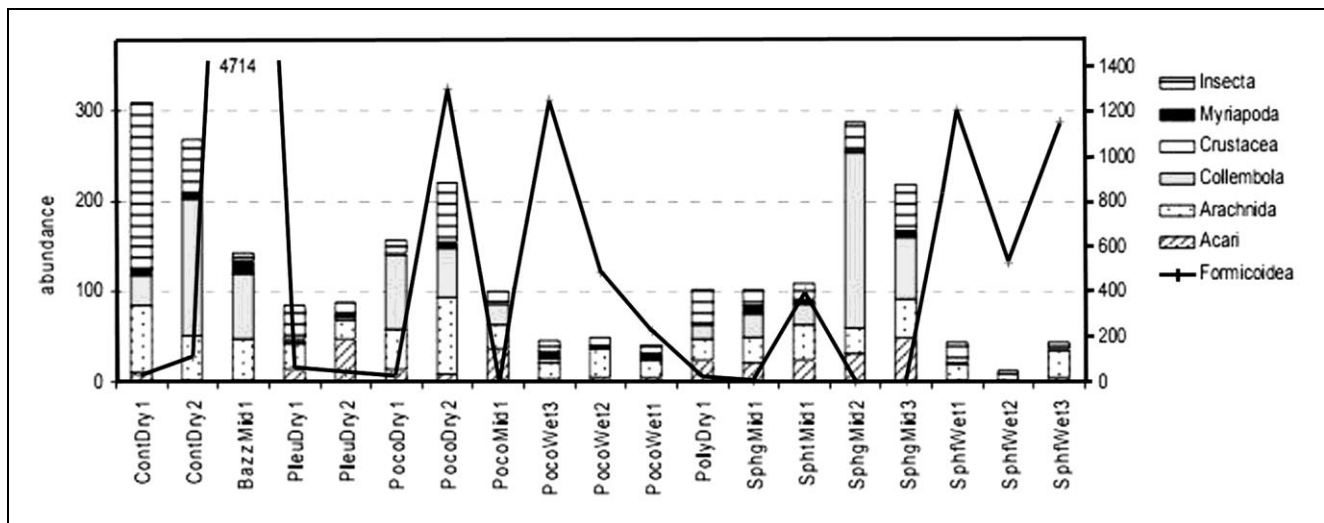


Figure 79. Arthropods from mosses in the Podolánky area of the Czech Republic. Poco = *Polytrichum commune*, Poly = *Polytrichastrum formosum*, Sphf = *Sphagnum teres*, Sphg = *Sphagnum girgensohnii*, Sphf = *Sphagnum fallax*, Bazz = *Bazzania trilobata*, Pleu = *Pleurozium schreberi*, Eurh = *Eurhynchium angustirete*, Olig = *Oligotrichum hercynicum*, Spha = *Sphagnum* spp., Cont = litter; moisture Wet = high, Mid = middle, Dry = low. Modified from Drozd *et al.* 2009.

As Drozd and coworkers (2009) pointed out, bryophages and detritivorous arthropods "have no reason to move about," potentially causing a low capture rate in traps that require movement. But these researchers also suggested that bryophytes may serve only as shelter and a temporary place to prevent desiccation, referring to the oft held view that the bryophytes are low in nutrients. This latter assumption, however, has been contested, as you will see earlier in this chapter.

Few studies have attempted to find the uses made by the bryophyte inhabitants (Drozd *et al.* 2009). Rather, most have simply enumerated species, perhaps correlating them with other physical factors such as temperature and moisture.

One of the few studies that elaborates on the relationship between bryophyte species and the invertebrate inhabitants is that of Božanić *et al.* (2013). In this case, *Brachythecium curtum* on a decaying tree housed the greatest number of species. The layers of the forest were important, with type of substrate and height above ground proving to be the most important factors to determine the invertebrate distribution.



Figure 80. *Brachythecium curtum*, a species with a rich fauna of arthropods. Photo by Janice Glime.

Montane Tropical Rainforests

In the Atlantic Forest of Brazil, Maciel-Silva and dos Santos (2011) found a number of insects associated with the mosses *Hypopterygium tamarisci* (Figure 81) and *Lopidium concinnum* (Figure 82). These include **Lepidoptera** larvae, leafhoppers, aphids, and **Psocoptera**, as well as isopods, snails, mites, and spiders.



Figure 81. *Hypopterygium tamarisci*, home to several orders of insects. Photo by Peter Woodward, through Creative Commons.



Figure 82. *Lopidium concinnum*, a habitat for several orders of insects. Photo by Juan Larrain, through Creative Commons.

Epiphytes

A number of species of arthropods are associated with the epiphytes, including several groups of insects. Miller *et al.* (2008) compared the epiphyte arthropod fauna at three heights on red maple (*Acer rubrum*; Figure 83) trees in the Acadian forest of Maine, USA. They found that there was a close association between springtails and spiders and suggested that the spiders were there because of the abundance of springtail prey. When the bryophytes diminished following gap harvesting, the spiders and springtails did as well. One surprise was the abundance of **Diptera** associated with the epiphytes. Fifteen families of these flies were represented. Overall, the numbers of morphospecies was positively correlated with bryophyte abundance except for the springtail family **Isotomidae**. Abundance of the other springtail morphospecies were correlated with dense bryophyte cover at the bases of trees.

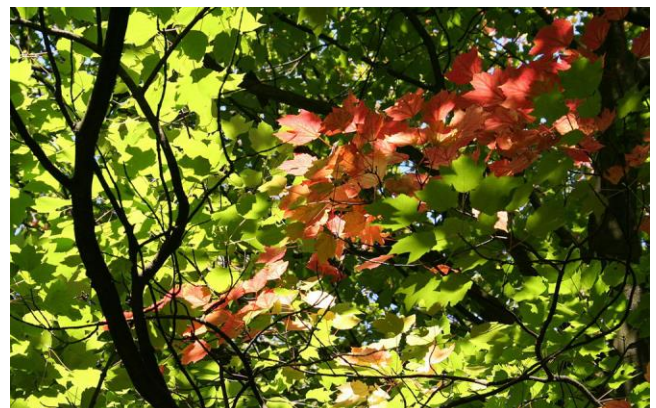


Figure 83. *Acer rubrum*, a species that supports arthropods living in epiphytic bryophytes. Photo by Jean-Pol Grandmont, through Creative Commons.

In the Pacific Northwest of North America, the epiphytic bryophyte mats in the subcanopy likewise house numerous insects. In collections of over 143,000 individuals, Peck and Moldenke (2011) recovered 205 morphospecies from 337 moss mats (less than 25 kg of mosses, fresh weight). These mosses were collected to determine the impact of moss harvesting on the insect community, but they also provide us with information on community structure. The faunal morphospecies composition between moss mats from the two shrubs, vine maple (*Acer circinatum*; Figure 84) and huckleberry (*Vaccinium parvifolium*; Figure 85) did not differ. Likewise, the fauna of the vine maple did not differ between the bases and branch tips of these shrubs, differing from their results in the Willamette National Forest (Peck & Moldenke 1999). Instead, the invertebrate fauna composition correlated with elevation, stand age, and vertical distance to water.



Figure 84. *Acer circinatum*, a shrub that supports growths of mosses that are often commercially harvested, with their accompanying invertebrate fauna. Photo by El Grafo, through Creative Commons.



Figure 85. *Vaccinium parvifolium*, a species with moss mats that hold arthropods. Photo by Walter Siegmund, through Creative Commons.

In the tropics, canopy bryophytes may be especially important for some of the invertebrates. Pócs (1982) estimated an excess of 1000 g m⁻² of bryophytes in the elfin forests. Trees in Costa Rican montane forests build canopy soils (including bryophytes) that house mites, amphipods,

isopods, beetles, springtails, ants, and insect larvae as the dominant invertebrate groups (Nadkarni & Longino 1990). The ground fauna had a mean density of 2.6 times that of the canopy. Only ants did not fit this pattern. However, it is difficult to assess these tropical mats because the mosses are typically only a minor component. Instead, the mats are primarily leafy liverworts and filmy ferns (Yanoviak *et al.* 2007). Yanoviak and coworkers found that these insect assemblages resembled the fauna of the soil mosses and accompanying humus layer. These are dominated by mites, springtails, ants, and minute beetles (Yanoviak *et al.* 2003, 2004). Unfortunately, the fauna of mosses in the canopy may be under-sampled because the fogging method used in many studies of canopy invertebrates is ineffective for sampling the tiny insects that inhabit the canopy bryophytes (Yanoviak *et al.* 2003).

Even within a mat of epiphytic bryophytes and other plants, vertical differences exist (Yanoviak *et al.* 2004). In a Costa Rican lower montane forest, the green portion of the mat housed twice as many individuals and species per gram dry mass compared to the brown portion. Morphospecies composition was similar, but some taxa differed significantly in relative abundance. Predators were randomly distributed in the larger patch sizes (up to 50 cm²). They found that interspecific interactions were more important than the environmental variables in determining the distribution of the mat fauna in small patch size (20 cm²).

Cryptogamic Crusts

The cryptogamic crusts are those habitats in arid ecosystems that are comprised of algae, bacteria, fungi, lichens, and bryophytes. These crusts are of major importance in these ecosystems, covering as much as 70% of the soil (Brantley & Shepherd 2004).

The arthropod fauna make use of the crusts for retreats and homes. In piñon-juniper woodland in central New Mexico, the crusts differ little in major groups from bryophyte habitats in other ecosystems, with tardigrades, nematodes, springtails, small insects, mites, and spiders predominating (Brantley & Shepherd 2004). Of the 38 taxa identified in the study, 27 occurred on mixed lichen and moss patches and 29 on moss patches. Only 21 were found on pure lichen patches. Of the three types of crusts, 15 arthropod taxa occurred on all three. Not only did the mosses have the highest number of arthropod species, but they also had the greatest abundance of arthropods. In this very dry climate, the greatest arthropod richness and abundance occurred in winter.

Altitude

Altitudinal gradients are complicated. Although the temperature tends to decrease and winds increase, moisture may be greater or less, and microhabitats abound. Vegetation changes and can increase or decrease shade. UV light may come into play.

Differences between elevations may be more due to microclimate differences than to those differences caused by elevations (Andrew *et al.* 2003). For example, Andrew and coworkers found that whereas altitude had a significant effect on diversity of insects in Tasmania and New Zealand, there was no general trend present along the altitudinal gradient. Mt. Field in Tasmania had the highest invertebrate and bryophyte diversity at 750 m. But Mt.

Rufus had low bryophyte and insect diversity throughout the altitudinal gradient. In Tasmania Mt. Otira had the highest diversity of both invertebrates and bryophytes at low altitudes, whereas Mt. Kaikoura had the highest invertebrate and lowest bryophyte diversity at the highest altitude. Clearly different factors are important for the bryophytes compared to those important for the invertebrates. Andrew and coworkers stressed the importance of scale and the need to sample both broad scale and microscale community patterns.

Tundra

Bryophytes are important ground cover in the tundra. In Spitsbergen, Bengtson *et al.* (1974) found a total arthropod abundance of 268,000 individuals m⁻² on wet moss tundra, compared to 42-63,000 on lichen tundra and 518,000 on grassland. The mites and springtails comprised 96-99% of the arthropod fauna, with small numbers of spiders, flies, and **Hymenoptera**. These major groups were similar in abundance to those of the high alpine in southern Norway.

Boreus in Norway takes advantage of mosses to provide protective space. This is a safe space in which they lay their eggs (Håvar 2001). And it appears that it might be a site of copulation, an event rarely observed on the snow. The chambered air spaces most likely also provide space for this winter-active scorpionfly. Adults of *Boreus elegans* (Figure 86) and *B. californicus* (Figure 87-Figure 88) feed on *Racomitrium heterostichum* (Figure 89-Figure 90); larvae and pupae of *B. elegans* can be found under *Brachythecium* (Figure 91) and other mosses (Russell 1979).

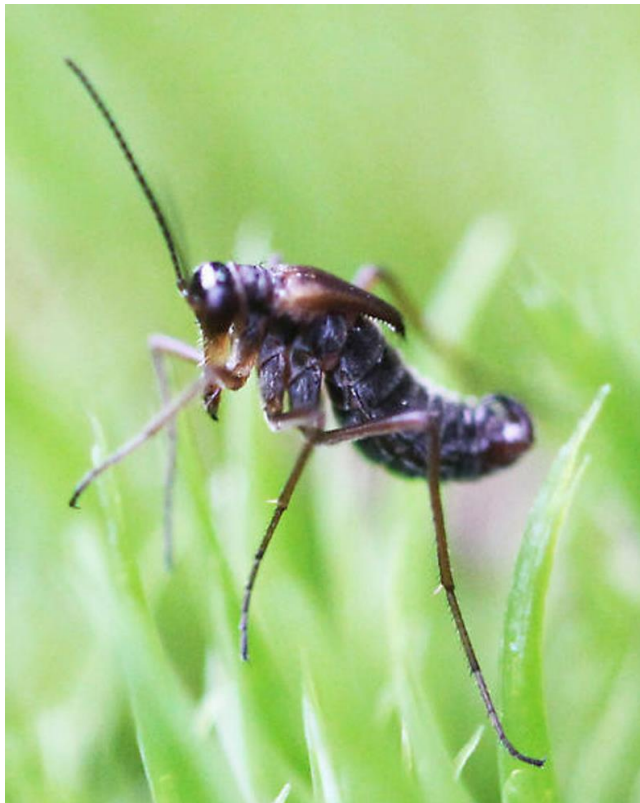


Figure 86. *Boreus elegans* adult, a winter-active scorpionfly that lays eggs among mosses. Photo by Megan Asche, with permission.



Figure 87. *Boreus californicus* adult female, a species that feeds on *Racomitrium heterostichum*. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

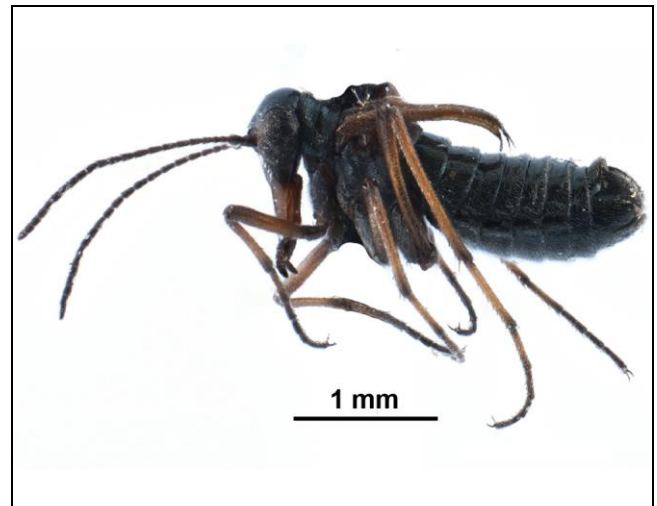


Figure 88. *Boreus californicus* adult male, a species that feeds on *Racomitrium heterostichum*. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

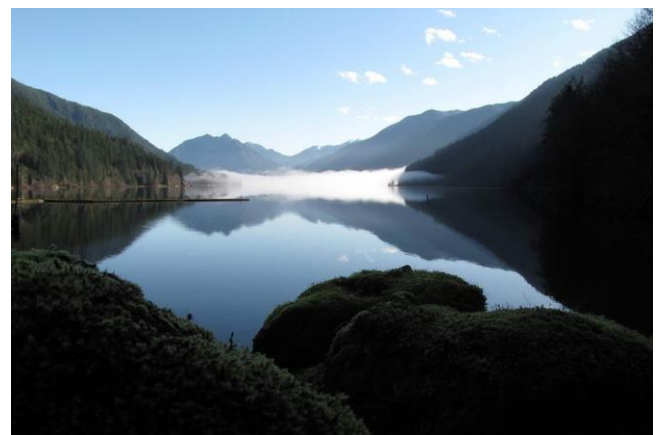


Figure 89. *Racomitrium heterostichum* habitat and home for *Boreus californicus* and *B. elegans*. Photo by Andrew Spink, with permission.



Figure 90. *Racomitrium heterostichum*, food for *Boreus californicus* and *B. elegans*. Photo by J. C. Schou <www.biopix.com>, with permission.



Figure 91. *Brachythecium rutabulum*, home for larvae and pupae of *Boreus elegans*, with capsules. Photo by Tim Waters, through Creative Commons.

The family **Apteropanorpidae** has a single genus, *Apteropanorpa* (Figure 92), with only four species (Wikipedia 2011). These are the Tasmanian snow scorpionflies, and they live among mosses in Tasmania and southern Australia. The adults are predators, but the larvae live among the mosses.



Figure 92. *Apteropanorpa tasmanica*, a moss dweller that is often infested with one or two species of parasitic mites. Photo by Simon Grove ©, Tasmanian Museum and Art Gallery, with permission.

The best-known species, *Apteropanorpa tasmanica* (Figure 92), is known to carry two species of parasitic mites (Seeman & Palmer, 2011). These are *Leptus agrotis* (Erythraeidae) and *Willungella rufusanus* (Microtrombidiidae).

Antarctic

In the Antarctic, bryophytes form the dominant vegetation and house the most arthropods (mites, springtails, insects) (Gerson 1969). Gerson reported that the *Polytrichum-Dicranum* (Figure 93) mats housed more arthropods than did *Pohlia* (Figure 94-Figure 95). The former was less wet and cold in the summer and its open texture made it easier for movement, especially of larger arthropods.



Figure 93. *Polytrichum juniperinum* in *Dicranum scoparium* mat, a species combination that is home for many arthropods. Photo by Kirill Ignatyev, through Creative Commons.



Figure 94. *Pohlia nutans* with capsules, a common sight in the Arctic and Antarctic. *Pohlia* species house arthropods there. Photo by Michael Lüth, with permission.



Figure 95. *Pohlia nutans* with capsules, a genus that is home to arthropods. Photo by Michael Lüth, with permission.

The Antarctic is dominated by small organisms. In that regard, bryophytes are an important habitat for invertebrates. Davis (1981) compared the invertebrates on two kinds of moss communities on Signy Island: a moss turf dominated by *Polytrichum alpestre* (= *P. juniperinum*; Figure 96) and *Chorisodontium aciphyllum* (Figure 97- Figure 98) and a moss carpet composed of *Warnstorfia sarmentosa* (Figure 99), *Sanionia uncinata* (Figure 100), and *Calliergidium austrostramineum* (Figure 101), with the liverwort *Cephaloziella varians* (Figure 102). The trophic structure, organic matter transfer, and production of primary producers (which included lichens and algae in addition to the bryophytes) were similar in these two community types, but the standing crops of **Collembola** (springtails; Figure 33) and **Acari** (mites) differed. These differences may have related to the differences observed in turnover of mosses and accumulation of dead organic matter.



Figure 96. *Polytrichum juniperinum*, a common moss on Signy Island and home to **Protozoa**, **Rotifera**, **Tardigrada**, **Nematoda**, **Acari**, and **Collembola**. Photo by Juni, through Creative Commons.



Figure 97. *Chorisodontium aciphyllum* in Antarctica, home to a variety of invertebrates. Photo from Polar Institute, through Creative Commons.

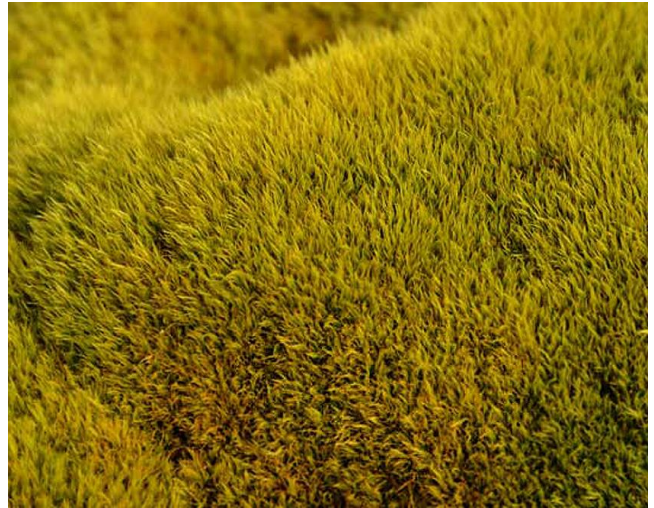


Figure 98. *Chorisodontium aciphyllum* in the Antarctic, a primary producer and home for the same groups of organisms as *Polytrichum juniperinum*, but with different proportions. Photo by Zicheng Yu, through Public Domain.



Figure 99. *Warnstorfia sarmentosa*, home for a variety of invertebrates, including **Collembola**, on Signy Island. Hermann Schachner, through Creative Commons.



Figure 100. *Sanionia uncinata*, home for invertebrates in the Antarctic. Photo by Hermann Schachner, through Creative Commons.



Figure 101. *Calliergidium austro-stramineum*, home for invertebrates in the Antarctic. Photo by Bill Malcolm, with permission.



Figure 102. *Cephaloziella varians* with *Polytrichum* sp., home for invertebrates in the Antarctic. Photo by Christian Peters, with permission.

The maritime Antarctic has a flora that is predominately bryophytic (Tilbrook 1967). The invertebrate fauna has few species with any great abundance. This area produced a number of indigenous insects: only seven species of *Collembola* (springtails) and one of *Diptera* (flies), but 20 species of mites. The dominant arthropod is *Cryptopygus antarcticus* (*Collembola*). The highest densities of insects are among the vegetation, but some occur in areas free of permanent

ice. Habitat specificity is uncommon. It is likely that the ability of bryophytes to absorb radiation and affect the microhabitat temperature, coupled with the insulation of snow, makes the bryophyte habitat a suitable habitat for the arthropods. Geothermal areas, as discussed below, further provide a bryophytic habitat that is suitable for arthropods.

Strong (1967) considered the Antarctic mosses to serve primarily as shelter and concluded that they do not provide a significant source of nourishment. Humidity seems to be the major controlling factor, with temperature playing a secondary role. Wind is an important feature that modifies temperature and humidity. The primary consumers include springtails and the midge *Belgica* (Figure 103). Adaptations to the climate seem to be primarily physiological rather than developmental or behavioral.



Figure 103. *Belgica antarctica*, a moss consumer, mating. Photo, through Creative Commons.

Usher and Booth (1984) cut five sets of 96 contiguous samples from moss turf on Signy Island in the maritime Antarctic. They found only 10 taxa of arthropods, comprised of mites and springtails. Of the six species with enough abundance to analyze, they found a vertical separation of the species, with three occurring near the surface, two in an intermediate position, and one deep in the mat, resulting in many negative correlations arthropod between species at any given depth. However, when the depths were combined, there were no negative correlations, and many positive correlations were present. Even within a species the vertical distribution differed with life cycle stage. Overall, two distinct communities were present – the green moss community (0-1.5 cm) and the dead moss community (below 3 cm). Nevertheless, the two communities were composed of the same six species, but the proportions differed.

Geothermal

Cold climates are harsh and many organisms do not have the life cycle and physiological adaptations needed to survive in them. However, one habitat provides the year-round warmth for survival of more temperate organisms that are able to arrive there. These are the geothermal areas that are in polar regions of both the Antarctic and Arctic landscapes.

Bryophytes serve as buffers in these habitats. Their own depth insulates the tips of the plants from the heat beneath, and the "steam" emanating from the vents keeps the habitat moist (Glime & Iwatsuki 1990). Lichens seem

unable to survive these hot but moist environments, but the bryophytes protect their own growing tips and survive at higher moist temperatures than those suitable for lichens.

Elmarsdottir *et al.* (2003) address the paucity of knowledge about the geothermal ecosystems. Most studies have been descriptive, with little attention to the interactions of this unique ecosystem. Soil temperatures dominate the limiting factors, with soil pH and carbon content also influencing species composition. Nevertheless, a number of bryophytes have been able to tolerate the heat or escape it by providing their own insulation through decaying lower parts. These bryophytes provide homes for invertebrates.

Historically, geothermal areas most likely served as refugia from glaciers, and once glaciers receded, these heated areas permitted recolonization of nearby non-geothermal regions. Fraser *et al.* (2014) tested this hypothesis, based on the expectation that the greatest diversity would occur closest to the geothermal areas. Using Antarctica as a test, they did indeed find the greatest diversity closest to the geothermal areas.

Convey and Lewis Smith (2006) reported that the bryophytes on South Sandwich Islands in the Antarctic had the greatest richness in geothermally influenced ground. In fact, only four of the mosses on the islands were never associated with geothermal areas; 35 moss species and 9 liverwort species were present in all. On the other hand, 8 liverwort and 50% of the mosses occurred only on heated or recently heated geothermal areas. *Campylopus introflexus* was the only bryophyte to tolerate the maximum temperatures (40–47°C) of the upper 0.5 cm of the bryophyte layer. The flora of the unheated ground is similar to that of the maritime Antarctic (Convey *et al.* 2000). The heated ground contains species common to both the maritime and sub-Antarctic areas, supporting the importance of the geothermal areas for successful colonization elsewhere.

Given the success of bryophytes in geothermal areas, it is easy to imagine that the ubiquitous insects would likewise be represented there, likewise taking advantage of the extra warmth. Even in Hawaii, geothermal areas permit ants to extend to higher elevations than would otherwise be possible (Wetterer 1998).

Boothroyd and Browne (2006) found that the invertebrate species occupying geothermal areas of New Zealand tended to be common species. Willoughby *et al.* (2015) found that the bryophytic fauna in the Waikato Region of New Zealand did not correlate with the soil temperature.

Some studies are focussing on the impact of human activity, especially for harvesting geothermal heat and power, on the flora and fauna (Miller *et al.* 1995). Human activity poses a threat to these fragile systems. Connectivity between suitable sites is important to maintain these communities and their fauna.

Pollution Effects

Bryophytes are well known for their ability to collect air pollutants, especially heavy metals. As a result, we might expect that the bryophagous insects would also have higher concentrations than those feeding on plants that are less efficient collectors (Steiner 1994).

We might also predict that these high concentrations could be lethal for some of the inhabitants. Varga (1992) tested *Plagiobryum zierii* (Figure 104) and *Saelania glaucescens* (Figure 105) from a polluted roadside in Hungary and found higher lead concentrations in them. Concomitantly, the invertebrate fauna, including insects, was lower than that found in mosses from an unpolluted control site. Furthermore, the invertebrates from the polluted mosses exhibited high concentrations of lead.



Figure 104. *Plagiobryum zierii* from Europe, a moss that accumulates lead that can then accumulate in bryophagous insects. Photo by Michael Lüth, with permission.



Figure 105. *Saelania glaucescens*, a moss that accumulates lead that can then accumulate in bryophagous insects. Photo by Michael Lüth, with permission.

Pollution can have positive or negative effects on insects. When mosses in an area polluted with heavy metals were analyzed, those from less polluted areas had more molybdenum, whereas those from the polluted areas had increased levels of cadmium and chromium (Soltes 1996). These increased Cd and Cr contents corresponded with the areas of spruce bark beetle outbreak.

Climate Change

Pollution with CO₂ is generally blamed for global climate changes. It not only means that some areas will be hotter, some will be colder, more severe storms will occur, water levels will rise, and seasons will have different periodicities, but nutrient levels will change as well.

Richardson *et al.* (2002) examined the impact of changes in nutrients and warming in a sub-Arctic heath on vegetation and insect herbivores. The bryophagous **Heteroptera** in fertilized plots was reduced to as little as 6% that of the unfertilized controls. **Homoptera** that fed on grasses became 400% more abundant. The changes in the insect community was driven primarily by the subordinate plant groups (grasses and mosses), emphasizing the importance of the mosses in this tundra habitat. Nutrients had a greater impact than the rise in temperature.

Summary

Bryophytes serve as habitat for numerous kinds of insects. They provide moisture (an important limiting factor for insects), food, shelter, refuge from predators, and a buffer against the climate. The insects that live there are limited in their adaptations, but some are wingless, have cryptic coloration, are able to eat bryophytes, and are small and flexible enough to maneuver among the bryophytes.

Those that live in northern regions often use mosses as a winter home. They may eat bryophytes to survive in winter and it is possible these bryophytes may help to adapt them to the winter cold, possibly through providing **arachidonic acids**.

Because bryophyte dwellers typically have limited mobility, their dispersal is limited. Fragmented landscapes and separated microhabitats often require corridors that connect the habitats with suitable microhabitats to permit recolonization of disturbed sites.

Although most of the bryophyte inhabitants seem to use the associated invertebrates, algae, bacteria, and fungi as food, some do eat the bryophytes and some are even liverwort specialists. Bryophytes often have secondary compounds that prevent herbivory and those insects that eat bryophytes do have preferences. Some bryophytes are so effective at deterring herbivores that they are being developed as pesticides.

Again because bryophytes have limited mobility, typical insect sampling methods are often inappropriate and biased. Using heat to cause the insects to fall into traps or using pitfall traps may miss whole taxonomic groups that fail to move away from the bryophytes. Hand sorting of bryophyte clumps is the only (nearly) unbiased method, but it is destructive and therefore limits the number of samples.

The most common bryophyte-dwelling arthropods worldwide are spiders, springtails, and mites. The typical orders of insects present include **Collembola**, **Odonata**, **Notoptera**, **Psocoptera**, **Hemiptera**, **Megaloptera**, **Neuroptera**, **Coleoptera**, **Hymenoptera**, **Trichoptera**, **Lepidoptera**, **Mecoptera**, and **Diptera**.

In bogs and wetlands, ants are common *Sphagnum* inhabitants making nests of the *Sphagnum*. **Lepidoptera** are common and depend on plants that depend on the environment created by the bryophytes. Several families of beetles, especially **Carabidae**, live among the bryophytes.

Forest bryophytes have fewer species and the bryophyte fauna there seems to be less well known. In the tropical rain forests, epiphytes provide important habitats, especially for ants and springtails. In cryptogamic crusts of the desert, bryophytes provide a refuge from the hot sun and a place where moist periods last longer, but the life cycle needs to be attuned to the short moist periods or the insects must be able to burrow deep into the soil.

At high altitudes, in the tundra, and in the Antarctic, the bryophytes are the most hospitable habitat for terrestrial insects, providing a buffer against the extreme temperatures, maintaining moisture, and harboring smaller food organisms. It is also likely that they protect against UV light. Geothermal areas in these cold regions provide a haven for species normally found in warmer habitats, and the bryophytes are usually the dominant vegetation.

Bryophytes are known accumulators of air pollutants, so insects that eat them or eat other invertebrates that eat them may be seriously affected by the accumulated heavy metals. A warming climate is likely to decrease the bryophytes in northern climates and thus affect the insect herbivores. Furthermore, increases in nutrients resulting from climate warming cause decreases in bryophagous **Heteroptera** and increases in **Homoptera** that feed on grasses.

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CHAPTER 12-2

TERRESTRIAL INSECTS:

HEMIMETABOLA – COLLEMBOLA

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CHAPTER 12-2

TERRESTRIAL INSECTS:

HEMIMETABOLA – COLLEMBOLA



Figure 1. *Hypogastrura* sp. on *Schistidium apocarpum*. Photo by Christophe Quintin, through Creative Commons.

Meet the Collembola

These tiny creatures, the springtails, are easily overlooked until they start popping about before your eyes. Previously considered to be insects, they are currently placed in the class **Entognatha**, where the name **Collembola** has been elevated from an order to a subclass. Among the bryophytes, they blend with the dark crevices between the leaves. Numerous studies attest to their frequency among bryophytes (e.g. Bonnet *et al.* 1975; Acon & Simon 1977; Skarzynski 1994). The bryological habitat is likely to yield some surprises, even new species (Acon & Simon 1977; Skarzynski 1994).

Their diversity includes the tiny non-jumping ones to the larger ones equipped with a **furcula** (Figure 2) that permits them to spring like those metal cricket toys some of us remember (Kinchin 1992). A **collophore** (Figure 3) holds the furcula in place and ready to spring. The collophore may be used in osmoregulation, water intake, and excretion (Wikipedia 2016). By comparative body size, these 15-cm jumps are equivalent to a human jumping over the Eiffel Tower (Shockley 2011). Like other insects,

they shed their outer covering (**exuvia**; Figure 4-Figure 5) in order to grow.

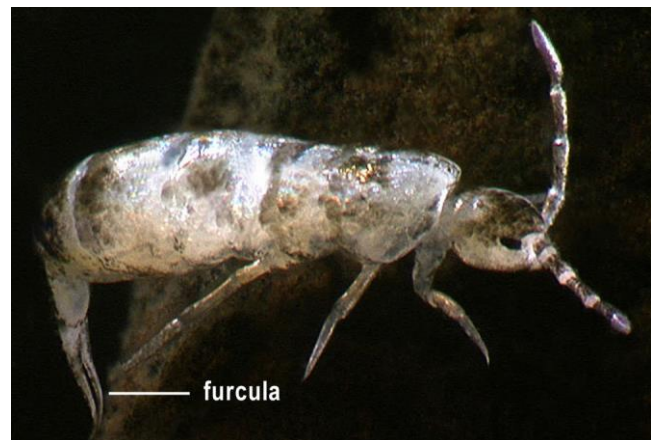


Figure 2. *Arthropleona oruarangi* showing **furcula**. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 3. *Isotoma* (springtail) showing **collophore** (arrow). Photo by U. Burkhardt, through Creative Commons.



Figure 4. *Kalaphorura burmeisteri* molting. Note the clean new covering exposed on the thorax as the old one splits to become the **exuvia**. Photo by Andy Murray, with permission.



Figure 5. *Dicyrtoma fusca* with **exuvia**. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

Swan (1992) suggests that "insects" such as the primitive **Collembola** may have invaded land even before the early bryophytic land plants. Mosses are often present as a photosynthetic band at the edge of **Aeolian** (wind erosion) zones, benefitting from nutrients delivered by the winds. But these windborne nutrients were available even before mosses arrived, with organic compounds collecting along the Aeolian zone. It is not hard to imagine, then, that when mosses appeared, **Collembola** colonized them.

Moisture Needs

It is easy to imagine that bryophytes can help to maintain moisture for **Collembola** in many habitats. But in many habitats both bryophytes and **Collembola** are susceptible to desiccation stress (Verhoef & Witteveen 1980). Some **Collembola** produce a special grooming fluid (Figure 6) that keeps their heads moist (Shockley 2011). They have two inflatable tubes (Figure 6) that help them to distribute the fluid. These tubes double as "arms" if the springtail lands on its back – the tubes are used to stick to the substrate and pull the springtail over to its proper position or to attach it to the substrate to prevent it from tumbling on an incline.



Figure 6. *Sminthurus* cf. *wahlgreni* with its inflatable **adhesion tube** attached to its abdomen. Note drops of grooming fluid on the head and abdomen. Photo by Jan van Duinen, with permission.

Reproduction

Mating is a bit unusual in the springtails. Rather than depositing sperm into the female, the male produces a small packet (**spermatophore**; Figure 7-Figure 8) that he attaches on a short stalk onto a substrate (Shockley 2011). The female must then take the spermatophore into her reproductive tract. The mating itself can take many forms in an attempt to insure that a female will attain the sperm. These include

1. random deposition of spermatophores across the landscape.
2. deposition of a spermatophore followed by the male using antennae to drag the female across it.
3. locating a female and depositing multiple spermatophores; male then tries to lure the female through this "garden" of spermatophores.
4. locating a female and surrounding her with spermatophores so she must contact one or more to escape.
5. holding a male-female courtship dance [e.g. *Deuterosminthurus pallipes* (Figure 9) – a species found among mosses in the floodplain meadow of the Kargy River in Russia (Bretfeld 2010)], doing a face-to-face push and retreat ritual to establish a rhythm. As the female tries to get away, the male continues to woo her. If the female accepts, the male deposits the spermatophore directly in front of her; she picks it up

and either deposits it in her reproductive tract or – eats it.



Figure 7. *Lepidocyrtus* sp. with a spermatophore at the lower far right. Photo by Andy Murray, with permission.



Figure 8. *Isotominae* spermatophore. Photo by Jan van Duinen, with permission.



Figure 9. *Deuterosminthurus pallipes* courting; the female is the larger one. Photo by Jan van Duinen, with permission.

Some species, e.g. *Folsomia candida* (Figure 10-Figure 11) (*Isotomidae*), are **parthenogenetic** (giving birth without fertilization). This is helpful in the disconnected bryophyte patches where contact is limited.



Figure 10. *Folsomia candida* with eggs. Photo by Steve Hopkin, with permission.



Figure 11. *Folsomia candida* with young. Photo by Steve Hopkin, with permission.

Christiansen *et al.* (1992) reported a generation time of about one month for most laboratory-reared **Collembola** species. But some species are **univoltine** (one generation per year) and others are **multivoltine** (more than one generation per year) (Hopkin 1997). Mitchell (1977) provided evidence that **Collembola** communities have seasonal fluctuations in composition and numbers.

Dispersal

Data for dispersal rates for **Collembola** dwelling among the bryophytes seem to be lacking. But those living in soil and those living within the bryophyte clumps may be similar. Ojala and Huhta (2001) determined the rate for soil **Collembola** to be 0.5-1 cm per week, compared to 1-2 cm per week for cryptostigmatic mites. This of course is likely to be different if they must migrate between patches where they can hop much longer distances than the

distances travelled within the confines of the moss mat itself.

For the moisture-requiring **Collembola**, winter is often the time for dispersal, a feat often accomplished across the snow (Figure 12) (Leinaas 1981a, b, c; Hågvar 1995; Zettel 1984, 1985; Zettel & Zettel 1994).



Figure 12. **Collembola** – snow flea on snow. Photo by Bob Armstrong, with permission.

It might be useful to consider the possibility of springtails being dispersed along with the bryophytes, a phenomenon already considered for tardigrades (Janiec 1996). Although this may be a rare occurrence for larger adults, might small species or the eggs get dispersed on bryophyte fragments in the winter when bits can travel long distances across the snow and even glaciers (Miller & Howe Ambrose 1976)?

Collembola appear early in succession of new moss colonies. The first organisms to appear are rotifers and protozoa (Mukerji *et al.* 2000). These are followed by nematodes, mites, and **Collembola** once the moss has formed a detrital layer. In high altitudes, the **Collembola** abound among colonizing mosses, which also serve as their food (Mani 1962).

On the other hand, Sinclair *et al.* (2003) found that **Collembola** not only graze on bryophytes, but that mosses may be essential to their temperature maintenance in the Antarctic. When the springtail *Desoria klovstadi* (**Isotomidae**; see Figure 105) was collected while foraging on moss, it had a high **supercooling point** (point of crystallization), but when the animals were starved for 2-8 hours, the supercooling point shifted towards the low group. But acclimating them with lichen or algae for five days resulted in even higher supercooling points than if supplied with moss, while those starved (with free water or 100% relative humidity) displayed a trimodal supercooling point distribution. On the other hand, the supercooling point of this springtail was lower when they were acclimated for five days and provided with moss than when supplied with algae or lichens. Sinclair and coworkers found that other pretreatments, including cold, heat, desiccation, and slow cooling, did not induce any supercooling point shifts, suggesting that their diet of mosses, algae, and lichens may have been the controlling factors. They suggested that vertical migration might permit the springtails to escape the cooler temperatures of night. In other Antarctic locations, vertical distributions indicate distinct communities (Usher & Booth 1984).

Bryophytes as a Habitat for Springtails

Kinchin (1990) considered the **Collembola** to be one of the two most abundant groups among bryophytes, the

other being the mites. Studies from wide-ranging locations have demonstrated the importance of the bryophytes as habitats (e.g. Mexico: Varga 1989, 1991; Varga & Vargha 1992; Brazil: Abrantes *et al.* 2010; Hungary: Traser *et al.* 2006; Antarctica: Seppelt & Ochyra 2008). In Brazil, *Brachystomella agrosa* (see Figure 13), *B. contorta* (**Brachystomellidae**), *Seira melloi* (see Figure 14), *S. subannulata* (**Entomobryidae**), and *Ballistura fitchi* (**Isotomidae**) inhabit mosses (Abrantes *et al.* 2010).



Figure 13. *Brachystomella parvula* juvenile, a moss dweller. Pigment protects it from UV light. Photo by Andy Murray, with permission.



Figure 14. *Seira dollfusi*, from a genus that inhabits mosses in Brazil. Photo by Andy Murray, with permission.

Božanić (2011) considered the bryophytes to be important habitats for hiding from predators and unfavorable weather, for feeding, and for laying eggs. Bryophytes absorb water rapidly, reduce substrate evaporation, and insulate against temperature and wind (Gerson 1982; Smrz 1992; Andrew *et al.* 2003). By ameliorating the habitat conditions, they permit **Collembola** to aggregate (Figure 190), thus avoiding dry conditions (Joose & Verhoef 1974; Leinaas & Sømme 1984; Usher & Booth 1984).

For those who are eager to find new species, bryophytes are a good habitat for finding such treasures. Skarzynski (1994) found two species new to the Polish flora by looking at *Sphagnum* (Figure 15) inhabitants. Their small size makes these springtails easy to overlook, and sorting through samples with a microscope is time-consuming and destructive. Because of the chambered structure of the mosses, most extraction techniques are not as effective as in other kinds of samples. (See Sampling below.)



Figure 15. *Sphagnum angustifolium*, a moss where one might find new springtail species by careful sorting. Photo by Michael Lüth, with permission.

Species and Abundance

Species numbers, abundance, and dominance in bryophyte **Collembola** communities can vary widely between locations, as can be seen in Figure 17 (Traser *et al.* 2006). Traser and coworkers collected 60 species (3,451) of **Collembola** in 18 moss species in three habitats in Hungary. The highest diversity was in the reed bed (Tómalom), accompanied by very low abundance and more evenness than the other two sites: Fertőrákos is a dry grass habitat and Sopron is a Botanic Garden, both with lower diversity and higher richness. Interestingly, the **bryobiont** (animal that occurs exclusively associated with bryophytes) *Hymaphorura dentifera* was absent, but several **bryophilic** (bryophyte-loving) species (e.g. *Xenylla boernerii*; Figure 144) were present. None of the dominant species is restricted to bryophytes. The two most abundant species were *Cryptopygus bipunctatus* (Figure 28) and *Folsomia manolachei* (Figure 29). *Sphaeridia pumilis* (Figure 53) and *Parisetoma notabilis* (Figure 187) occurred on *Calliergonella cuspidata* (Figure 16) in two locations. *Brachythecium rutabulum* (Figure 161) housed four species whereas *Hypnum cupressiforme* (Figure 18) housed 14. *Entomobrya nivalis* (Figure 86) occurred on *H. cupressiforme* in two locations. The most abundant species were different for each location (Figure 17). The dominant species primarily belong to the families **Isotomidae** and **Hypogastruridae** [followed by **Entomobryidae** and **Symphyleona** (spherical springtails)]. Moss-dwelling species included:

Hypogastruridae (Figure 1): *Hypogastrura socialis*, *Hypogastrura vernalis* (Figure 19), *Xenylla boernerii* (Figure 144), *Xenylla maritima* (Figure 82), *Xenylla brevicauda*, *Willemia virae* (see Figure 20)

Brachystomellidae: *Brachystomella parvula* (Figure 13)

Neanuridae: *Friesea truncata* (see Figure 157), *Anurida pygmaea* (Figure 21), *Neanura muscorum* (Figure 166)

Onychiuridae: *Supraphorura furcifera* (Figure 22), *Protaphorura armata* (Figure 23)

Tullbergiidae: *Doutnacia xerophila* (see Figure 24), *Mesaphorura critica*, *Mesaphorura hylophila* (Figure 25), *Tullbergia krausbaueri*, *Tullbergia macrochaeta* (Figure 26), *Metaphorura affinis* (Figure 27)

Isotomidae: *Pachytoma crassicauda*, *Cryptopygus bipunctatus* (Figure 28), *Folsomia manolachei* (Figure 29), *Folsomia penicula* (Figure 30), *Folsomia quadrioculata* (Figure 88), *Isotomiella minor* (Figure 31), *Parisetoma notabilis* (Figure 187), *Isotoma viridis* (Figure 32), *Isotoma riparia* (Figure 33), *Isotomurus* cf. *palustris* (Figure 34), *Isotomurus prasinus* (Figure 35)

Entomobryidae: *Entomobrya corticalis* (Figure 36), *Entomobrya handschini* (Figure 37), *Entomobrya multifasciata* (Figure 38), *Entomobrya nigriventris*, *Entomobrya nivalis* (Figure 86), *Lepidocyrtus cyaneus* (Figure 120), *Lepidocyrtus lanuginosus* (Figure 39), *Lepidocyrtus lignorum* (Figure 40), *Lepidocyrtus paradoxus* (Figure 41), *Lepidocyrtus peisonis*, *Lepidocyrtus violaceus* (Figure 42), *Pseudosinella alba* (Figure 43), *Pseudosinella octopunctata* (Figure 44)

Orchesellidae: *Orchesella cincta* (Figure 68), *Orchesella bifasciata* (Figure 150), *Orchesella xerothermica* (Figure 45), *Heteromurus major* (Figure 46), *Heteromurus nitidus* (Figure 47)

Tomoceridae: *Tomocerus* cf. *baudoti* (Figure 48), *Tomocerus minor* (Figure 164-Figure 165)

Cyphoderidae: *Cyphoderus albinus* (Figure 49)

Oncopoduridae: *Oncopodura crassicornis* (Figure 50)

Neelidae: *Megalothorax minimus* (Figure 51), *Neelides minutus* (Figure 52)

Sminthuridae: *Sphaeridia pumilis* (Figure 53)

Katiannidae: *Sminthurinus elegans* (Figure 54), *Sminthurinus aureus* (Figure 55)

Dicyrtomidae: *Dicyrtoma fusca* (Figure 5)

Bourletiellidae: *Deuterosminthurus bicinctus* (Figure 56), *Fasciosminthurus strigatus*, *Heterosminthurus bilineatus* (Figure 57)



Figure 16. *Calliergonella cuspidata*, home to the springtails *Sphaeridia pumilis* (Figure 53) and *Parisetoma notabilis* (Figure 187) in Hungary. Photo by Michael Lüth, with permission.

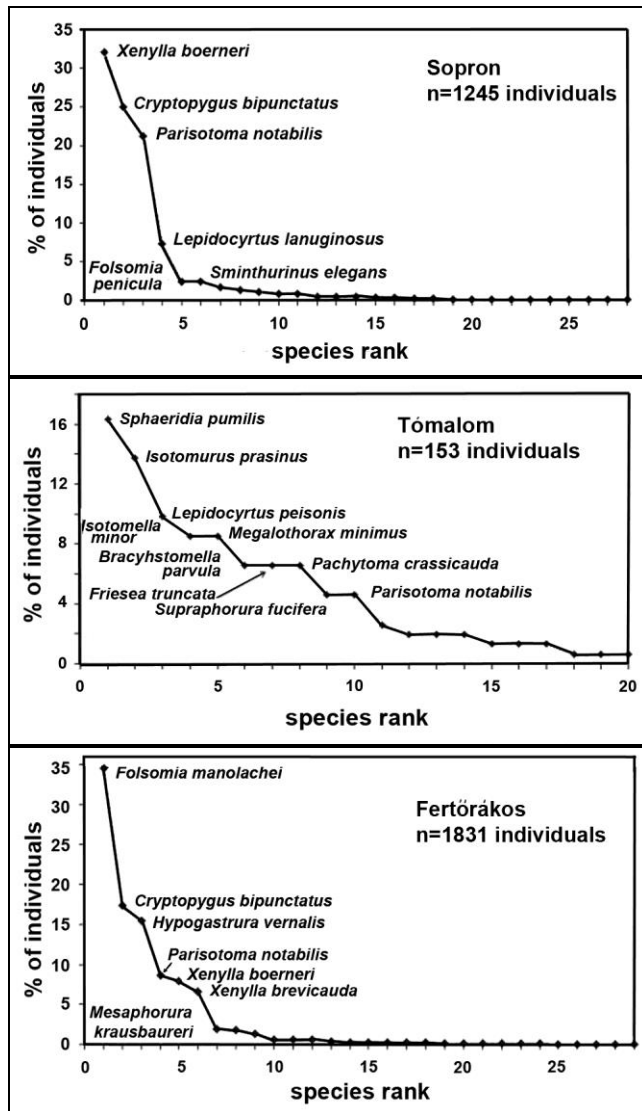


Figure 17. Comparison of dominant species and percent of individuals at three locations in Hungary. Redrawn from Traser *et al.* 2006.



Figure 18. *Hypnum cupressiforme*, home for at least 14 species of springtails in Hungary. Photo by Michael Lüth, with permission.



Figure 19. *Hypogastrura vernalis*, a moss dweller in Hungary. Photo by Arne Fjellberg, through Creative Commons.

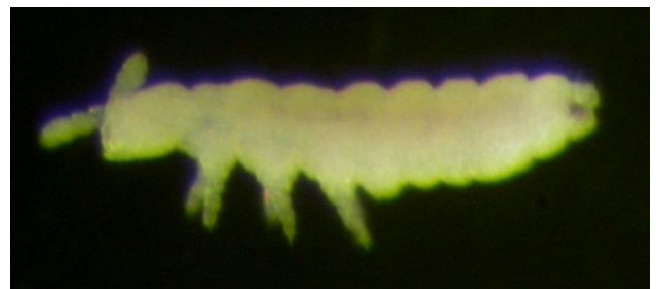


Figure 20. *Willemia similis*, a moss dweller in Hungary. Photo by Arne Fjellberg, through Creative Commons.



Figure 21. *Anurida pygmaea*, one of the tiny moss-dwelling Collembola. Photo by David Porco, through Creative Commons.



Figure 22. *Supraphorura fucifera*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 23. *Protaphorura armata*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 24. **Tullbergiidae**; several members, including *Doutnacia xerophila*, occur among mosses in Hungary. Photo by Andy Murray, through Creative Commons.

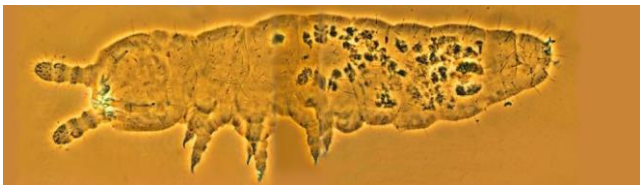


Figure 25. *Mesaphorura hylophila*, a moss dweller in Hungary. Photo by Steve Hopkin, with permission.



Figure 26. *Tullbergia macrochaeta*, a moss dweller in Hungary. Note the absence of eyes. Photo by Andy Murray, through Creative Commons.



Figure 27. *Metaphorura affinis*, a blind moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.

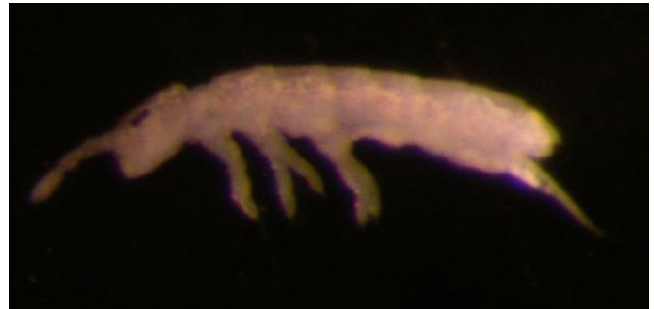


Figure 28. *Cryptopygus bipunctatus*, a common species among mosses in Hungary. Photo by Arne Fjellberg, through Creative Commons.



Figure 29. *Folsomia manolachei*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 30. *Folsomia penicula*, a moss dweller in Hungary. Photo by Galina Bushmakiu, through Creative Commons.



Figure 31. *Isotomiella minor*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 34. *Isotomurus palustris*, a species associated with both aquatic and terrestrial bryophytes. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.



Figure 32. *Isotoma viridis* var. *violacea*. This species lives among mosses in Hungary. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.



Figure 35. *Isotomurus prasinus* or *I. gramineus*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 33. *Isotoma riparia*, a moss dweller in Hungary. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.



Figure 36. *Entomobrya corticalis*, a bryophyte dweller in Hungary. Photo by Miroslav Deml, through Creative Commons.



Figure 37. *Entomobrya handschini*, a moss dweller in Hungary. Photo by Steve Hopkin, with permission.



Figure 38. *Entomobrya multifasciata*, a moss dweller in Hungary. Photo by Valter Jacinto, through Creative Commons.



Figure 39. *Lepidocyrtus lanuginosus*, a moss dweller in Hungary. Photo by Andy Murray, with permission.



Figure 40. *Lepidocyrtus lignorum*, a moss dweller in Hungary. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.



Figure 41. *Lepidocyrtus paradoxus*, a moss dweller in Hungary. Photo by Christophe Quintin, through Creative Commons.



Figure 42. *Lepidocyrtus violaceus*, a moss dweller. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.



Figure 43. *Pseudosinella alba*, an inhabitant of mosses in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 44. *Pseudosinella octopunctata*, a moss dweller in Hungary. Photo by Galina Bushmakiu, through Creative Commons.



Figure 45. *Orchesella xerothermica*, a moss dweller in Hungary. Photo by Galina Bushmakiu, through Creative Commons.



Figure 49. *Cyphoderus albinus*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 46. *Heteromurus major*, a moss dweller in Hungary. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.



Figure 50. *Oncopodura crassicornis*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 47. *Heteromurus nitidus*, a moss dweller in Hungary. Photo by Steve Hopkin, with permission.



Figure 51. *Megalothorax minimus*, a tiny moss dweller. Photo by Andy Murray, through Creative Commons.



Figure 48. *Tomocerus baudoti*, a moss dweller in Hungary. Photo by Louis Deharveng, through Creative Commons.



Figure 52. *Neelides minutus*, a tiny moss dweller. Photo by Andy Murray, through Creative Commons.



Figure 53. *Sphaeridia pumilis* on mosses. Photo by Andy Murray, through Creative Commons.



Figure 54. *Sminthurinus elegans*, a springtail with markings that could hide it among mosses. Photo by Scott Justis, with permission.



Figure 55. *Sminthurinus aureus* forma *maculata*, a moss dweller shown here with *Cyanobacteria*. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.



Figure 56. *Deuterostminthurus bicinctus*, a springtail that lives among mosses in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 57. *Heterosminthurus bilineatus* female, a moss dweller. Photo by Jan van Duinen, with permission.

The greatest numbers of bryophyte-dwelling **Collembola** seem to be those in the Antarctic. But abundance numbers seem to be rare in the literature. Matveyeva (1972) found that moss carpets in the tundra sedge-moss community of Taimyr, USSR, supported 4000 **Collembola** per square meter. That moss carpet area accumulates more snow than areas with turf and the mosses may provide a protected habitat in which the **Collembola** can move and find sufficient food without being detected.

At Spitsbergen, mites and springtails comprised 96-99% of the total arthropods, numbering 268,000 individuals m^{-2} in the wet moss tundra compared to 42,000-63,000 on lichen tundra and 518,000 on grassland there (Bengtson *et al.* 1974).

Božanić (2011) reported 1341 Collembola in individual samples from the Litovelské luhy National Nature Reserve, Czech Republic, compared to only 137 in the control samples (soil, wood, *etc.*). These numbers compared to 2946 mites and 320 isopods. Other groups exhibited lesser numbers.

In the Antarctic, mites and springtails typically dominate the bryophyte habitat. **Collembola** [especially *Parisotoma octooculata* (Figure 58) and *Cryptopygus antarcticus* (Figure 78)] ranged up to 20,540 individuals per 100 cm^2 of *Polytrichastrum alpinum* (Figure 64) (Schenker & Block 1986).



Figure 58. *Parisotoma octooculata*, a common bryophyte inhabitant in the Antarctic. Photo by Te Papa, through Creative Commons.

Food

Collembola are opportunists, feeding on fungi, detritus, and mosses (Gerson 1969; Peterson & Luxton 1982; Hodkinson *et al.* 1994; Chen *et al.* 1995; Varga *et al.* 2002a, b). Ponge (2000) demonstrated that **Collembola** living in soil of 13 Belgian beech forests had gut contents that corresponded with the available food in their immediate proximity. Nevertheless, the **Onychiuridae** (Figure 59) exhibited plasticity of food items based on depth.



Figure 59. *Onychiurus* sp., a species with adaptable food preferences. Photo by Andy Murray, through Creative Commons.

At least some **Collembola** eat bryophytes. And they have actually been seen eating mosses in Antarctica (Pryor 1962; Janetschek 1967). In addition, Pryor (1962) successfully reared them on mosses in the lab. *Gomphiocephalus* (Figure 60 - Figure 61) (**Hypogastruridae**) prefers mosses over **Cyanobacteria**, red lichens, and the mold *Penicillium* (in Gerson 1969). Gerson (1969) reported that *Isotoma* feeds extensively on mosses. *Desoria klovstadi* (see Figure 105) prefers mosses over fungi and feeds extensively on them (Pryor 1962). Nevertheless, Davis (1981) found no evidence of

Collembola feeding on bryophytes in two Antarctic terrestrial moss communities. Despite the dominance of bryophytes in the flora of Antarctica, Block (1985) similarly found that arthropods feed on epiphytic algae, micro-flora, and detritus.



Figure 60. *Gomphiocephalus* feeding on algae that are growing on *Bryum argenteum* on the continent of Antarctica. Photo courtesy of Catherine Beard.



Figure 61. *Gomphiocephalus* feeding on the lichen *Caloplaca setrina* growing on dead *Bryum argenteum* in the Antarctic. Photo courtesy of Rod Seppelt.

Merrifield (2000) suggested that **Collembola** may graze on some bryophytes, possibly causing the increased dependence on gemmae for reproduction. A search of the moss *Syntrichia laevipila* (Figure 62) revealed considerable grazing, but this could also have been the activity of slugs.



Figure 62. *Syntrichia laevipila* with capsules, a species that is grazed, possibly by *Collembola*. Photo by Michael Lüth, with permission.

Megaphorura arctica (Figure 63) (*Onychiuridae*) in West Spitsbergen feeds mostly on living and dead bryophytes, detritus, and sometimes algal cells (Hodkinson *et al.* 1994). The bryophytes include *Sanionia uncinata* (Figure 184-Figure 185), *Polytrichastrum alpinum* (Figure 64), and *Racomitrium lanuginosum* (Figure 65-Figure 66).



Figure 63. *Megaphorura arctica*, a species that feeds on living and dead bryophytes in Spitsbergen. Photo by Arne Fjellberg, through Creative Commons.



Figure 64. *Polytrichastrum alpinum*, a springtail habitat and food in cold places. Photo by John Hribljan, with permission.



Figure 65. *Racomitrium lanuginosum* hummocks, common *Collembola* habitat in the Arctic. Photo by Janice Glime.



Figure 66. *Racomitrium lanuginosum*, a source of food and shelter for *Collembola*, as snow is melting. Photo by Michael Lüth, with permission.

The fungi within bryophyte mats can serve as a food source for bryophyte dwellers (Varga *et al.* 2002b). McMillan and Healey (1971) found mosses in guts of the genus *Tomocerus*. But even the fungi they eat might be moss inhabitants. The springtails *Tomocerus longicornis* (Figure 67) (*Entomobryidae*) and *Orchesella cincta* (Figure 68) (*Entomobryidae*) feed on fungi living on the moss *Tortella tortuosa* (Figure 69) preferentially over other fungi (Varga *et al.* 2002b). One can recognize *T. longicornis* because when it is disturbed, it curls the ends of its antennae (Figure 67). Gut contents of these two species consisted of detritus (55 & 63%), moss particles (20 & 33%), and fungal propagules (10 & 24%), respectively. The fungal gut contents were not in the same proportion as those on the moss, indicating that the springtails were selective in their choice of fungi.



Figure 67. *Tomocerus longicornis* showing coiled antennae in response to disturbance. Photo by Steve Hopkin, with permission.



Figure 68. *Orchesella cincta*, a moss dweller that feeds on the fungi living there. Photo by G. Drange, through Creative Commons.



Figure 69. *Tortella tortuosa*, home of fungi that serve as food for springtails. Photo by Michael Lüth, with permission.

Many springtails that live among mosses are treated to choices of fungi that grow in the association. At least some springtails are able to use olfactory cues – scents provided by the fungi – to both locate the fungi and to distinguish those that are poisonous (Staadén *et al.* 2011).

Bengtsson *et al.* (1988) further supported this discriminatory ability in the springtail *Onychiurus armatus* (Onychiuridae; see Figure 59). This species locates **hyphomycetous** fungi (fungi in Hyphomycetes; molds) by volatile compounds released by the **mycelium** (fungal threads). However, their choice of species differs depending on whether the fungus was grown on agar or on soil.

Sarah Lloyd sent me images of a Tasmanian endemic springtail species of *Acanthanura* (Figure 70) apparently dining on the plasmodium of the slime mold *Diderma* sp. (Figure 70-Figure 71) which is growing on a moss.

Predators

Bryophytes can be safe sites for the smaller creatures such as springtails. They make movement and even striking difficult for larger predators. But when the springtails are in the open spaces (Figure 72), their best protection is their powerful spring.



Figure 70. *Acanthanura* sp. (springtail genus endemic in Tasmania) on slime mold plasmodium (probably *Diderma* sp) on a moss. Photo courtesy of Sarah Lloyd.



Figure 71. *Diderma* fruiting bodies on moss. Photo courtesy of Sarah Lloyd.



Figure 72. The ant *Lasius flavus* with springtails (*Cyphoderus albinus*) and no immediate place for the springtails to hide. Photo by Andy Murray, through Creative Commons.

Miller *et al.* (2008) found a positive correlation among the bryophytes, springtails, and spiders in the Acadian Forest of Maine, USA. However, they found no correlation between number of **Collembola** and adult spiders (Miller *et al.* 2008). They considered spiders to be potential predators on bryophyte-inhabiting **Collembola**, thus confounding the correlations. The relationship between spiders and **Collembola** was sensitive to a decline in bryophyte abundance. This relationship with spiders might influence the abundance of the Brown Creeper (*Certhia americana*; Figure 73) (Miller *et al.* 2008), a bird that feeds on spiders that feed on springtails that live among bryophytes at the bases of trees (Mariani & Manuwal 1990; Weikel & Hayes 1999).



Figure 73. *Certhia americana* (Brown Creeper), part of the food web of bryophytes, springtails, and spiders at tree bases in Maine, USA. Photo by B. J. Stacey, through Creative Commons.

In the coastal grey dunes of France, Bonte and Mertens (2003) found that dwarf spiders considered springtails to be dinner there as well. They found a positive relationship between the phenology of the preferred springtails and the **stenotopic** (tolerating a narrow range of habitats) dwarf spiders. This was especially true for the female spiders because of their dependence on their prey, usually springtails, for reproduction. The spiders and springtails likewise have similar spatial aggregations. And the springtail aggregations typically occur among mosses.

The distribution of the spider *Coelotes terrestris* (Figure 74-Figure 75) was positively related to the cover of mosses and negatively related to litter cover in a beech-dominated (*Fagus sylvatica*; Figure 76) forest floor habitat in Europe (Sereda *et al.* 2012). But Sereda and coworkers did not find an association of spiders to prey-rich areas (**Collembola**) at the scale of 100 m, based on pitfall traps. It could be that the moss dwellers were within the moss clumps and not active near the traps, but these **Collembola** did have a positive relationship to medium deadwood pieces (**Entomobryidae** except *Lepidocyrtus* spp., Figure 77).



Figure 74. *Coelotes terrestris*, a predator spider that hangs out in mossy areas to catch **Collembola**. Photo by James K. Lindsey, with permission.



Figure 75. *Coelotes terrestris* nest among mosses and needles. Photo by James K. Lindsey, with permission.

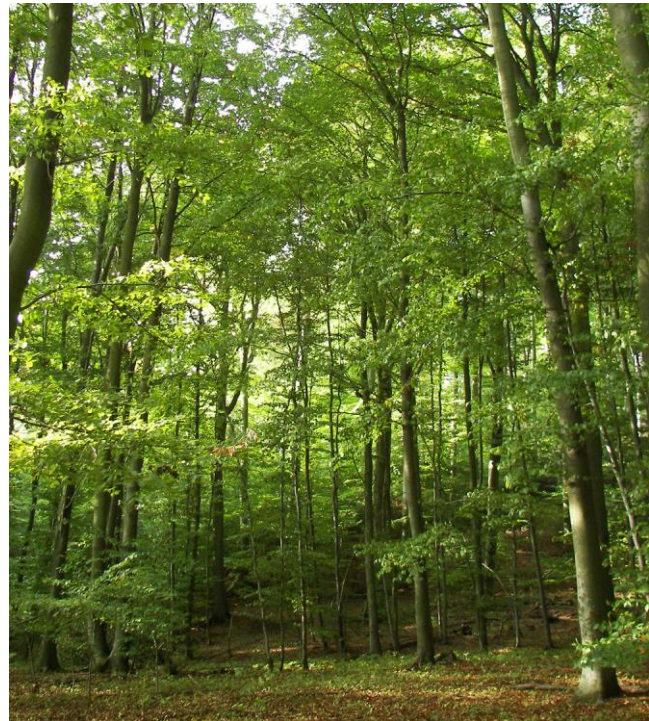


Figure 76. *Fagus sylvatica* forest floor, habitat where the spider *Coelotes terrestris* (Figure 74-Figure 75) is positively related to the cover of mosses. Photo by Nikanos, through Creative Commons.



Figure 77. *Lepidocyrtus* sp., a genus that has no relationship to medium deadwood pieces but does have moss dwellers. Photo by Andy Murray, through Creative Commons.

The Antarctic herbivore *Cryptopygus antarcticus* (Figure 78) is abundant in areas with bryophytes (Block 1985). The single arthropod predator, the mite *Gamasellus racovitzai* (see Figure 79) (*Ologamasidae*), feeds primarily on *C. antarcticus*, the most abundant of the available prey. In the summer this predator is non-selective and in the winter it does little feeding. Block considers it unlikely that such a predator ever has a shortage of food in bryophyte habitats. This aggregation has a strong relationship to moss cover. However, Usher and Booth (1986) considered *Gamasellus* (Figure 79-Figure 80) to have a random distribution. It is probably more accurate to say that the aggregations are random.



Figure 78. *Cryptopygus antarcticus*, the most abundant moss-dweller in Antarctica. Photo by Richard E Lee Jr., with permission.



Figure 79. *Gamasellus*; *G. racovitzai* is a common predator on *Collembola* in the Antarctic. Photo by Monica Young, Biodiversity Institute of Ontario, through Creative Commons.



Figure 80. *Gammarellus angulosus*, member of a genus that is a *Collembola* predator among mosses. Photo by Hans Hillewaert, through Creative Commons.

Wandering Salamanders (*Aneides vagrans*, Figure 81) prey on *Collembola* in the old-growth redwood forest of western USA (Camann 2011). In the canopy the springtails and mites are the most abundant arthropods, with springtails being by far the more abundant group. The salamanders hide in humus moss mats and other more moist locations in the crown of the tree and dine on these abundant springtails.



Figure 81. *Aneides vagrans*, a predator on *Collembola* that dwell in bryophyte refuges. Photo by Todd Pierson, with permission.

Adaptations

So how does a primitive, tiny, land-invader springtail survive among the bryophytes? First, being tiny is an advantage, making it possible for it to crawl about easily amid bryophyte leaves and stems and hide from predators. Some are blind (Figure 26), but that may be an adaptation to living in soil, with bryophytes also being a suitable habitat. Salmon and Ponge (2012) suggest that blind species may have better developed chemical senses. The ability to survive winter helps too. And its need for water is coupled with the ability to survive desiccation (Leinaas & Sømme 1984), making it well attuned to the wet-dry cycling in bryophytes.

Little has been written about adaptations to living among bryophytes, but Leinaas and Sømme (1984) described adaptations for *Collembola* that live among lichens on alpine rocks. Those should apply for many bryophytes as well, although the species of *Collembola*

may be different. The springtails *Xenylla maritima* (Figure 82) (**Hypogastruridae**) and *Anurophorus laricis* (Figure 83) (**Isotomidae**) in South Norway have seasonal cold hardiness. They prevent formation of ice crystals by gut evacuation in preparation for winter and accumulate cryoprotective substances during autumn in preparation for winter cold. These activities permit them to supercool below normal expected winter temperatures. However, those springtails in unprotected areas of the rocks were killed by an exceptionally cold period, suggesting the importance of lichens (or bryophytes) as a refuge. These two species are able to survive **anaerobic** (no free oxygen) conditions, permitting them to survive when their habitat is encased in ice. Both are able to survive drought stress. Reproduction later in the season than other **Collembola** species permits the hatchlings to emerge after the driest periods of summer.



Figure 82. *Xenylla maritima*, a lichen-dwelling species with seasonal cold hardiness in Norway. Photo by Jan van Duinen < www.janvanduinen.nl>, with permission.



Figure 83. *Anurophorus laricis*, a lichen-dwelling species with seasonal cold hardiness in Norway. Photo by Jan van Duinen < www.janvanduinen.nl>, with permission.

Salmon and Ponge (2012) speculated on adaptations for living among bryophytes and other communities associated with tree bark. They considered a short furcula, dark color, stocky body, and limited number of eyes (Figure 84) to be adaptations to living in concealed environments. These are accompanied by small size and limited movement. Pigmentation provides protection from UV light.



Figure 84. *Neelus murinus* showing few eyes and spherical body typical of epiphyte dwellers. Photo by Andy Murray, through Creative Commons.

Collembola commonly form aggregations (Figure 190). Benoit *et al.* (2009) suggest that in the Antarctic, where exposure is more dangerous, the **Collembola** *Cryptopygus antarcticus* (Figure 78) and *Friesea grisea* (see Figure 157) emit chemical cues (**pheromones**) that help them to locate each other, particularly for mating.

Sampling Methods

Pitfall traps are often used for trapping insects in the soil and have also been used to trap those inhabiting bryophytes (Drozd *et al.* 2009; Sereda *et al.* 2012). Drozd and coworkers express concern that the moss clumps are too dense for ease of movement by most invertebrates. Furthermore, the patchy, random distribution of aggregations of springtails necessitates a large number of samples.

Predators are active on the surface, but they are unable to navigate the "bushy obstacle" created by the mosses. On the other hand, **bryophagous** (eating bryophytes) and **detritivorous** (eating dead organic matter – detritus) arthropods such as **Collembola** have no reason to leave the moss clump, again avoiding traps. Similar problems are encountered when using **fogging** techniques (pesticides) to collect arthropods from canopy bryophytes (Yanoviak *et al.* 2003). The bryophyte dwellers fail to drop from the moss clumps.

Shaw (2013) suggested the use of "inert" pads to collect small arthropods as a nondestructive method in areas with sensitive cover of bryophytes. Standard scouring pads are ideal because of their relatively large pore spaces that somewhat resemble moss clumps. The accumulated arthropods can then be extracted using a Tullgren funnel (see below). He found that the percent of total species of sampled **Collembola** communities were between those of soil and those of bark (Figure 85). The numbers were slightly less than those of soil. I have to wonder if the paucity of food would not greatly decrease the number potential.

Heat gradients are common methods for extracting invertebrates from soil and bryophytes (Tuf & Tvardik 2005; Božanić *et al.* 2013). Nadkarni and Longino (1990)

used a Winkler sifting apparatus to extract insects, including **Collembola**, from tropical canopy samples. Hoyle and Gilbert (2004) used a similar method with the Tullgren funnel. The Berlese funnel is a similar method (Briones 2006). Block (1982) used a gradient of temperature and moisture for six days to extract **Collembola** from bryophytes and soil, based on a method used for lichens (Goddard 1979). Brantley and Shepherd (2004) used heptane flotation to extract springtails and other invertebrates from lichens and mosses in cryptogamic crusts in the piñon-juniper woodland in New Mexico, USA. See Chapter 4-1 of this volume for more information and an illustration on heat gradients.

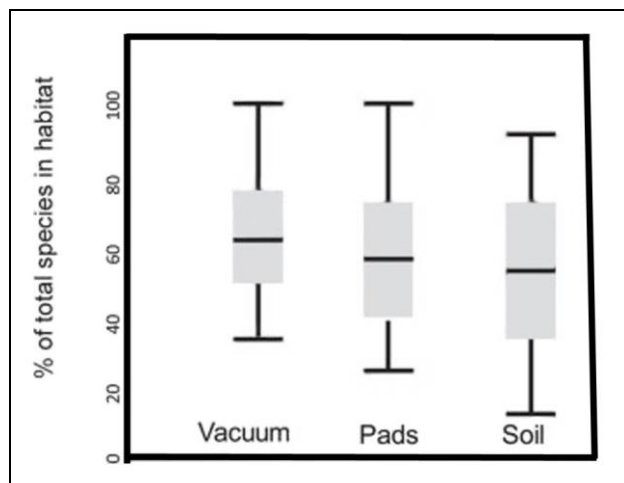


Figure 85. The proportion of **Collembola** collected by three different sampling techniques. Modified from Shaw 2013.

Andrew and Rodgeron (1999) found that the kerosene phase separation was especially more effective in extracting larger numbers of mites and springtails when compared to heat separation with the Tullgren funnel or sucrose flotation (Pask & Costa 1971; see Chapter 12-1 in this volume). Especially for **Collembola**, they concluded that two samples should be used and extracted as replicates, rather than a bulk sample, because of the important effect that spatial scales have on the distribution of these invertebrates.

Temperature Survival

Zettel (1999) examined the cold hardiness of alpine **Collembola**. He found that the winter-inactive hibernator *Entomobrya nivalis* (Figure 86) (**Entomobryidae**), an inhabitant of mosses on boulders, builds up cold hardiness in an anticipatory fashion, using photoperiod and temperature as cues, whereas the winter-active *Isotoma hiemalis* (**Isotomidae**) only responds to sub-zero ($<0^{\circ}\text{C}$) temperatures. Alpine populations of *E. nivalis* living among the lichens on trees hibernate through the winter in crevices under bark flakes. This was the only alpine species Zettel found to increase its low-molecular-weight antifreeze in the winter, making it more sluggish compared to its behavior at the same temperatures in summer. But when this species overwinters in Norway where the temperatures are even colder, it hibernates under the snow (Leinass 1983).



Figure 86. *Entomobrya nivalis*, a moss-dwelling species that anticipates oncoming cold based on photoperiod and temperature. Photo by Steve Hopkin, with permission.

Some alpine **Collembola** survive winter by going deeper into the soil (Zettel (1999)). Soil surfaces under the snow are typically above 0°C , despite subzero air temperatures. And deeper in the soil the temperature is typically even warmer. Spaces in the soil make such migrations to deeper locations possible.

Pigmentation provides a mechanism for absorbing heat, even at low temperatures. Zettel (1999) reported that only one snow-dwelling, winter-active collembolan in the European alpine area had a light color. All others were dark in color. This dark color simultaneously protects them from the high UV radiation present in the alpine zone.

Since **Collembola** are common among bryophytes in the Antarctic, it is easy to understand that the **Collembola** there must have special means to tolerate the low temperatures. These can include physiological adaptations that protect them against the formation of internal ice crystals, the ability to supercool, and life cycle adaptations in which they are dormant during the long, cold winters. Coulson and Birkenmoe (2000) found that the springtails *Hypogastrura tullbergi* (Figure 87) (**Hypogastruridae**) and *Folsomia quadrioculata* (Figure 88) (**Isotomidae**) survived for four years at temperatures below -22°C in soil samples in the lab.



Figure 87. *Hypogastrura tullbergi*, a species that can survive for four years at -22°C . Photo by Arne Fjellberg, through Creative Commons.



Figure 88. *Folsomia quadrioculata*, a species that can survive for four years at -22°C . Photo by Andy Murray, through Creative Commons.

One mechanism in two common Antarctic *Collembola* species is the ability to **supercool** (Block *et al.* 1978). *Cryptopygus antarcticus* (Figure 78) can supercool to -30°C . To do this, they must evacuate the gut by starvation prior to winter cold. This can protect them against internal ice crystal formation by removing water. Such behavior seems to be common among *Collembola* that must endure low temperatures. They lack freeze tolerance, so supercooling is their only physiological survival mechanism (Sømme 1981). For this to work, the gut must be empty to avoid the danger of **ice nucleation** (formation of crystals around proteins and other nucleators). Accumulation of **glycerol** or other **cryoprotectant** (substance that protects against damage by low temperatures) further helps them to survive. Glycerol is used to keep insects from drying out completely in museum collections. Could it serve a similar function for the live animal?

Cannon (1986) likewise demonstrated the importance of evacuation of the gut in preparation for cold weather. He investigated the common *Cryptopygus antarcticus* (Figure 78) (*Isotomidae*) from Signy Island in the Antarctic. If the animal has a diet of moist algae and distilled water at 5°C , it loses most of its ability to supercool. The guts of field-collected animals contain unicellular green algae, dead mosses, fungi, and mineral particles, but living mosses are absent in the gut. As winter approaches, these springtails exhibit a decline in feeding activity. Those foods containing potential **ice nucleators** (small particles such as proteins that serve as the centers for ice crystal formation; such crystals damage cell membranes) are eliminated and replaced by alcohols such as **glycerol**. The glycerol renders a **cryoprotective** (protection against cold) role and is produced in response to low temperatures.

Some Antarctic *Collembola* survive because they live among bryophytes in geothermal areas where temperatures remain warm year-round. In the heat-tolerant *Campylopus introflexus* (Figure 89), the upper 0.5 cm of the moss remains at $40\text{--}47^{\circ}\text{C}$ (Convey & Lewis Smith 2006). More *Collembola*-friendly temperatures occur in slightly cooler geothermal sites. The mosses *Anisothecium hookeri*, *Sanionia georgico-uncinata*, *Pohlia nutans* (Figure 90- Figure 91), and *Notoligotrichum trichodon* (Figure 92), and the liverworts *Cryptochila grandiflora* (Figure 93) and *Marchantia berteriana* (Figure 94) live where

temperatures are $25\text{--}35^{\circ}\text{C}$ and subsurface temperatures are $50\text{--}60^{\circ}\text{C}$.



Figure 89. *Campylopus introflexus*, a common springtail habitat in geothermal areas. Photo by Michael Lüth, with permission.



Figure 90. *Pohlia nutans*, showing extensive bed of the ubiquitous moss that houses springtails in geothermal areas of Antarctica. Photo by Michael Lüth, with permission.



Figure 91. *Pohlia nutans*, a ubiquitous moss that houses springtails in geothermal areas of Antarctica. Photo by Michael Lüth, with permission.



Figure 92. *Notoligotrichum trichodon*, a moss that provides suitable temperatures for **Collembola** in geothermal areas of Antarctica. Photo by Jan-Peter Frahm, with permission.



Figure 93. *Cryptochila grandiflora*, a leafy liverwort that provides a suitable habitat for **Collembola** in geothermal areas of the Antarctic. Photo by Juan Larrain, with permission.

Fertilizing Mosses

The most exciting bryological discovery this century, at least for me, has been that of arthropod fertilization of mosses. This was presented to us in a video at the biennial meeting of the International Association of Bryologists in Kuala Lumpur, Malaysia. Cronberg *et al.* (2006) found that the relationship between mosses and mites (*Scutovertex minutus*, *Scutoverticidae*) or **Collembola** (*Isotoma caerulea*, *Isotomidae*, Figure 95) can be **mutualistic** (both benefitting). In their experiments, these arthropods served as sperm vectors for the moss. This relationship permits sperm to reach females 10 cm, even 1

m, away (Milius 2006). In experiments, if the mosses were even as close as 2-4 cm, they did not reproduce unless they had one of these arthropod vectors to transfer the sperm. The springtails are more effective than the mites in making the transfer. Both seem to be attracted by something in the female moss because they visit it more often than they do the males (Figure 96 (see also Chapter 6-3 in this volume). That's good, because one visit to a male could potentially carry many sperm and thus fertilize a number of females.



Figure 94. *Marchantia berteroa* female, a thallose liverwort that provides a suitable habitat for **Collembola** in geothermal areas of the Antarctic. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 95. *Isotoma caerulea* on mosses, a species that fertilizes some moss species. Photo by Andy Murray, through Creative Commons.

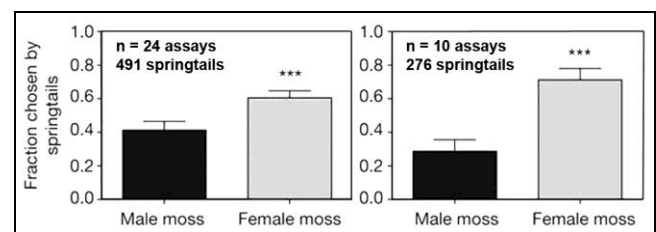


Figure 96. Gender preference of *Ceratodon purpureus* by springtails in Petri dishes (**left**) and olfactometer (**right**). Bars are means with error bars. *** $P < 0.0001$. From Milius 2006.

Both of the mosses *Ceratodon purpureus* (Figure 97) and *Bryum argenteum* (Figure 98-Figure 99) use springtails (*Folsomia candida*, Figure 10-Figure 11,

Figure 97) to transfer their sperm (Cronberg *et al.* 2008; Rosenstiel *et al.* 2012). It is ironic that this species that lacks sexual reproduction itself helps to accomplish it in mosses. Rosenstiel *et al.* demonstrated that springtails are attracted by volatile substances emitted from the moss *Ceratodon purpureus*. Furthermore, these volatile chemicals are sex-specific. Much as in flowering plant pollination, the springtails significantly increase moss fertilization rates (Figure 100). But unlike in pollination, water is important in springtail transfer of sperm. Rosenstiel and coworkers found that water alone and springtails alone were equally effective at fertilizing mosses, but when the two were present together, moss reproduction was more than twice as successful (Figure 100).

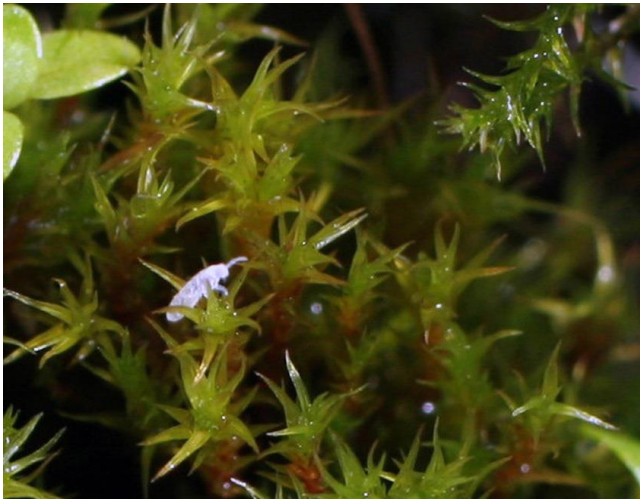


Figure 97. *Folsomia candida* on *Ceratodon purpureus*, a springtail that fertilizes this moss. Photo courtesy of Erin Shortlidge.



Figure 98. *Bryum argenteum* males with perigonia. Photo by George J. Shepherd, through Creative Commons.



Figure 99. *Bryum argenteum* male with perigonia. Photo by George J. Shepherd, through Creative Commons.

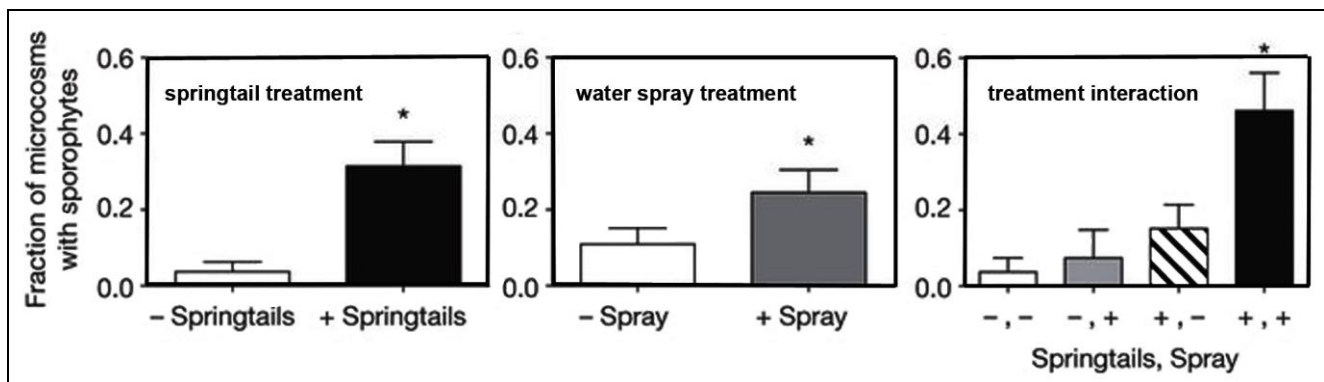


Figure 100. Fertilization success in *Ceratodon purpureus* and *Bryum argenteum*, measured as the fraction of microcosms that developed sporophytes. Bars are means \pm standard error. Plus and minus symbols represent the presence and absence of springtails and water spray. $n = 108$ microcosms. * $P < 0.05$. Modified from Rosenstiel *et al.* 2012.

Bisang and Hedenäs (2015) suggest that springtails, and perhaps other organisms, may be more widespread among bryophytes as agents of fertilization than we have realized. They found *Xenylla humicola* (Figure 101) in great numbers on *Tortula cernua* (Figure 101). Further examination revealed a mix of immature and mature antheridia and mature archegonia. They postulated that the mosses produce a volatile substance at this stage that

attracts the springtails. The springtails, in return, increase the fertilization success. This moss, unlike the previous examples in dioicous mosses, is **autoicous** (antheridia & archegonia in different clusters on the same plant). Hence, we have three examples in three different moss families (**Bryaceae**, **Ditrichaceae**, **Pottiaceae**) to demonstrate moss fertilization by **Collembola**. Thus far no examples are known for pleurocarpous mosses or liverworts.



Figure 101. *Xenylla humicola* on *Tortula cernua* during fertilization season for the moss. Photo courtesy of Lars Hedenäs & Irene Bisang.

There is yet another case of a member of *Xenylla* that can live in the spent antheridial cup of *Polytrichum piliferum* (Fjellberg *et al.* 2017). This species, *Xenylla maritima* (Figure 102), presents a puzzle because two individuals were curled up there when the splash cup was already producing new growth from the center, indicating that the sperm had already been dispersed much earlier. Hence, we are left to wonder what attracted them to this location, and in the right season do they facilitate dispersal of the sperm.



Figure 102. *Xenylla maritima*, an isopod, in the male splash cup of the moss *Polytrichum piliferum*. Note the new, green growth in the center of the cup. Photo by Arne Fjellberg, with permission.

Habitat Differences

Bryophytes in different habitats house different species of *Collembola*. These differences seem to be primarily the result of the habitat differences, not the bryophyte differences. In either case, moisture is an important determinant (Lek-Ang *et al.* 2007).

Bogs and Wetlands

Blackith (1974) pulled together the known literature on *Collembola* from blanket bogs in Ireland and assessed their ecological needs. He found that they are sensitive to

waterlogging, being driven from the peat in spring when the water level rises. This is time of high mortality for them, in part because they have lost their shelter. They benefit from the heat sink provided by the bog mosses, and only a small number of them have a dark color as would be typical of tundra species. This lack of dark color is more typical of tropical species. The *Collembola* are very specific in their choice of host (food) plants, essentially eliminating competition between *Collembola* species.

Many bog *Collembola* are also associated with a particular layer/depth of the peat. Krab *et al.* (2010) experimented with the parameters that determine that depth by literally turning the bog layers upside down with their *Collembola* inhabitants still in them. The responses were of two sorts. The **stayers** remained with the stratum they were in, thus remaining with the substrate of choice. The **movers** left the original position and returned to the vertical position corresponding to their original position. Presumably, the latter group sought a suitable moisture and temperature level. These *Collembola* are important in making the peat suitable for decomposers, and the behavior of the mover group suggests that if the bogs were to undergo warming, this would affect the faunal composition and decomposition rate of the bog.

In a further study of this decomposition relationship, Krab *et al.* (2013) found that in a high-latitude ecosystem, increased litter from birch (*Betula pubescens*), a predictable event from global warming, changed the feeding habits of the resident *Collembola*. Instead of their normal levels of the peat moss *Sphagnum fuscum* (Figure 103) in the diet, all species switched to a strong dietary preference (67%) for *Betula*-associated food sources instead of *Sphagnum*. This resulted in slower decomposition of the *Sphagnum* litter while the *Collembola* species composition remained the same.



Figure 103. *Sphagnum fuscum*, home of *Collembola* with non-specific feeding habits. Photo by Jutta Kapfer, with permission.

In 13 mire habitats of Norway, Fjellberg (1976) found 35 species of surface-active species of *Collembola*. He even found three species new to Norway: *Isotoma tenuicornis* (see Figure 104), *Arrhopalites cochlearifer*, and *Sminthurides pseudassimilis*. Typical mire inhabitants included *Desoria olivacea* (Figure 105), *Isotoma neglecta*, *I. tenuicornis*, *Isotomurus plumosus* (Figure 106),

Sminthurides aquaticus (Figure 107), *Arrhopalites principalis* (Figure 108), and *Heterosminthurus novemlineata* (Figure 109). As is typical with other insects, the highest species richness occurred in the transition zone between the mires and the forest.



Figure 104. *Isotoma anglicana*; *I. tenuicornis* and *I. neglecta* are typical mire inhabitants in Europe. Photo by Arne Fjellberg, through Creative Commons.



Figure 105. *Desoria olivacea*, a bog moss dweller in Norway. Photo by Andy Murray, through Creative Commons.



Figure 106. *Isotomurus plumosus*, a bog moss dweller in Norway. Photo by Arne Fjellberg, through Creative Commons.



Figure 107. *Sminthurides aquaticus* on a moss. This is a common bog species. Photo by Andy Murray, through Creative Commons.



Figure 108. *Arrhopalites principalis*, a typical mire inhabitant in Norway. Photo by Andy Murray, through Creative Commons.



Figure 109. *Heterosminthurus novemlineata*, a typical species in Norwegian mires. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Sławska (2000) found that even the small basin bogs of pine forests have **stenotypic** (able to live in only a narrow range of environmental conditions) species of **Collembola**. These included many typical mire species: *Ceratophysella mosquensis* (see Figure 110), *C. scotica*, *Isotomurus plumosus* (Figure 106), *Ballistura crassicauda*, *Arrhopalites principalis* (Figure 108), *Sminthurides schoetti* (Figure 111), *S. malmgreni* (Figure 112), *S. parvulus* (Figure 113), and *S. pseudassimilis*. Rare species included *Isotoma neglecta*, *I. tenuicornis*, *Desoria fennica* (Figure 114), *Folsomia bisetosa* (Figure

115), *Pseudanurophorus binoculatus* (Figure 116), *Arrhopalites spinosus*, and *Stachorutes sphagnophilus*. Seven of these species are the same as those found by Fjellberg (1976) as typical of the Norwegian mires. Slawska found that the species composition and diversity varied with the size of the peatland, mire type, water conditions, plant communities, and topography, but that the boreal-alpine species in basin bogs did not seem to relate to these parameters. Instead, geography seemed to be an important determinant of the boreal-alpine communities.



Figure 110. *Ceratophysella denticulata*; *Ceratophysella mosquensis* and *C. scotica* are typical mire species in Europe. Photo through Creative Commons.



Figure 111. *Sminthurides schoetti* on moss, a typical bog species in Europe. Photo by Andy Murray, through Creative Commons.



Figure 112. *Sminthurides malmgreni*, a typical bog species in Europe. Photo by Jan van Duinen, with permission.



Figure 113. *Sminthurides parvulus*, a typical bog species in Europe. Photo by Andy Murray, through Creative Commons.



Figure 114. *Desoria fennica*, a rare bog species. Photo by Arne Fjellberg, through Creative Commons.

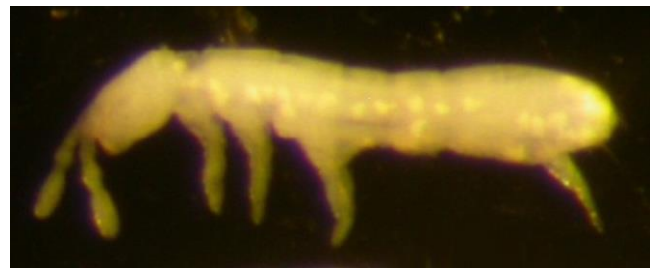


Figure 115. *Folsomia bisetosa*, a common bog species in Europe. Photo by Arne Fjellberg, through Creative Commons.



Figure 116. *Pseudanurophorus binoculatus*, a typical bog species in Europe. Photo by David Porco, through Creative Commons.

Kuznetsova (2002) found that *Vaccinium myrtillus* and green mosses serve as indicators of mesic conditions where one can find **mesophilous** (loving mid-moisture conditions) **Collembola**. The *Sphagnum* communities

typify wet sites and house **hygrophilous** (water-loving) **Collembola** communities. Saraeva *et al.* (2015) identified **continuous** and **spotty distributions** of **Collembola** in **Sphagnum** pine forests of Karelia, Russia. But these patterns are influenced little by relative humidity, mass of moss cover, and litter thickness.

Predators are important in reducing springtail numbers. Bardwell and Averill (1997) found 24 spider genera that possessed prey items in cranberry bogs in Massachusetts, USA. Among 7009 spiders, 2.7% of them possessed prey. The prey items represented 11 orders of insects; 18.6% of these were **Collembola**.

Forests

Moisture seems to be a primary driving factor in delineating differences among collembolan communities. Lek-Ang *et al.* (2007) examined the gradient from forest to peat bog in the French Pyrenees and found a total of 63 species using 48 samples in the bog and 20 in the forest. They found that the peat bog communities were always distinct from those of the forest. Variations were strongly correlated with substrate water content, **Sphagnum** (Figure 117), and grass cover. In this case, the **ecotone** (transition zone between two biological community types) between the forest and bog did not display a greater **species richness** (number of species). (Generally an ecotone has species of both communities, resulting in greater species richness).



Figure 117. *Sphagnum squarrosum*, a collembolan home in forest transition habitats. Photo by J. C. Schou, through Creative Commons.

Snider (1967) reports collecting *Bourletiella arvalis* (**Bourletiellidae**, Figure 118) from *Sphagnum* (Figure 117) in Michigan, USA, forests. *Sminthurinus quadrimaculatus* (**Katiannidae**; Figure 119) occurred in forest moss scrapings and *Lepidocyrtus cyaneus* (Figure 120) and *L. helenae* among mosses.



Figure 118. *Bourletiella arvalis* a species that lives among *Sphagnum* in Michigan forests. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.



Figure 119. *Sminthurinus quadrimaculatus*, a species from forest mosses in Michigan, USA. Photo by Tom Murray, with permission.



Figure 120. *Lepidocyrtus cyaneus*, a species from forest mosses in Michigan, USA. Photo by Steve Hopkin, with permission.

Miller *et al.* (2007) found that the abundance of most of the **Collembola** species in the Acadia Forest in Maine, USA, were correlated with the dense bryophyte cover at the base of sampled trees. Only the family **Isotomidae** (Figure

10-Figure 11) seemed to decrease in abundance as bryophyte cover increased. Instead, this family was primarily associated with the epiphytic lichen *Usnea subfloridana* (Figure 121) higher up the trees. Nevertheless, Snider (1967) listed few *Collembola* from bryophytes outside of bogs in his treatment of Michigan, USA, *Collembola*. Could it be that the human collectors have the same problem as the predators – the *Collembola* are too difficult to see or capture when they live among the bryophytes?



Figure 121. *Usnea subfloridana*, preferred home for *Isotomidae* compared to mosses. Photo by Jerzy Opiola, through Creative Commons.

Majzlan and Fedor (2003) found that springtails may "crawl" up trees, observing this activity on the trunks of *Aesculus hippocastanum* (horse chestnut) in Slovakia (but they were unable to observe downward movement). They determined that this activity might relate to their trophic preference (bryophytes, lichens, algae) or to their tolerance of soil humidity. [Davies (1928) found that the optimum humidity for *Collembola*, except *Entomobrya*, at 25°C was a saturated atmosphere.] Majzlan and Fedor (2003) documented that there were four times as many springtails in the lower (1 m) tree samples compared to the upper ones (5 m), but in autumn, this number increased to ten times as many in the lower samples.

Rodgers and Kitching (1998) examined the vertical stratification of *Collembola* in the subtropical rainforest site at Lamington National Park in southeast Queensland, Australia. They found that the vertical stratification was complex for the arthropods. The greatest homogeneity existed among samples on the forest floor and the greatest dissimilarity in the upper canopy. They considered that dispersal barriers might account for some of the observed differences, accompanied by a greater risk of extinction in the upper canopy. These two limiting factors could account for the greater heterogeneity of canopy *Collembola* species. Since Rodgers and Kitching used leaf litter as a substrate to sample the *Collembola*, suspending the samplers in canopy epiphytes, it is unclear how these differences relate to stratification of bryophyte-*Collembola* communities.

Forest Floor

Deciduous forests and conifer forests have very different ground flora. Bryophytes in deciduous forests are restricted to emergent structures such as logs, stumps, tree bases, vertical inclines, and rocks. This is because the leaf litter buries them elsewhere. These bryophytes serve as important habitats for *Collembola*.

In a boreal forest in northern Sweden, removal of mosses, such as that following fire, strongly negatively impacted both abundance and diversity of the *Collembola* (Bokhorst *et al.* 2014). On the other hand, the species diversity of the *Collembola* community gradually increased with forest decline in Tam Dao National Park, Vietnam (Vu & Nguyen 2000). A major reason for the correlation of *Collembola* with bryophytes is the need of these springtails for moisture, whether it be in the bryophyte mat or is the soil beneath them (Jucevica & Melecis 2005).

For some species, mosses are a seasonal habitat. In a spruce forest of the High Tatra Mountains, Slovakia, there is a mosaic cover of the mosses *Dicranum scoparium* (Figure 122) and *Hylocomium splendens* (Figure 123) (Čuchta *et al.* 2012). *Vertagopus cinereus* (Figure 124) lives in that moss layer in winter and in early spring, but it migrates into the soil during summer (Prat & Massoud 1982). On the other hand, Čuchta *et al.* (2012) found that in this same spruce forest, *Orchesella cincta* (Figure 68) and *Xenylla tullbergi* are far more common among bark pieces and tree mosses and lichens than in the litter layer.

Ponge *et al.* (1993) experimented with litter perturbations to see the effects on the *Collembola* community. They found that the bog species *Sminthurides schoetti* (Figure 111) and *S. parvulus* (Figure 113) increased in abundance following litter disappearance in the forest. These two species are typical of *Sphagnum* bogs (Stach 1956; Gisin 1960; Sławska 2000). Ponge (1993) concluded that vegetation does not itself directly influence the *Collembola*, but that it may affect them indirectly by humus formation.



Figure 122. *Dicranum scoparium*, a dominant moss in the spruce forests where one can find several *Collembola* species in the moss layer. Photo by Janice Glime.



Figure 123. *Hylocomium splendens*, a dominant moss in the spruce forests where one can find several **Collembola** species in the moss layer. Photo by Andrew Spink <www.andrewspink.nl>, with permission.



Figure 124. *Vertagopus cinereus* juvenile on bryophytes, a species that migrates into the soil in summer. Photo by Jan van Duinen, with permission.

In *Picea sitchensis* (Figure 125) plantations, succession after cutting starts with unvegetated needle litter and progresses to well-developed herb or shrub layers that then become suppressed by shade during canopy closure about 15-20 years after clear-cutting (Butterfield 1999). Depending on thinning, little ground vegetation may remain, but sparse moss cover may be present. **Collembola** densities were high in spring when the canopy was open, decreasing in summer. Under closed canopy, the opposite relationship occurred, with drying most likely accounting for the low summer densities in the open. The closed canopy also supported higher **Collembola** densities in the upper soil layer than in the drier ones under the open canopy.



Figure 125. *Picea sitchensis* with storm damage, showing areas of open canopy. Photo by Max East, through Creative Commons.

The Checklist of Nordic **Collembola** notes mosses among the habitats for many **Collembola** species (Fjellberg 2007b). These include *Micranurida anophthalmica* (Neanuridae), a rare species among mosses on rotten wood; *Appendisotoma abiskoensis* (Isotomidae) among boreal forest mosses; *Pseudisotoma sensibilis* (Figure 141, common) (Isotomidae), *Orchesella spectabilis* (Entomobryidae; Figure 126), *Pogonognathellus flavescens* (Tomoceridae; Figure 127), and *Lipothrix lubbocki* (Sminthuridae; Figure 128-Figure 129) in moss and forest litter; *Orchesella cincta* (Figure 68) common in moss and dry forest litter; *Orchesella flavescens* (Figure 130) in moss and litter in damp forests, mainly conifers; *Pogonognathellus longicornis* (Figure 131) among mosses and forest litter, mainly hardwoods; *Sminthurinus aureus signatus* (Katiannidae; Figure 132) in moss and litter of damp habitats in forests; and *Gisinianus flammeolus* (Katiannidae; Figure 133) in moss and litter of rich, moist hardwood forests.



Figure 126. *Orchesella spectabilis* male among mosses. Photo by Gábor Keresztes <xespok.net>, with permission.



Figure 127. *Pogonognathellus flavescens*, a species of Nordic forest mosses and litter. Photo by Anki Engström at <www.krypinauren.se>, with permission.



Figure 130. *Orchesella flavescens*, a species living among mosses and litter in damp conifer forests of Nordic countries, shown here on a species of *Polytrichum*. Photo by Jan van Duinen, with permission.



Figure 128. *Lipothrix lubbocki* adult, a species of forest mosses and litter in Nordic countries. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.



Figure 131. *Pogonognathellus longicornis*, a species that lives among Nordic hardwood forest mosses and litter. Photo by S. D. Lund, through Creative Commons.



Figure 129. *Lipothrix lubbocki* juvenile, a species of forest moss and litter. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.



Figure 132. *Sminthurinus aureus* orange form on moss, a species from mosses and litter in damp Nordic forest habitats. Photo by Andy Murray, through Creative Commons.

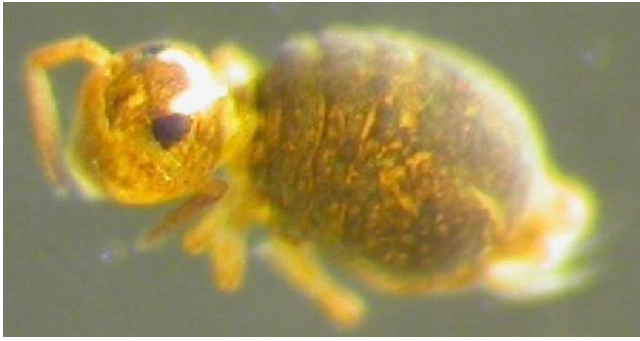


Figure 133. *Gisinianus flammeolus*, a species that lives among Nordic hardwood forest mosses and litter. Photo by Arne Fjellberg, through Creative Commons.

Tetrodontophora bielanensis (Onychiuridae; Figure 134) is common on the forest floor of the Bielany Hills near Kraków, Poland, where it lives among dead leaves, mushrooms, and on mosses (Klag 1982). In Hungary, *Xenylla brevisimilis* and *Tetracanthella franzi* (Isotomidae) occur in mosses and litter (Dány & Traser 2008). *Tetracanthella wahlgreni* (Figure 135) lives among xerophilous (dry-loving) mosses and lichens.



Figure 134. *Tetrodontophora bielanensis* on mosses, a forest dweller on dead leaves, mushrooms, and mosses in Poland. Photo by Steve Hopkin, with permission.



Figure 135. *Tetracanthella wahlgreni*, a species that lives among xerophilous mosses and lichens. Photo by Andy Murray, through Creative Commons.

Andy Murray (2015) describes chasing *Sminthurides schoetti* (Sminthuridae; Figure 136) through a "forest of moss" in order to get its picture. It at least appears to use mosses to escape as well as being a common bog dweller. Murray describes finding *Stenacidia violacea* (Sminthuridae; Figure 137-Figure 139) among mosses. This forest species is relatively common and may even use bryophytes for mating sites (Figure 137).



Figure 136. *Sminthurides schoetti* on moss. Photo by Andy Murray, through Creative Commons.



Figure 137. *Stenacidia violacea* courtship ritual. Photo by Andy Murray, through Creative Commons.



Figure 138. *Stenacidia violacea* juvenile checking out the mosses. Photo by Andy Murray, through Creative Commons.



Figure 139. *Stenacidia violacea* juvenile on moss. Photo by Andy Murray, through Creative Commons.

Some species that live on rotten wood also take advantage of the mosses occurring there. Such is the case for *Sminthurinus bimaculatus* (Figure 140) as seen in this picture by Andy Murray. *Pseudisotoma sensibilis* (Isotomidae; Figure 141) prefers cushions on logs not far above the ground (Bauer & Christian 1993).



Figure 140. *Sminthurinus bimaculatus* on moss. Photo by Andy Murray, through Creative Commons.



Figure 141. *Pseudisotoma sensibilis*, a common species among mosses on logs in Nordic countries. Photo by Arne Fjellberg, through Creative Commons.

Entomobrya muscorum (Figure 142) has been a puzzle for me. This species has a name that suggests that it

should live among mosses. But instead, I was able to verify it as living on soil. Finally, as I was preparing the final formatting of this sub-chapter, I made one more search. A study on nematode predators on other invertebrates verified that it does indeed live among mosses as well, and it eats nematodes there (Heidemann *et al.* 2014).

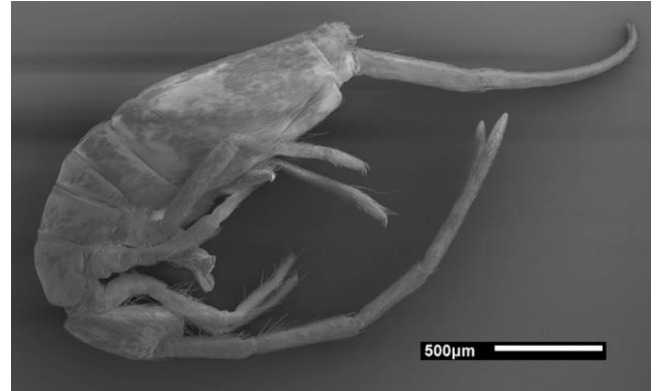


Figure 142. *Entomobrya muscorum*, a soil dweller and sometimes a moss dweller. Photo by Jürgen Schulz, with permission.

Epiphytes

The epiphytic bryophytes seem like an unlikely habitat for an insect with a spring on it. But not all "springtails" have springs. Hence, they may be small and round, lack a furcula, be small, and produce a glue that helps to hold them to the tree or catch them like a tether when they fall.

Dicyrtoma fusca (Figure 5) is well adapted to living among epiphytic bryophytes by its small, globular shape (Figure 143) (Traser *et al.* 2006; Nature Spot 2015). It feeds on mold and other fungi. Dány and Traser (2008) found that *Xenylla boernerii* (Figure 144) is **corticophilous** (bark-loving), living among epiphytic mosses in Hungary; its furcula is reduced to two small warts. Fjellberg (2007b) reported *Entomobrya albocincta* (Figure 145) (**Entomobryidae**) and *Pseudachorutes boernerii* (Figure 146) (**Neanuridae**) in mosses and lichens on trees in the Nordic countries. These two genera do have well-developed furculas.



Figure 143. *Dicyrtoma* (left) and *Sminthurinus* (right) showing differences in size among collembolans. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.

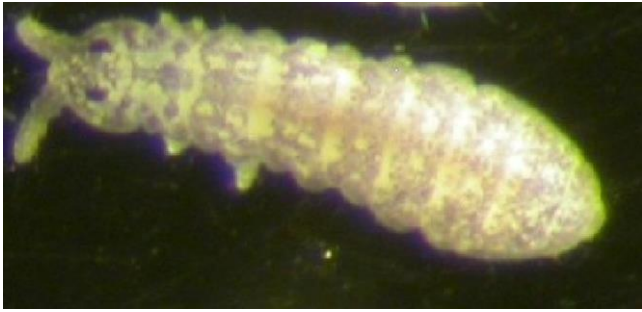


Figure 144. *Xenylla boernerii*, a springtail that inhabits epiphytic mosses in Hungary. Photo by Arne Fjellberg, through Creative Commons.



Figure 145. *Entomobrya albocincta*, a springtail of Nordic mosses and lichens on trees. Photo by Andy Murray, through Creative Commons.



Figure 146. *Pseudachorutes* sp.; *P. boernerii* lives among mosses on boulders and tree trunks in Nordic Countries. Photo by Andy Murray, through Creative Commons.

Both epiphytic bryophytes and **Collembola** are affected by gap harvesting. Wagner *et al.* (2007) found that springtails, mites, and spiders were most abundant near the tree bases in the Acadian forest of central Maine, USA. Gap harvesting reduced the abundance of all three of these groups on the bark of red maple (*Acer rubrum*; Figure 147). There was a positive correlation among these three groups. It is likely that the spiders preyed on the **Collembola** and that gap harvesting affected the spiders by affecting their prey. Miller *et al.* (2008) found that spiders tended to be where the **Collembola** were, but they also found indications of an association between six families of **Diptera** (flies) and members of the **Collembola** family **Entomobryidae**.



Figure 147. *Acer rubrum* in autumn, home of springtails, mites, and spiders among epiphytic bryophytes. Photo by Anderson & Ryser (2015), through Creative Commons.

Cutz-Pool *et al.* (2010) examined **Collembola** communities at three different heights among epiphytic mosses on trees in Mexico, where they collected 12 **Collembola** species. Both species richness and density decreased with increasing height on the tree. Height on the tree had a significantly negative effect on the densities of *Pseudachorutes subcrassus* (**Hypogastruridae**; see Figure 146), *Entomobrya* cf. *triangularis* (**Entomobryidae**), *Americabrya arida* (**Entomobryidae**; Figure 148), and *Ptenothrix marmorata* (**Dicyrtomidae**; Figure 149).



Figure 148. *Americabrya arida*, an epiphytic moss dweller. Photo by Jesse Christopherson, through Creative Commons.



Figure 149. *Ptenothrix marmorata*, an epiphytic moss dweller. Photo by Tom Murray, with permission.

The epiphyte mats of tropical cloud forests provide important niches for a diverse microarthropod community, including the **Collembola** among the most abundant (Yanoviak & Nadkarni 2001). The bryophytes buffer the environment against the wind, retain moisture, provide foraging sites, provide shelter for egg deposition, and provide safe sites against predators (Gerson 1982; André 1983; Nadkarni 1994; Kitching *et al.* 1997; Yanoviak *et al.* 2004). Yanoviak *et al.* (2004) investigated the differences in arthropod communities in the green vegetative portion and brown humic portions of these epiphytic mats, a portion of which was comprised of bryophyte species. The dominant arthropods were mites, ants, and springtails. The green portion of the mats housed twice as many arthropod individuals and species per gram compared to the brown portion and **Collembola** were more abundant in the green portion.

In a neotropical montane forest in Costa Rica, Nadkarni and Longino (1990) found that while the relative abundance of arthropods, including **Collembola**, are essentially the same on the forest floor and in the canopy. The densities of all groups except ants are significantly higher on the ground by a factor of 2.6. Among these, mites, beetles, ants, and springtails are consistently the most abundant arthropod taxa in the mats of epiphytes and humus (Longino & Nadkarni 1990; Nadkarni & Longino 1990; Paoletti *et al.* 1991; Yanoviak & Nadkarni 2001; Yanoviak *et al.* 2003).

A number of additional species of **Collembola** live among bryophytes on both tree trunks and boulders, as discussed below.

Boulders and Rock Canyons

As in trees, some bryophytes can provide the necessary moisture for collembolans in the harsh environment of boulders and rock walls. Hence, bryophytes on boulders share many of the same **Collembola** species that live among bryophytes on tree trunks. Fjellberg (2007a) included *Vertagopus arboreus* (Figure 151) (**Isotomidae**), *Vertagopus westerlundii* (Figure 152), *Vertagopus pseudocinereus* (Figure 153), and *Pseudisotoma sensibilis* (Figure 141) (**Isotomidae**) among boulder and tree trunk mosses in Fennoscandia and Denmark. Likewise, the Nordic **Collembola** include many species common to mosses of both boulders and tree trunks (Fjellberg 2007b): *Orchesella bifasciata* (**Entomobryidae**; Figure 150), *Xenylla boernerii* (**Hypogastruridae**; Figure 144), *Tetracanthella strenzkei* (**Isotomidae**; see Figure 158), *Vertagopus arboreus* (**Isotomidae**; Figure 151), *Vertagopus westerlundii* (northern; Figure 152).



Figure 150. *Orchesella bifasciata*, a Nordic species of mosses on boulders and tree trunks. Photo by Anki Engström <www.krypinnaturen.se>, with permission.



Figure 151. *Vertagopus arboreus*, a species that lives among mosses on boulders and tree trunks. Photo by Andy Murray, through Creative Commons.

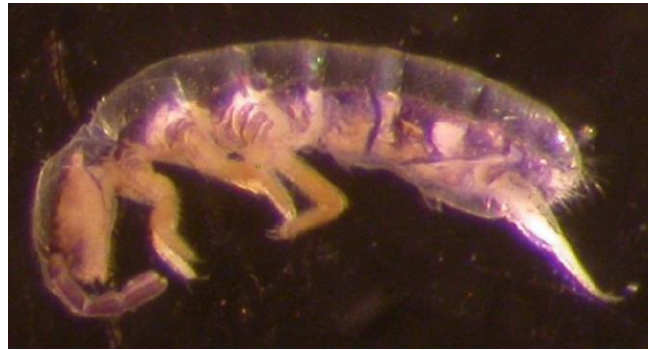


Figure 152. *Vertagopus westerlundii*, a species that lives among mosses on boulders and tree trunks. Photo by Arne Fjellberg, through Creative Commons.



Figure 153. *Vertagopus pseudocinereus*, a species that lives among mosses on boulders and tree trunks. Photo by Jan van Duinen, with permission.

But boulders can also have unique assemblages of bryophyte-dwelling **Collembola**. In beech and spruce forests in Bohemia, Rusek (2001) found that the **Collembola** communities among mosses on boulders differed significantly from other forest communities. Forest age and microhabitat characteristics were important in determining the forest collembolan inhabitants, and some species were restricted to only one or two microhabitats. As in a number of other studies, Rusek demonstrated the importance of examining both local patch variation and broader ecosystem differences.

Onychiurus armatus (Onychiuridae; see Figure 59) lives exclusively in moss cushions on granite boulders in Australia where the microclimate is stable, taking advantage of the supercooling ability and avoiding the need to cross bare rock (Bauer & Christian 1993). *Xenylla boernerii* (Figure 144) is the dominant species when the microclimate is unstable in cushions on boulders and does not share any aversion to bare rock. The mosses may help these collembolans to survive the winter.

Wood (1967) found it difficult to categorize communities associated with moorland soils in Yorkshire, England, based on the species assemblages of 200 species of mites and springtails. However, on limestone boulders one indicator emerged – the springtail *Anurophorus laricis* (Isotomidae; Figure 83) seemed to be characteristic of the moss genus *Grimmia* (Figure 154) and lichens on these boulders.



Figure 154. *Grimmia pulvinata* on a wall where **Collembola** live among them. Photo from Botany Department Website, University of British Columbia, Canada, with permission.

In Fennoscandia and Denmark, Fjellberg (2007a) adds the rock/boulder-dwelling *Isotomurus antennalis* (Entomobryidae; Figure 155) in damp moss of rocky habitats and *Vertagopus sarekensis* (Isotomidae; Figure 156) among mosses and lichens on alpine rocks. Among the Nordic **Collembola** (Fjellberg 2007b), rock and boulder dwellers include *Friesea claviseta* (Neauridae; Figure 157), *Anurophorus fulvus* (Isotomidae) and *Anurophorus laricis* (Isotomidae; Figure 83) (common) in moss/lichen patches on rocks, *Vertagopus sarekensis* and *Vertagopus arcticus* among alpine mosses on rocks, *Megaphorura arctica* (Onychiuridae; Figure 63) common in the Arctic on rocks with moss/algae growth, *Tetracanthella arctica* (Isotomidae; Figure 158) in the Arctic among mosses and lichens on seashore rocks, and *Isotomurus antennalis* among wet mosses on rocks of seashores. In Michigan, USA, Snider (1967) reports *Isotoma nigrifrons* (Isotomidae) from mosses on a rocky bluff.



Figure 155. *Isotomurus antennalis*, a species of damp mosses on rocks and boulders. Photo by G. Drange, through Creative Commons.



Figure 156. *Vertagopus sarekensis*, a species that lives among mosses and lichens on alpine rocks. Photo by Arne Fjellberg, through Creative Commons.

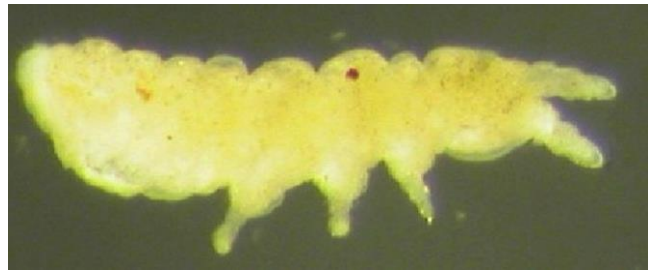


Figure 157. *Friesea claviseta*, a moss-lichen dweller on boulders in Nordic countries. Photo by Arne Fjellberg, through Creative Commons.



Figure 158. *Tetracanthella arctica*, a species that lives in the Arctic among mosses and lichens on seashore rocks. Photo by Arne Fjellberg, through Creative Commons.

Some boulder-dwelling **Collembola** are more specific in their locations. *Mackenziella psocoides* (Mackenziellidae) occurs in rock fissures and among mosses on sand (Fjellberg 2007b). *Folsomia*

coeruleogrisea (*Isotomidae*; Figure 159) lives among mosses on **bird cliffs** (steep cliffs with numerous small shelves that serve as nesting locations for bird colonies).

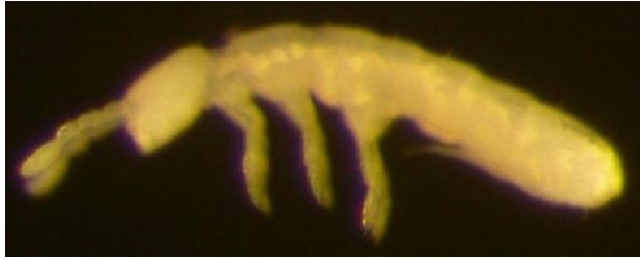


Figure 159. *Folsomia coeruleogrisea*, a species among mosses on bird cliffs. Photo by Arne Fjellberg, through Creative Commons.

Boulders can present harsh conditions for **Collembola**, particularly on a hot summer day. And some boulders are subject to frequent disturbance. Inhospitable conditions make it difficult for the tiny springtails to navigate from one moss patch to another. Hoyle and Gilbert (2004) studied the role of bryophyte corridors in movement of **Collembola** and other arthropods among bryophyte [*Homalothecium sericeum* (Figure 160), *Brachythecium rutabulum* (Figure 161), *Hypnum lacunosum* var. *lacunosum* (Figure 162)] patches on a wall habitat, a good model for boulders as well. They found 12 morphospecies of **Collembola**, including *Entomobrya nivalis* (*Entomobryidae*; Figure 86), *Orchesella villosa* (*Entomobryidae*; Figure 163), *Tomocerus minor* (*Entomobryidae*; Figure 164-Figure 165), *Neanura muscorum* (*Neanuridae*; Figure 166), *Pseudisotoma sensibilis* (*Isotomidae*; Figure 141), *Dicyrtomina minuta* (*Dicyrtomidae*; Figure 167-Figure 168), and *Lepidocyrtus curvicolis* (*Entomobryidae*; Figure 169). These were represented by 314 individuals per moss patch, on average. Numbers were positively correlated with patch weight. They found no evidence that populations of predators were more affected by fragmentation than non-predators. Hoyle and Gilbert suggested that corridors of mosses might be more important during extreme conditions.



Figure 160. *Homalothecium sericeum* on a stone wall where **Collembola** are able to live among them. Photo by Michael Lüth, with permission.



Figure 161. *Brachythecium rutabulum*, a species that provides shelter for **Collembola** on stone walls. Photo by Michael Lüth, with permission.



Figure 162. *Hypnum lacunosum*, a species that provides shelter for **Collembola** on stone walls. Photo by Michael Lüth, with permission.



Figure 163. *Orchesella villosa*, a species that lives among mosses on stone walls, shown here on a thallose liverwort. Photo by Steve Hopkin, with permission.



Figure 164. *Tomocerus minor* juvenile, a species among mosses on stone walls. Photo by Steve Hopkin, with permission.



Figure 165. *Tomocerus minor* adult, a species among mosses on stone walls. Photo by Andy Murray, through Creative Commons.



Figure 166. *Neanura muscorum*, a species among mosses on stone walls. Photo by Andy Murray, through Creative Commons.



Figure 167. *Dicyrtomina minuta* eating algae. Photo by Jan van Duinen <www.janvanduinen.nl>, with permission.



Figure 168. *Dicyrtomina minuta*, a species that lives on mosses on rock walls. Photo by Tom Murray, with permission.



Figure 169. *Lepidocyrtus curvicolis*, a springtail that lives among mosses on stonewalls. Photo by Steve Hopkin, with permission.

Limestone outcrops are absent in many parts of the world. Some **Collembola** prefer living among mosses in such habitats. In Moldova, several species of *Orchesella* (Figure 150) and *Entomobrya* (Figure 86) occurred in these habitats, with *Orchesella maculosa* occurring in most of the canyons in the Moldova study, but not in other ecological conditions (Buşmachi *et al.* 2015).

Considering this problem of migrating from one patch to another, Starzomski and Srivastava (2007) examined the effect of fragmentation of moss patches and the importance of disturbance on mites and springtails – two taxa comprising more than 200 morphospecies in <20 m². The moss community covered a granite outcrop in British Columbia, Canada, and was comprised of *Polytrichum* (Figure 170) and *Bryum* (Figure 171) moss species. Starzomski and Srivastava determined that the disturbance

rate, size, and connectivity were the most important factors affecting species richness and abundance in local patches. Reductions in patch size had little effect unless there was also an absence of connectivity between patches. Repeated disturbance also caused rapid declines in both richness and abundance and caused considerable change in the community composition.



Figure 170. *Polytrichum piliferum*, a moss that can grow on rocks and house **Collembola** there. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 171. *Bryum capillare* with capsules, a moss that can grow on rocks and house **Collembola** there. Photo by Lairich Rig, through Creative Commons.

Vertical Gradients

The transition from soil to soil bryophytes to boulder bryophytes creates a gradient of moisture, light, and food sources. Bonnet *et al.* (1975) considered this gradient for 26 species of **Collembola**, but restricted the observations to the soil and aerial mosses and ignored the soil mosses. On the south faces of rocks, the habitat is dry with highly drained mosses. On the north sides of the rock the soil is deep. The gradients of **Collembola** in these locations emphasize the importance of humidity and temperature in determining the distribution of these moss-inhabiting springtails.

Mountains, Alpine, and Arctic

Fjellberg (2007b) has contributed much to our knowledge of **Collembola** among the bryophytes in alpine and Arctic areas. These records include *Folsomia binoculata* (**Isotomidae**; Figure 172) in wet mossy habitats, Arctic Islands only; *Folsomia agrelli* (**Isotomidae**; Figure 173), rare in high alpine wet moss communities; *Desoria tolya* (**Isotomidae** Figure 174) in moss and forest litter, more common in alpine rocky habitats; *Sminthurinus concolor* (**Katiannidae**; Figure 175) in damp moss on rocks of the Arctic tundra.

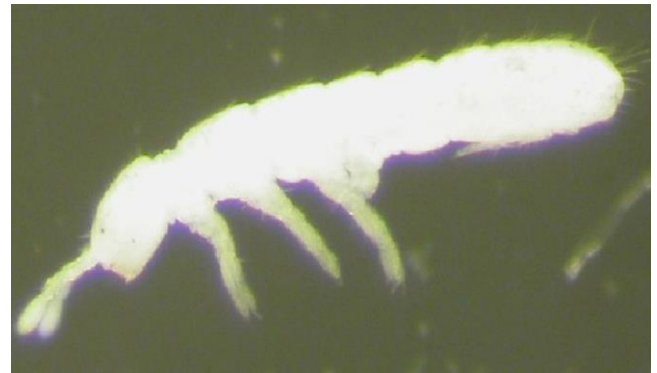


Figure 172. *Folsomia binoculata*, a species of wet, mossy Arctic habitats. Photo by Arne Fjellberg, through Creative Commons.

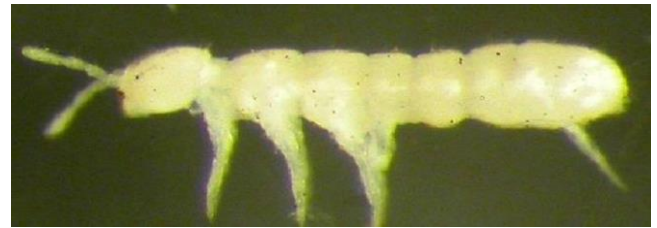


Figure 173. *Folsomia agrelli*, a rare species among high alpine wet mosses. Photo by Arne Fjellberg, through Creative Commons.

In the poor high mountain areas of the North Swedish Mountains, Agrell (1941) found the **Collembola** to be well represented by **stenotopic** species (able to tolerate only a restricted range of habitats or ecological conditions) with few stenotopic **Coleoptera** (beetles), but he found no characteristic bog species there.



Figure 174. *Desoria tolya*, a species of mosses and forest litter, especially in alpine rocky habitats. Photo by Arne Fjellberg, through Creative Commons.



Figure 175. *Sminthurinus concolor*, a species of damp moss on rocks of the Arctic tundra. Photo by Arne Fjellberg, through Creative Commons.

In the Russian tundra, Bretfeld (2010) reported *Arrhopalites principalis* (Arrhopalitidae; Figure 176) in moss, *Sminthurinus alpinus* (Katiannidae; Figure 177) in moss-lichen tundra, *S. oiskiyensis* in moss on rocks along a river in a small forest with *Abies sibirica* at 1300 m altitude, and *Sminthurus cogsonzavi* (Sminthuridae) in an alpine moss-lichen tundra at 1500-1800 m altitude.



Figure 176. *Arrhopalites principalis*, a species of moss-lichen tundra in Russia. Photo by Andy Murray, through Creative Commons.



Figure 177. *Sminthurinus alpinus*, a species of moss-lichen tundra in Russia. Photo by Arne Fjellberg, through Creative Commons.

Altitudinal Gradients

Cutz-Pool *et al.* (2008) examined altitudinal gradient effects on the structure of the collembolan community among **epiphytic** (bark) mosses in a sub-humid forest in Mexico. Density was greatest at the highest altitude (3250 m asl), but species richness was highest at the lowest altitude in the study (2750 m asl). Density had a significant positive relationship with altitude. *Americabrya arida* (Figure 148) and *Willowsia mexicana* (Figure 178) (both **Entomobryidae**) were the dominant species among these epiphytic mosses.



Figure 178. *Willowsia platani*; *Willowsia mexicana* is among the dominant springtails among epiphytic mosses in Mexico. Photo by Andy Murray, through Creative Commons.

Antarctic Bryophyte Communities

The Antarctic continent is covered with ice except for about 2% of the surface (Seppelt & Ochyra 2008). The vegetation is comprised of lichens, bryophytes, algae, Cyanobacteria, and fungi. **Collembola**, **Diptera**, and mites are the predominant arthropod fauna (Strong 1967; Tilbrook 1967), and the lichens and bryophytes provide a suitable cover (Tilbrook 1973 – Signy Island; Lewis Smith 1996). In the drier areas, the bryophytes are covered with algae and Cyanobacteria (Green & Broady 2001).

Even bryophytes with very different species can have similar trophic levels. Davis (1981) examined two moss communities on Signy Island in the Antarctic. One was a moss turf dominated by *Polytrichum juniperinum* (Figure 179) and *Chorisodontium aciphyllum* (Figure 180-Figure 181). The second was a moss carpet of *Calliergon sarmatosum* (Figure 182), *Calliergidium austrostramineum* (Figure 183), and *Sanionia uncinata* (Figure 184-Figure 185) along with the leafy liverwort *Cephaloziella varians* (Figure 186). The two communities had similar productivity levels, trophic structure, and organic matter transfer efficiencies, but the standing crops of **Collembola** and mites, turnover of mosses, and accumulation of dead matter differed.



Figure 179. *Polytrichum juniperinum*, a turf-former in the Antarctic and home for **Collembola**. Photo by Janice Glime.



Figure 182. *Calliergon sarmentosum*, home for **Collembola** in the Antarctic. Photo by Michael Lüth, with permission.



Figure 180. *Chorisodontium aciphyllum* in Antarctica, a **Collembola** home. Photo from Polar Institute, through Creative Commons.



Figure 183. *Calliergidium austro-stramineum*, home for **Collembola** in the Antarctic. Photo by Bill Malcolm, with permission.

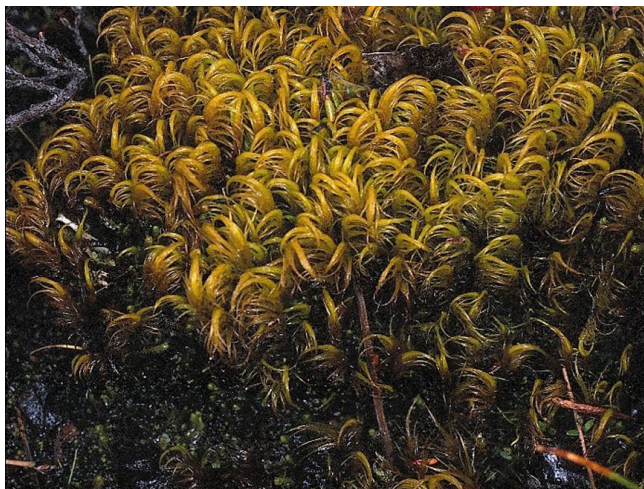


Figure 181. *Chorisodontium aciphyllum*, home for **Collembola** in the Antarctic. Photo by Jan-Peter Frahm, with permission.



Figure 184. *Sanionia uncinata* with grass in Antarctica. *Sanionia uncinata* is a suitable **Collembola** habitat. Photo from Polar Institute, through Creative Commons.



Figure 185. *Sanionia uncinata*, Antarctic home for *Collembola*. Photo by Michael Lüth, with permission.



Figure 186. *Cephaloziella varians* with *Polytrichum*, a *Collembola* habitat in the Antarctic. Photo by Kristian Peters, with permission.

Who Dares to Live Here?

With temperatures reaching extremes within a single day, a long, harsh winter, and elevated UV radiation, it is little wonder that the flora and fauna of the Antarctic are limited. But some *Collembola* (as well as mites and *Diptera*) are relatively common here. Bryophytes serve as important habitats for many of these arthropods, providing cover and protection and ameliorating the microclimate.

On the Schirmacher Oasis, a 25 km long and up to 3 km wide ice-free plateau with more than 100 freshwater lakes on the Antarctic continent, Mitra (1999) reported two families of *Collembola* inhabiting mosses. The springtail *Cryptopygus antarcticus* (Figure 78) is the dominant arthropod in the maritime Antarctic (Tilbrook 1967). Gressitt (1967) reports *Gomphioccephalus hodgsoni* (*Hypogastruridae*; see Figure 60), *Friesea* (*Neanuridae*; Figure 157), and *Parisotoma* (*Isotomidae*; see Figure 187) as common in moss clumps. Block (1982) reported *Friesea grisea*, *Parisotoma octooculata* (see Figure 187), and *Cryptopygus antarcticus* in the *Polytrichum-Chorisodontium* moss turf (Figure 179-Figure 181) of Signy Island, where they had a density of 49,928 individuals per m². In the *Calliergon-Calliergidium-Drepanocladus* moss carpet (Figure 182-Figure 185) *Collembola* averaged 9913 individuals m². *Cryptopygus antarcticus* was present in 99% of the moss turf samples and 100% of the moss carpet samples. This species was

significantly more abundant in *Polytrichum* (Figure 179) than in dead moss or bare peat. But this is not a bryophage – it feeds on unicellular green algae that grow on the mosses (see also Green & Broady 2001).



Figure 187. *Parisotoma notabilis*, a common species among mosses in the maritime Antarctic. Photo by Andy Murray, through Creative Commons.

On Anvers Island of the Antarctic Peninsula, *Cryptopygus antarcticus* (Figure 78) is again abundant in the moss *Dicranum* (*Chorisodontium aciphyllum*?; Figure 180-Figure 181) (Lippert 1971). These live mostly at about 5 cm depth in the moss mat, with few in the first cm. *Polytrichum* (Figure 179) had this same species, but also provided home to *Parisotoma* (*Isotomidae*; Figure 187), *Friesea* (*Neanuridae*; Figure 157), as well as several mite species. And as usual, *C. antarcticus* was the most abundant. This dominant species also occurred in wet *Sanionia uncinata* (Figure 184-Figure 185).

Species are often arranged vertically by temperature and moisture preference (Sømme 1995). These behavioral adaptations permit them to move up or down as the moisture and temperature conditions change on daily and seasonal regimes. For example, *Cryptopygus antarcticus* (Figure 78) occurs mostly in the upper 1.5 cm of moss, preferring the moisture content there. *Friesea woyciechowskii* (*Neanuridae*) is absent in that zone, but is distributed below it down to 9 cm or more. For *F. woyciechowskii*, water content of the moss seems to be of little importance.

Geothermal Areas

For several arthropods in polar regions, the **geothermal** (steam vent) areas provide cozy homes with suitable temperatures. The higher temperatures support a richer vegetation with a longer growing season (Convey & Lewis Smith 2006). These plants, largely bryophytes, support a more diverse and abundant fauna than other areas of Antarctica, including species that are non-native and unknown elsewhere on the continent (Greenslade *et al.* 2012). The bryophytes are restricted by moisture (Kennedy 1993; Convey 2001), and geothermal areas provide them with moisture coming from the warmer air arising from the soil in heated areas. This same moisture is favorable for the *Collembola* (Hogg *et al.* 2006). Greenslade *et al.* (2012) found *Proisotoma minuta* (Figure 188) and *Hypogastrura viatica* (Figure 189-Figure 190), both non-indigenous species, on heated ground where bryophytes dominate. They suggest that the moisture there may be more important than the temperature.



Figure 188. *Proisotoma minuta*, a non-native species that is able to survive among mosses in geothermal areas of Antarctica. Photo by Andy Murray, through Creative Commons.



Figure 189. *Hypogastrura viatica*, an invasive species among mosses in geothermal areas of Antarctica. Photo by Andy Murray, through Creative Commons.



Figure 190. *Hypogastrura viatica* showing its common habit of forming aggregations. Photo by Mick Talbot, through Creative Commons.

Habitat Suitability and Collembolan Adaptations

Water is one of the most important factors in determining the species composition of Antarctic moss-turf communities (Booth & Usher 1984). For example, *Cryptopygus antarcticus* (Figure 78) has an optimum water content, but this species has a relatively wide acceptable moisture range.

Most of the arthropods in the maritime Antarctic are concentrated in the upper layers among vegetation (Tilbrook 1967), including mostly mosses and grasses. The soil and mosses absorb the solar radiation and winter snow insulates, creating temperature regimes that are more suitable for the **Collembola** than elsewhere in the area. Gressitt (1967) found that temperatures in clumps of the moss *Polytrichum* (Figure 179) could exceed the air temperatures by as much as 13°C. Temperatures in mat-forming *Drepanocladus* s.l. (most likely *Sanionia uncinata*; Figure 184-Figure 185) had temperatures closer to ambient air temperatures.

Like so many other invertebrates, the **Collembola** exhibit differences in vertical distribution (Usher & Booth 1984). And it appears that the Collembolans use the mosses to survive winter in the Antarctic. But it is not the protection of the bryophyte cushion cover that saves them from the cold. Rather, they may eat the mosses and gain the ability to survive lower temperatures (Sømme & Block 1982). When fed moss turf homogenate, *Cryptopygus antarcticus* (Isotomidae; Figure 78) from Signy Island, Antarctica, exhibited evidence of efficient nucleators in their moss substrate. When fed purified green algae, a high proportion of low group supercooling points were retained, i.e. it required a lower temperature for tissue freezing to occur, suggesting a lack of nucleators in the algae. In *C. antarcticus* the concentrations of cryoprotective substances increase at -5°C, concurrent with lowering of the mean supercooling point. The primary substances of this cryoprotectant system were **trehalose**, **mannitol**, and **glycerol**.

Collembola can migrate vertically to achieve the best combination of conditions within the mosses. The relationship between the green zone of *Polytrichum* (Figure 179) and the **Collembola** is weak; chemical characteristics seem to be the most important influence on the distribution of the arthropods in the green zone (Booth & Usher 1984). There seems to be no relationship of the arthropod communities with the dead moss zone.

On Signy Island, 78-88% of the **Collembola** were in the top 6 cm of *Polytrichum-Chorisodontium* (Figure 179-Figure 181) turf and 96-99% were in the top 6 cm of the *Calliergon-Calliergidium-Drepanocladus* carpet (Figure 182-Figure 185) (Block 1982). *Cryptopygus antarcticus* (Figure 78) responded to seasonal changes by migrating vertically. In summer it reached as many as 94% of its individuals in the top 3 cm, but in winter this percentage dropped to as low as 48%. Some were as deep as 21 cm, but they rarely went below 6 cm in the moss carpets. The carpets have less extreme temperatures and accumulate more snow than does the turf, ranging 25 to -20°C. The **Collembola** need temperatures of -5 to +5°C to be able to move, and hence to feed. But the moss carpet presents a different problem – it periodically floods, a condition intolerable for the **Collembola** (Kühnelt *et al.* 1976).

Usher and Booth (1986) looked at the relationship of scale in the bryophyte faunal communities. The common *Cryptopygus antarcticus* (Figure 78) demonstrates different patterns at scales of 10 and 60 cm depth in the surface layer of the moss turf. *Friesea grisea* (see Figure

157), on the other hand, occurs deeper – at 5 cm – and has only a single scale of pattern. Their predator, the mite *Gamasellus* (Ologamasidae; Figure 79), is distributed randomly. The moss *Polytrichum* (Figure 179) exhibits moisture trends along transects and at smaller scales, perhaps accounting for the patterns seen in at least some of the *Collembola*.

In contrast to its abundance among mosses, *Cryptopygus antarcticus* (Figure 78) is not desiccation tolerant and is thus absent from the drier rock platform habitat (Hayward *et al.* 2004). Instead, *Friesea grisea* (Neanuridae; see Figure 157) is the only collembolan able to survive there. Nevertheless, *F. grisea* has a stronger preference for 98% relative humidity conditions than does *C. antarcticus*, suggesting that the former species can take advantage of such refuges when available.

Temperatures in the Antarctic summer can vary considerably between day and night. Some of the Antarctic *Collembola* exhibit a bimodal supercooling point (SCP) distribution (Sinclair *et al.* 2003). Mosses may play a slight role in setting the supercooling point. *Desoria klovstadi* (Isotomidae) that was foraging on mosses had high SCPs (froze at higher temperatures), but these shifted to the low group when the springtails were starved for 2-8 hours. They developed even higher SCPs when fed with lichen or algae for five days, compared to those supplied with mosses. *Friesea grisea* (Neanuridae; see Figure 157), on the other hand, had unimodal distribution of SCPs that did not vary between day and night.

Eat and Be Eaten

Suitable food is always a requirement in any habitat. In some cases, food preferences may determine where organisms live. In the Antarctic, food sources can be limiting as few organisms can survive the harsh climate. Furthermore, provision of cryoprotectants can play a role in determining suitable food sources, providing the springtails with cryoprotectants in preparation for winter or for cold events during the growing season.

Gressitt (1967) found that many *Collembola* eat fungal hyphae and lichens in the Antarctic. *Friesea* (Figure 157) lays eggs among the mosses, suggesting that the young probably find their food among the mosses, most likely eating fungal mycelia.

But larger organisms among the bryophytes also need to eat, and for the carnivores, these springtail aggregations (Figure 190) may be an ideal food source. On the Antarctic Peninsula of Antarctica, predators on *Collembola* include the mites *Rhagidia* (Rhagidiidae) and *Cyrtolaelaps* (Ologamasidae) (Strong 1967). Strong considers the live mosses to provide little nourishment for insects and mites, serving mostly as a site of shelter. Nevertheless, the mosses provide a suitable environment for other sources of food, including fungi and algae, for the *Collembola* (Figure 191). These springtails typically spend the winter in the same habitat, probably enjoying at least some insulation among the moss cushions while having adequate moisture.



Figure 191. These Antarctic *Collembola* are common on this *Bryum subrotundifolium*. Photo courtesy of Catherine Beard.

Glacier Mice – Moss Balls

One unusual habitat for arthropods is among "glacier mice." These are actually unattached moss balls that form from wind-blown mosses on the glaciers. Coulson and Midgley (2012) explored this unusual habitat on glaciers in Iceland. In this case, the moss was a species of *Racomitrium* (Figure 65-Figure 66), a common genus in Iceland. The 8-10 cm balls always contained invertebrates and housed two species of *Collembola*. *Pseudisotoma sensibilis* (Isotomidae; Figure 141) numbered 12-73 individuals per ball, with *Desoria olivacea* (Isotomidae; Figure 192) comprising far fewer inhabitants. Tardigrades numbered approximately 200 while nematodes numbered near 1000. Surprisingly, there were no mites or arachnids and no annelids.



Figure 192. *Desoria olivacea*, a springtail that can be found in glacial moss balls. Photo by Andy Murray, through Creative Commons.

Pollution

Air pollution can be harmful not only to bryophytes, but also to the fauna within, including *Collembola* (Steiner 1995). Species richness decreases as a function of increased pollution. This is especially true for mites, possibly giving the springtails a small advantage if their predators diminish in numbers. Alterations in relative humidity, substrate type, and pH can have further influence on the species richness. Nevertheless, the arthropods are less sensitive than are nematodes and tardigrades.

The subalpine mosses *Plagiobryum zierii* (Figure 193) and *Saelania glaucescens* (Figure 194) near a busy road in the Bükk Mountains of Hungary are protected species there, but they are subject to pollution from the traffic on the road (Varga 1992). They exhibit a higher lead level and poorer fauna, including *Collembola*, than mosses from an unpolluted site.



Figure 193. *Plagiobryum zierii*, a moss that houses *Collembola* in the subalpine. Photo by Michael Lüth, with permission.



Figure 194. *Saelania glaucescens*, a moss that houses *Collembola* in the subalpine zone. Photo by Michael Lüth, with permission.

Summary

Collembola were once considered insects but are now considered a subclass instead of an order. Most species spring by a **furcula**, a structure that is absent among some of the epiphyte dwellers. These springtails most likely existed before bryophytes did and moved to inhabit them later. They are sensitive to moisture and use bryophytes to maintain it. They eat algae, detritus, fungi, and slime molds among the bryophytes, and occasionally the bryophytes themselves, depending on the springtail species. Some are parthenogenetic and others deposit the sperm in a spermatophore that the female places into her reproductive tract. Their

dispersal is slow and traversing bare rock or other non-vegetated areas brings the risk of desiccation. Bryophytes can provide safe channels for migration; *Collembola* are among the first arthropods to colonize mosses.

Bryophytes provide cover, feeding sites, and egg-laying sites. Some *Collembola* are important in transferring sperm from male to female mosses. The bryophytes are moist and may help in lowering the supercooling point and protect the *Collembola* from freezing damage when the gut is empty. Vertical migration in the bryophyte mat can also help them find the best temperature and moisture where they can aggregate, further reducing water loss. Bryophytes provide safe sites against predators, especially spiders and mites, but also some salamanders. Few true *bryobionts* exist, one being *Hymaphorura dentifera*. The dominant families seem to be *Isotomidae*, *Hypogastruridae*, and *Entomobryidae* as well as the spherical springtails (*Symphyleona*).

The *Collembola* are adapted by small size and pigmentation where they live exposed to light. Those living among bryophytes on tree bark often have short furculas, dark color, stocky body, few eyes, small size, and limited movement. Sampling is usually done by pit traps or collecting the bryophytes. Bryophytes can be placed in funnels with a heat gradient that causes the *Collembola* to drop into a preservative or by using a flotation technique. But many won't leave the bryophytes to be sampled by these techniques. The springtails may number hundreds of thousands in a square meter, especially in Arctic and Antarctic regions.

Bogs seem to be important for some species, with water content being a controlling factor. Species living among epiphytic bryophytes are often the same as those among bryophytes on boulders. In forests they are usually in moist sites such as log or soil mosses, especially in wetter areas. In the Antarctic, *Cryptopygus antarcticus* is by far the most abundant, often reaching 95-100% of the springtail community among bryophytes. Some live in mobile homes known as glacier mice – moss balls on glaciers.

Acknowledgments

I appreciate the help of Richard Snider who, many years ago, helped me identify the *Collembola* in my bryophyte collections. He and other entomologists introduced me to the willingness of experts to help with identifications. Thank you to Sarah Lloyd for sharing her interesting finds with me. Rod Seppelt and Catherine Beard kindly offered their Antarctic pictures and provided me with a sense of the habitat. My sister, Eileen Dumire, proofread an earlier version of the sub-chapter and made suggestions to improve clarity for beginners.

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CHAPTER 12-3

TERRESTRIAL INSECTS:

HEMIMETABOLA – ODONATA

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CHAPTER 12-3

TERRESTRIAL INSECTS: HEMIMETABOLA – ODONATA



Figure 1. *Uropetala chiltoni* naiad emerging from burrow hidden among leafy liverworts. Photo by Rod Morris, with permission.

ODONATA – DRAGONFLIES AND DAMSELFLIES

Most of the **Odonata** are discussed in Chapter 11-5 with the aquatic insects, but some are terrestrial even as naiads and are appropriately discussed here. The **Odonata** are **hemimetabolous**. That is, they have an incomplete life cycle, one in which the immature animal resembles the adult and has no **larval** or **pupal** stage. Rather, the **naiad** (Figure 2), or **nymph**, develops directly into the adult. Naiads are the aquatic nymphs and thus the term doesn't apply in the strict sense to the terrestrial species. The large eyes (Figure 3) and scoop mouth enable these to be formidable carnivores. The odonate wings develop within the wingpads of the nymphs/naiads and expand when the last nymphal skin is shed. These adults must climb upward and pump fluids into the wing veins to expand them. They are vulnerable at this time because they are not yet ready to fly. Refer to Chapter 11-5 for more detailed discussion of this order of insects.



Figure 2. *Aeshna interrupta* naiad, a species whose naiads are not tolerant to drying. Photo by Donald S. Chandler <www.discoverlife.org>, with permission.



Figure 3. *Sympetrum striolatum* head showing large eyes. Photo by Anki Engström <www.krypinauren.se>, with permission.

Both dragonflies (**Anisoptera**) and damselflies (**Zygoptera**) have members that spend their nymphal life among bryophytes on land. These habitats provide cover and help the **Odonata** retain moisture. Others deposit eggs among mosses near water bodies where it is easy for nymphs to reach water through flooding, crawling, and or dropping into the water.

Biology

The **Odonata** are voracious carnivores and are preyed upon as naiads primarily by fish in their aquatic habitat. On land, this larger predator is absent and birds and amphibians are the most likely predators for both nymphs and adults. But their larger danger as nymphs on land is drying out. Hence, enter the bryophytes.

Paulson and Buden (2003) collected **Odonata** on the Eastern Caroline Islands of Micronesia, bagging 448 specimens. These comprised 15 species, six of which were damselflies in the genus *Teinobasis* (**Coenagrionidae**), a genus with known bryophyte dwellers. *Teinobasis ponapensis* (see Figure 4) was taken only in areas with moss and fern cover, suggesting that even adults can find some advantage in association with bryophytes. On that island they found that body size increases with an increase in altitude.



Figure 4. *Teinobasis sjupp* adult. *Teinobasis ponapensis* is a species whose adults live only in areas with mosses and ferns. Photo by V. J. Kalkman, through Creative Commons.

Terrestrial Naiads

Terrestrial nymphs are known for some families of **Odonata**, and moist forests, especially montane rainforests, seem especially suited for the moisture needs of this

"aquatic" insect. Oppel (2005) reported on the **Odonata** of Papua New Guinea, where its 61 species were predominately among the **Zygoptera** (damselflies). Most were associated with moving or standing water, but one group was associated with temporary water sources or forest sites with high non-seasonal rainfall and high humidity. No **Anisoptera** (dragonflies) were among these terrestrial associations. Surprisingly to me, there was a negative correlation between the **Odonata** and mosses among this group.

Nevertheless, bryophytes can play an important role for some species. In Australia, the nymphs of *Pseudocordulia* (**Corduliidae** or **Pseudocorduliidae** – dragonflies) occur among leaf litter in the rain forests and moss forests of northern Queensland far from water (Watson 1982). Thus it should be no surprise to find **Odonata** nymphs among mosses as well, and many records of **Odonata** in litter may include mosses – soil biologists typically include mosses as part of the litter layer. *Austropetalia patricia* and *A. tonyana* (Figure 5-Figure 6) (**Austropetaliidae** – dragonflies) nymphs live on logs or among mosses in waterfalls and on streambanks (Theischinger & Hawking 2006). These alpine species are often rare due to limited habitat.



Figure 5. *Austropetalia tonyana* adult, a species whose nymphs can live among terrestrial mosses. Photo by Reiner Richter, with permission.



Figure 6. *Austropetalia tonyana* habitat where nymphs live above water among mosses. Photo by Reiner Richter, with permission.

Some **Odonata** use water-filled tree holes for their naiads. It is interesting that the rare damselfly naiads of *Podopteryx selysi* (**Megapodagrionidae** – damselflies; Figure 7) occur in such tree holes in the rainforest of north Queensland, Australia, but Watson and Dyce (1978) surmise that this species must lay its eggs on moss-covered stones or bushes. They apparently base this on finding the adults clinging to shrubs along paths and to the use of mosses for egg laying by other rainforest **Odonata**.



Figure 7. *Podopteryx selysi* adult, a species that may lay its eggs among mosses near tree holes in the rainforest. Photo by Reiner Richter, with permission.

In the Northern Sierra Madre Natural Park, Philippines, *Risicnemis elegans* (**Cordulegasteridae** – dragonflies; Figure 8) nymphs occur in shaded seepages and on the moist forest floor several meters from water (Villanueva *et al.* 2009). In these locations, the females lay eggs on moist mosses.



Figure 8. *Risicnemis cf. elegans*, a species that lays its eggs on moist mosses. Photo through Project Noah, with permission.

The genus *Gomphomacromia* (**Corduliidae** – dragonflies) also has at least semi-terrestrial nymphs. Von Ellenrieder and Garrison (2005) found nymphs under stones about 3 m from a moist, rocky area in Chile. Louten *et al.* (1996) found *G. cf. fallax* (Figure 9) on a moist, moss-covered slope along a dirt trail in Pakitza, Peru. That Beckemeyer (2002) found *Gomphomacromia fallax* laying eggs in dripping mosses on a cliffside suggests that nymphs of this species live there as well.



Figure 9. *Gomphomacromia cf. fallax* adult, a species that sometimes lays eggs in dripping mosses. Photo by Roy J. Beckemeyer, with permission.

Bryophytes can be a refuge for aquatic **Odonata** naiads when their habitat dries up. Willey and Eiler (1972) observed this in *Somatochlora semicircularis* (**Corduliidae**; Figure 10) from subalpine pools in Colorado, USA. When their pond dried up, they could be found under rocks, in moss mats, under logs, and at the bases of sedge clumps. This species dries more slowly than the dragonflies *Aeshna interrupta interna* (Figure 2, Figure 11) and *Libellula quadrimaculata* (Figure 12). It takes *S. semicircularis* twice as long to reach the same lethal state of dryness as that experienced by these two less tolerant species. This advantage seems to be incurred by a lower transpiration rate, and further protection is afforded by the early formation of snow pack over the dry pond. The mosses and other substrata are sufficient to protect the naiads from drought until the snow arrives.



Figure 10. *Somatochlora semicircularis* adult; this species has naiads that use wet mosses when its pond dries up. Photo by Belinda Lo through Creative Commons.



Figure 11. *Aeshna interrupta* adult. Photo by Kam's World, through Creative Commons.



Figure 12. *Libellula quadrimaculata* adult, a species with poor desiccation tolerance as a naiad. Photo by Böhringer Friedrich, through Creative Commons.

Donnelly (1990) found damselfly naiads of the dominant Fijian genus *Nesobasis* (Coenagrionidae; Figure 13) near a stream, crawling over wet mosses. As Donnelly cautiously pointed out, these may not be truly terrestrial. Rather, normally aquatic insects often climb above the water level in search of food, or perhaps to avoid excessive flow – or just because they can. In other cases, receding water levels after a rainstorm may leave them above the water surface. There is sufficient moisture for them to maintain hydration until they return to the water. But naiads must leave the water to shed their naiadal skin and emerge as adults, perhaps also explaining this above-water observation.



Figure 13. *Nesobasis* sp., a species whose naiads are known to crawl over wet mosses occasionally. Photo through Creative Commons.

Mosses may aid in the selection of burrowing sites of terrestrial dragonflies. Rod Morris (2010) shows the giant mountain dragonfly (*Uropetala chiltoni*; Figure 1, Figure 14) nymph poking its head out of its burrow in the soil and into a bed of mosses in a small wetland in New Zealand.



Figure 14. *Uropetala chiltoni* nymph emerging from burrow to a bed of mosses. Photo by Rod Morris, with permission.

Emergence

Terrestrial bryophytes can serve as emergence sites where the naiads shed their exoskeleton, leaving it behind as an **exuvia** (Figure 15-Figure 16), to become adults (Needham *et al.* 1901). These researchers found layers of shed exuviae of both *Gomphus exilis* (Figure 17) and *G. spicatus* (Gomphidae – dragonflies; Figure 18-Figure 19) among the mosses on logs at the edge of a pond. Similarly, *Somatochlora elongata* (Corduliidae – dragonflies; Figure 20; see also Figure 21-Figure 22) left exuviae on mosses at the edge of a pond. Soriano and Gutiérrez (1998) found the exuviae of *Oplonaeschna magna* (Aeshnidae – dragonflies; see Figure 23-Figure 24), a new species at the time, clinging to mosses on the vertical rock walls of a canyon in Mexico. These exuviae were 0.80-1.25 m above the water, reaching as much as 3 m on tree trunks and shrubs. Bryophytes are easy to climb, provide moisture, and permit at times a refuge or limited camouflage.



Figure 15. *Lestes* sp. emerging on a reed, leaving behind its shed **exuvia**. Photo by Richard Orr, with permission.



Figure 16. *Tetragoneuria cynosura* emerging. Photo by Richard Orr, with permission.



Figure 17. *Gomphus exilis* adult, a species that uses mosses as emergence sites. Photo by Richard Orr, with permission.



Figure 18. *Gomphus spicatus* naiad, a species known to emerge among mosses on logs near water. Photo by Donald S. Chandler, with permission.



Figure 19. *Gomphus spicatus* male adult. Photo by Richard Orr, with permission.



Figure 20. *Somatochlora elongata* male, a species that emerges on mosses. Photo by Denis A. Doucet, with permission.



Figure 21. *Somatochlora tenebrosa* exuvia, shed here on a moss-covered surface. Photo by Richard Orr, with permission.



Figure 22. *Somatochlora tenebrosa* male adult. Photo by Richard Orr, with permission.



Figure 23. *Oplonaeschna armata* adult, a species that uses mosses for emergence. Photo by Jerry Oldenettel, through Creative Commons.



Figure 24. *Oplonaeschna armata* adult ovipositing in mud. Photo by Jerry Oldenettel, through Creative Commons.

Once the dragonflies shed their naiad exoskeleton, the newly emerged adults must climb or hang in place to spread their wings and pump fluids into those veins (Figure 25). I have watched them climb *Eleocharis* to the top, then climb down and climb another, apparently in search of a minimum height where they finally stayed to emerge. In the Huron Mountains of the Upper Peninsula of Michigan, USA, Kielb *et al.* (1996) observed emergent adults of *Stylogomphus albistylus* (Gomphidae – dragonflies; Figure 26) resting on vertical moss-covered rock faces below waterfalls and on nearby trees.

But not all naiads must assume a vertical position to emerge. *Aeshna juncea* (Figure 28-Figure 29) is able to emerge in a horizontal position on *Sphagnum* (Figure 33) (Maitland 1967).



Figure 25. *Anax junius* on *Eleocharis*, where it is has emerged and is preparing to pump fluids into its wings. Photo by Richard Orr, with permission.



Figure 26. *Stylogomphus albistylus* adult, a species that can emerge on vertical rocks covered by mosses. Photo by Richard Orr, with permission.

Perching and Mating

Although the adults are strong fliers, even they must rest at times. For some, mosses seem to be suitable sites (Figure 27), especially in bogs.



Figure 27. *Celtithemis martha tenera* adult resting on male *Polytrichum*. Photo by Richard Orr, with permission.



Figure 28. *Aeshna juncea* naiad with mosses. Photo by Tim Faasen, with permission.



Figure 29. *Aeshna juncea* in flight. Photo by Jens Nielsen Buurgaard, through Creative Commons.

Adults no longer must live in the water and these strong fliers (Figure 29) can often stray far from their naiadal home. For example, members of *Enallagma* (Figure 30) occasionally travel up to 1 km to a different lake to lay eggs (McPeck 1989). But some exhibit mass annual migrations of a much greater distance, a phenomenon noted as early as 1494 in Europe! (Calvert 1893; May 2013). Matthews (2007) used a hydrogen isotope ratio to track migrations of *Anax junius* from Ontario, Canada, to Veracruz, Mexico in late August to

October. Matthews found that about 90% of the individuals moved southward for a mean distance of ca. 900 km, but exhibited a maximum of nearly 3,000 km. During these migrations they often stop to feed, mate, or lay eggs (Russell *et al.* 1998; Wikelski *et al.* 2006; Matthews 2007). Distance travelled depends on species, sex, age, size, and weather (Angelibert & Giani 2003). They may seek a particular habitat as adults that differs from that adjacent to the water, at least in part to avoid predators such as frogs while mating.



Figure 30. *Enallagma divagans* mating pair. Photo by Richard Orr, with permission.

In New Guinea, the genus *Lathanusa* (Libellulidae – dragonflies) is restricted to high elevations above 1350 m (Lieftinck 1955). *Lathanusa lamberti* occurs in the moss forests at 2800-2850 m, the highest known elevation of any Libellulidae in New Guinea. The mosses there may simply like the same atmospheric conditions and habitat as the odonates, but the presence of the moss could also provide some aspect of the habitat that makes it more suitable for these dragonflies. One such possibility could be as sites for egg deposition and nymphal development.

Beckemeyer (2002) found *Gomphomacromia fallax* (Figure 9) adult males perching on mosses beneath cliff sides where there was dripping water. Females were flitting about nearby and flicking their abdomens to deposit eggs toward the mosses. A discussion of perching and mating in bogs (Figure 31) is in Chapter 11-5 of this volume.



Figure 31. The dragonfly *Sympetrum danae* rests here on the moss *Polytrichum*. It prefers *Sphagnum* peatlands for mating. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.

Oviposition

If a nymph is terrestrial, then the eggs must also be laid in a terrestrial habitat, although the converse is not necessarily true. (Hatched naiads could drop into the water from overhanging plants or crawl to the water.) Most aquatic Odonata are not moss inhabitants, but the female may nevertheless lay her eggs among mosses, providing them with a secure and hidden location for development. Such is the case for *Austroargiolestes chrysoides* (Figure 32) in Australian rainforest streams (Theischinger & Hawking 2006).

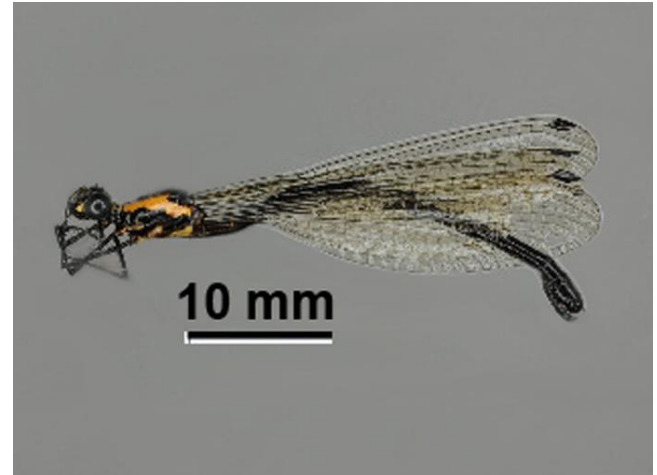


Figure 32. *Austroargiolestes chrysoides* adult, a species that lays its eggs among mosses in Australian rainforest streams. Photo from Biodiversity Centre, through Creative Commons.

Michiels and Dhondt (1990) described the selection of the oviposition site by the dragonfly *Sympetrum danae* (Libellulidae; Figure 33). This species deposits its eggs among *Sphagnum* (Figure 33), but given the choice of *Sphagnum* and *Mnium hornum* (Figure 34-Figure 35), some females will deposit eggs in the latter as well. Michiels and Dhondt attempt to explain the choice of these mosses, considering them to have similar form but distinctly different odors, at least to humans. They thus eliminate odors as determining the choice and consider moss form to be a more likely determining factor. They derived a list of advantages for depositing eggs among *Sphagnum*, based on a number of literature references:

1. Wet *Sphagnum* prevents summer drying of eggs and is likely to be submerged in the spring when eggs hatch and naiads develop.
2. Acid water associated with *Sphagnum* has fewer fish and other predator species.
3. Conditions are optimal for mycobacteria that feed Cladocera that in turn feed naiad Odonata.
4. *Sympetrum danae* (Figure 33) naiads are sprawling and need support and shelter found among *Sphagnum* (Figure 33).



Figure 33. *Sympetrum danae* male on *Sphagnum*, a suitable egg deposition site. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.



Figure 34. *Mnium hornum* hummock, giving a superficial similarity to *Sphagnum*. Photo by Michael Lüth, with permission.



Figure 35. *Mnium hornum* up close, showing that it is quite different from *Sphagnum*. Photo by Bob Klips, with permission.

These advantages would not be present in the terrestrial moss *Mnium hornum* (Figure 34-Figure 35), so the choice of *Sphagnum* for egg deposition is also dependent on its availability in the proximal habitat to that of the naiads. Nevertheless, mosses near water bodies and in rain forests do afford more limited protection from drying. One must wonder how the terrestrial nymphs are adapted for obtaining prey. The large jaws and watch and

wait behavior should still work on land, but the prey items will be different.

Egg-laying among bryophytes has been observed for a long time. Lucas (1900) noted that *Aeshna caerulea* (Aeshnidae – dragonfly) occurred on "moss-hags" around peaty tarns and laid its eggs in wet, mossy ground. A female *Aeshna juncea* (Figure 36) on the Brooks Peninsula of Vancouver Island, Canada, oviposited into the wet mosses clinging to a vertical rock surface at the edge of a drying pool (Cannings & Cannings 1983).

Wang (2000, in Reels & Dow 2006) found that *Bayadera brevicauda brevicauda* (Euphaeidae – damselflies; Figure 37) from Taiwan uses moss-covered stones or fallen leaves, often at some distance from water, as oviposition sites.

In Hawaii, the seepage damselfly *Megalagrion hawaiiense* (Coenagrionidae; Figure 38) deposits her eggs in dripping moss banks (Williams 1936). These damselflies are territorial (Moore 1983) and males guard the females while they lay eggs (Williams 1936; Polhemus 1994). The eggs hatch in about ten days.



Figure 36. *Aeshna juncea* ovipositing in *Polytrichum*. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.



Figure 37. *Bayadera brevicauda*, a species that uses moss-covered stones away from water for oviposition. Photo by Cao Heihua, through Creative Commons.



Figure 38. *Megalagrion hawaiiense*, a species that lays its eggs in dripping moss banks. Photo by Karl Magnacca, with permission.

The heaviest of all dragonflies, females of *Tetracanthagyna plagiata* (Aeshnidae; Figure 39-Figure 40), seem to prefer soft substrates (Leong & Tay 2009). One such substrate is decaying logs kept moist and soft by moss cover. Leong and Tay observed this behavior on a log next to a stream in Singapore.



Figure 39. *Tetracanthagyna plagiata* (dragonfly; Aeshnidae) adult in Malaysia. This is the heaviest of the dragonflies. Photo by Keith Wilson, through Creative Commons.

Matushkina and Klass (2011) suggest that the ovipositor of female *Phenes raptor* (Petaluridae; Figure 41) is particularly adapted for the substrate where the eggs are to be laid. This ovipositor (Figure 42) has numerous sensilla of different shapes and Matushkina and Klass suggest these may be able to detect suitable places for depositing eggs. These females choose loose substrata, including mosses, grass roots, and decaying plant matter. The ovipositor also lacks serration and the interlocking mechanism that connects the first two valves medially is reduced, both adaptations they suggest to relate to depositing eggs within soft substrata, including mosses.



Figure 40. *Tetracanthagyna plagiata* showing oviposition into soft wood. Photo by Marcus Ng, with permission.



Figure 41. *Phenes raptor* ovipositing into the soft end tissue of log. Mosses help to keep logs moist so they become soft. Photo by Eric LoPresti, with permission.



Figure 42. *Phenes raptor* female showing ovipositor. Photo by Eric LoPresti, with permission.

It would be interesting to see if the **Odonata** have preferences for growth forms of mosses. Dense cushions would seem appropriate for those adapted to a soft but solid substrate. Others that drop or "throw" the eggs to the substrate may prefer loose, thick mats, or at least be able to use them. If such correlations exist, the structure of the ovipositor may tell us the kinds of mosses or liverworts they would prefer.

Sampling

These nymphs are worth bringing home live for a closer look, but bring some smaller food items for observations of the interesting feeding. Keep them separate until you are ready to watch! Lucas (1900) suggests carrying the live specimens home in wet moss to avoid the jostling they would get in a jar. They can live this way for several hours to several days. Winstanley *et al.* (1981) were able to keep nymphs of *Uropetala carovei carovei* (**Petaluridae**; Figure 43) from New Zealand alive and rear them through emergence to adults by filling 2-liter containers with leaf mold, moss, and water.



Figure 43. *Uropetala carovei*, a species that can be reared using mosses, leaf mold, and water. Photo by Geoff Tutty, through Creative Commons.

Collection of terrestrial nymphs that live among bryophytes is a matter of collecting the bryophytes. Some may be collected by using traps, but small ones may not leave the bryophyte. Adults are usually collected with insect nets.

Life in a Thallus

Some of the **Odonata** use bryophytes as food for larvae and pupae, providing a safe, moist habitat for their survival in semiterrestrial habitats. For the dragonfly *Epiophlebia superstes* (**Epiophlebiidae**; Figure 44), an **endemic** (restricted to certain area or country) in Japan (Asahina & Eda 1982; Inoue 1983; Tabaru 1984), it appears that bryophytes also provide egg-laying substrata. This dragonfly is often confused with damselflies because

its hind wings are nearly equal to the forewings and it folds its wings over its back at rest like damselflies do. Furthermore, it lacks the jet propulsion typical of dragonflies but absent in damselflies (Tabaru 1984). But it has apparently branched from a dragonfly, then become separated from them when the Himalayas uplifted. Normally the adult lays her eggs in vegetation alongside a waterfall (Asahina & Sugimura 1981). However, in the absence of any nearby tracheophytes, females in locations in Nakamura, Kochi Prefecture, Japan, used bryophytes on the nearby rocks. The eggs were injected into the thallose tissues of the thallose liverworts *Dumortiera hirsuta* (Figure 45), *Conocephalum* (Figure 46), and *Pellia* (Figure 48). In China, *Epiophlebia diana* selects tracheophytes, and Carle (2012) considers the preferred plants of *E. superstes* there to be tracheophytes as well as the liverworts *Dumortiera*, *Conocephalum*, and *Pellia* (Asahina 1934, 1950; Asahina & Eda 1958, 1982; Asahina & Sugimura 1981; Tamiya & Miyakawa 1984; Tokunaga & Odagaki 1939).

In fact, it appears that the dragonfly *Epiophlebia superstes* (Figure 44) actually prefers the liverworts (Asahina & Eda 1958, 1982) for oviposition. Males stake out a "territory" over a patch of *Conocephalum conicum* (Figure 46), despite the presence of the usual tracheophyte egg depositories of *Petasites japonica* and *Eutrema wasabi*. Subsequently the female deposits her eggs in the tissues of this thallose liverwort (Figure 47). Upon dissection Asahina and Eda discovered that the eggs were precisely deposited in the air chambers of the thallus. Further egg deposits are also made into another thallose liverwort, *Pellia endiviifolia* (Figure 48). Because the liverwort thallus has an irregular shape compared to the symmetry of the tracheophyte leaves, the female has to keep changing her position relative to the surface, resulting in some of the eggs being laid in nearby tracheophytes.



Figure 44. *Epiophlebia superstes* (**Epiophlebiidae**) adult, a dragonfly that lays its eggs in thallose liverworts. Photo through Creative Commons.



Figure 45. *Dumortiera hirsuta*, a thallose liverwort that houses eggs injected into it by the dragonfly *Epiophlebia superstes*. Photo by Li Zhang, with permission.



Figure 46. *Conocephalum conicum* thallus, species where *Epiophlebia superstes* deposits its eggs. Photo by Li Zhang, with permission.

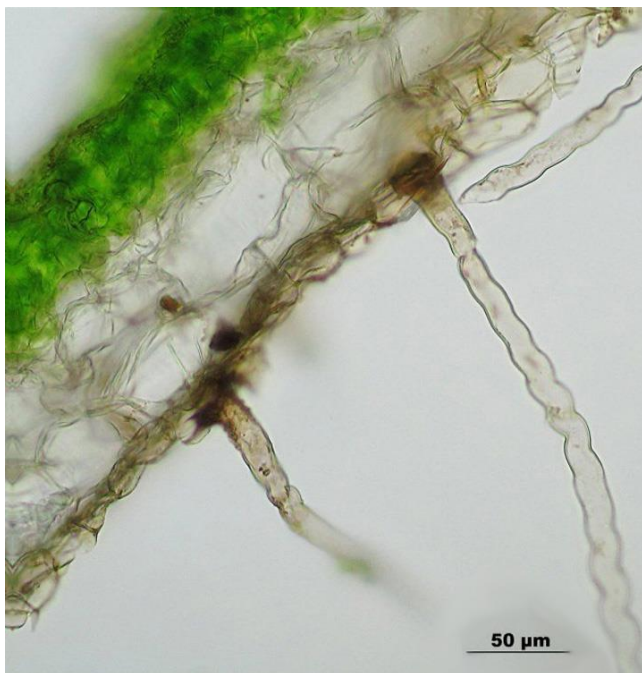


Figure 47. *Conocephalum conicum* thallus cross section showing chambering where nymphs of *Epiophlebia superstes* are able to live. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 48. *Pellia endiviifolia*, site of egg deposition for the dragonfly *Epiophlebia superstes*. Photo by Michael Lüth, with permission.

The ovipositor leaves a small "scar" on the liverwort thallus and the young nymphs later hatch through this hole. These holes permitted the researcher to identify thalli containing eggs and to count them. One thallus had 175 eggs! Others had lesser numbers of 24, 51, and 100. Development of the nymphs to become adults requires 5-8 years, perhaps setting the record for **Odonata** (Tabaru 1984). Use of the liverworts seems to vary between locations, with females in some areas seemingly avoiding the liverworts despite their suitable availability.

Asahina and Eda (1982) suggest that the related *Epiophlebia laidlawi* (**Epiophlebiidae**; Figure 49), a relict species from the Himalayas, might also use bryophytes for egg-laying. Now one can find in Wikipedia the statement that bryophytes are the preferred egg-laying substrate for that species, citing information from Silby (2001). At these high altitudes, mostly above 2000 m, the nymphs can take up to six years to develop before they emerge as adults.

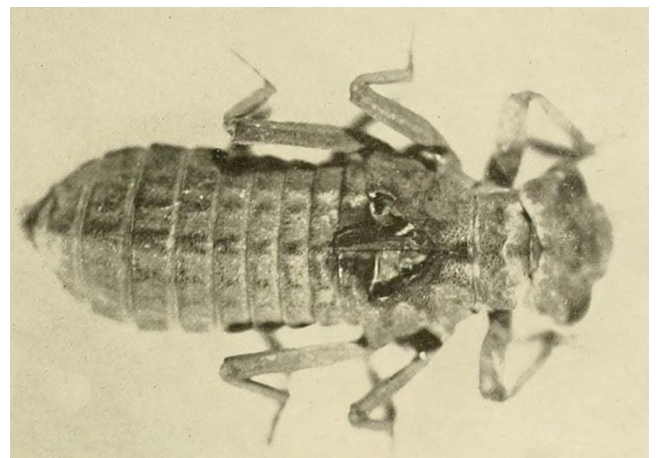


Figure 49. *Epiophlebia laidlawi*, dragonfly nymph that hatches from eggs laid in thallose liverworts. Photo by Shyamal, through Creative Commons.

It appears that *Epiophlebia* (Figure 44, Figure 49), which has only four species (Wikipedia 2007) and these are restricted to Asia, may not be the only odonate that uses a bryophyte thallus for oviposition (Villareal 2009). It's not

water, but it offers similar protection from desiccation – what better place than within the tissues of a plant that is seldom eaten? In this case, the nymphs were damselflies (**Zygoptera**; Figure 50-Figure 55), but their identity remains unknown. Although *Nothoceros aenigmaticus* (Figure 53) is not a true liverwort, but rather is a hornwort, its thalloid structure is similar to that of liverworts. This species is endemic to the southern Appalachian Mountains, USA, where, sadly, it is threatened to extinction resulting from a plague of hemlock woolly adelgids (*Adelges tsugae* – Hemiptera) on the hemlocks (*Tsuga canadensis*) that make its environment suitable for the hornworts (Jacobs 2005; Hyatt 2006).



Figure 50. Young damselfly from within the thallus of a hornwort. Photo courtesy of Juan Carlos Villareal.



Figure 51. Anal gills and abdomen of a young damselfly from within the thallus of a hornwort. Photo courtesy of Juan Carlos Villareal.



Figure 52. Young damselfly from within the thallus of a hornwort. Photo courtesy of Juan Carlos Villareal.

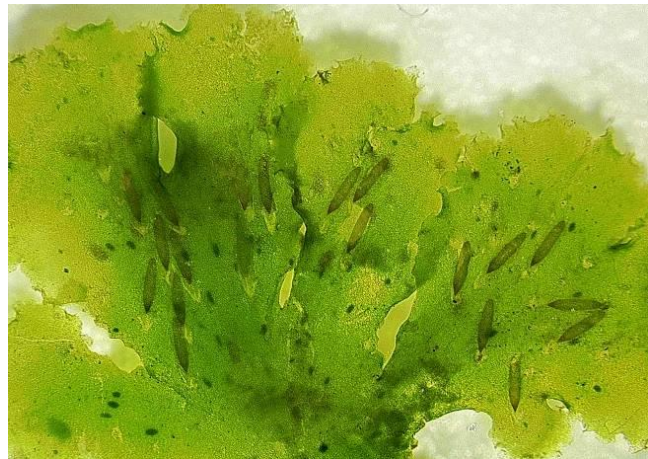


Figure 53. *Nothoceros aenigmaticus* thallus, a hornwort, with eggs that are probably those of a dragonfly or damselfly. Note that the small dark-green patches are *Nostoc* symbionts (blue-green bacteria that live in partnership with the hornwort, contributing converted atmospheric nitrogen). Dragonfly identification is by K. Tennessen. Photo courtesy of Juan Carlos Villareal.



Figure 54. Damselfly egg cases in *Nothoceros aenigmaticus*. Photo courtesy of Chris Cargill.



Figure 55. Damselfly egg case from *Nothoceros aenigmaticus*. Photo courtesy of Chris Cargill.

Juan Carlos Villareal (pers. comm. 23 December 2008) made a similar find in Mexican populations where the developing larvae were leaf miners on the thallus. The damselflies, identified by Ken Tennessen, were in the *Coenagrionidae*, possibly the genus *Argia* (Figure 56).



Figure 56. *Argia tibialis* adult, member of a genus whose nymphs may be one of those that live in hornwort thalli. Photo by Richard Orr, with permission.

I could find no observations on feeding by these thallus dwellers. How long do they remain in the thallus? What do they eat while they are there? This order of insects is highly adapted to be carnivorous. The chances that they find animal food items within the thallus seem slim.

Summary

The **Odonata** are predominately aquatic in the immature stage, but some nymphs are terrestrial, and some of these use bryophytes to protect themselves and to maintain moisture. These carnivores can find food among the bryophytes, including spiders, while hiding from their own predators – mostly amphibians and birds.

Bryophytes provide a good site for egg laying, and even aquatic species may lay eggs on streamside or poolside bryophytes. Some naiads may seek bryophytes as their water body dries up. Many more species climb to the banks of streams and lakes to

emerge from their nymphal skins, leaving behind evidence as numerous **exuviae** on the bryophytes. Others use moss hummocks as perching sites.

Live **Odonata** nymphs, including aquatic species, may be kept alive by placing wet moss in the container with them. Adults can be collected with insect nets.

A few **Odonata** actually live within the thalli of liverworts and hornworts. In particular, *Epiophlebia superstes* in Asia lays its eggs in several liverwort species and nymphs develop there. An unidentified damselfly develops within hornwort thalli; others appear to be in the genus *Argia*.

Acknowledgments

Thank you to Bob Marr for reviewing the chapter and providing me with an additional reference. And thank you to the many photographers who made their images available through Creative Commons or gave me permission to use their images.

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CHAPTER 12-4

TERRESTRIAL INSECTS:

HEMIMETABOLA – ORTHOPTEROIDEA

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CHAPTER 12-4

TERRESTRIAL INSECTS:

HEMIMETABOLA - ORTHOPTEROIDEA



Figure 1. **Orthopteran** moss mimic, blending with surrounding bryophytes. Photo courtesy of Matt von Konrat.

The **Orthopteroidea** (Figure 1) comprise a group of insects that used to be in the order **Orthoptera**. The group has recently been split into multiple orders, one of which is still called **Orthoptera**.

ORTHOPTERA – Grasshoppers and Crickets

Most grasshoppers are big, and in fields of tall grasses and **forbs** (non-grass herbaceous plants) they seem to be everywhere (Paranjape *et al.* 1988). But do they inhabit or use bryophytes? And what can bryophytes offer them?

At least some grasshoppers eat mosses (Appelqvist 1997). Uvarov (1977) suggested that the grasshoppers might eat mosses for their water content. But some seem to subsist primarily on mosses (Hochkirch *et al.* 2007). And some have color patterns that hide them well against the patterned moss surface (Figure 2-Figure 3) (Forsman & Appelqvist 1998). Others choose bryophytes for laying eggs (Langmaack 1997), presumably providing them with some protection (concealment) from predators and decreasing the danger of desiccation.



Figure 2. Forest grasshopper of Ecuador with liverwort color patterns on its sides and a moss hanging from its head. It appears that this hopper can help in dispersal. Photo by Arthur Anker, with permission.



Figure 3. Juvenile grasshopper in Ecuador with markings that look like leafy liverworts that are so common on tropical leaves. Photo by Arthur Anker, with permission.

Any increase in niches is likely to increase insect diversity, and bryophytes can play this role for some of the **Orthoptera**. Noting that the grasshopper family **Tetrigidae** (pygmy grasshoppers) included mosses in their diet (Hochkirch *et al.* 2000), Hochkirch *et al.* (2007) experimented with members of this family to determine how **sympatric** (having overlapping geographic distribution) species might co-exist. They used the mosses *Rhytidiadelphus squarrosus* (Figure 4) and soil algae as food sources. *Tetrix ceperoi* (Figure 5) and *T. subulata* (Figure 6), both sometimes moss inhabitants, were cultured together in the lab experiments. *Tetrix ceperoi* exhibited substantial decrease in copulations with its own species when in the presence of *T. subulata*. The males attempted more mating events with females of *T. subulata*, but the females rejected them. Although none of these two-species matings was successful in the lab, they substantially reduced the success of *T. ceperoi* in field experiments. It required much denser populations to have similar depression effects on *T. subulata*. Hochkirch *et al.* (2007) surmised that to prevent such reproductive interference the species may evolve different mating signals or different habitat preferences, spatial patterns, or temporal segregation. Having bryophytes in the habitat provides differences in available niches, including moisture and food item differences (Figure 7).



Figure 4. *Rhytidiadelphus squarrosus*, an acceptable food source for *Tetrix* species. Photo by Michael Lüth, with permission.



Figure 5. Mating grasshoppers, *Tetrix ceperoi*, on the moss *Atrichum subulatum* in the Czech Republic. Holes appear in the leaves where they have been eaten. Research continues on feeding preferences of these insects. Photo by Petr Kočárek, with permission.



Figure 6. *Tetrix subulata* female, a species that eats bryophytes and uses them for perching sites during mating. Photo by Joy Markgraf, with permission.

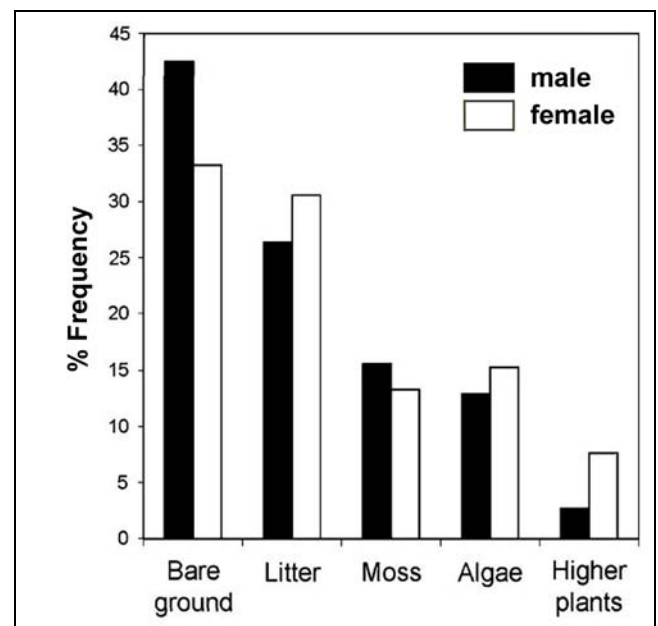


Figure 7. *Tetrix ceperoi* (Figure 5) frequency of perching on moss compared to other perching sites in its habitat. Modified from Hochkirch *et al.* 2007.

Tetrigidae – Pygmy Grasshoppers

The pigmy grasshoppers (Figure 8) are common moss dwellers and moss consumers (Hancock 1902; Chopard 1951; Bastow *et al.* 2002).



Figure 8. This grasshopper appeared to have protonemata cultured on its back. At the very least, it has cryptic coloration that makes it nearly invisible among these mosses – until it jumps! Photo by Janice Glime.

Tetrix

Tetrix granulata in Oregon, USA, lives in shaded meadows with damp mossy ground and short grass (Fulton 1930). Buckell (1921) noted that *Tetrix brunneri* (Figure 9) in the Chilcotin District of British Columbia, Canada, was present only in a small area where it lived among leaf litter and mosses under birch (*Betula*) and willow (*Salix*) surrounding an upland spring. This species occurs as high as 3,300 m among boulders in Colorado, USA (Alexander 1964). But the most widespread of these moss dwellers in North America is *Tetrix subulata* (Figure 6) (Rehn & Grant 1955).



Figure 9. *Tetrix brunneri*, a species that seems to prefer mossy areas. Photo by Lynette Schimming, through Creative Commons.

Tetrix subulata (Figure 6) has the somewhat unusual character of having both **brachypterous** (short-winged) and **macropterous** (large-winged) forms (Lock *et al.* 2006). There is a tradeoff in these insects between dispersal and reproduction, with the short-winged forms reproducing faster and the long-winged ones travelling farther and colonizing new habitats. The long-winged form consumes significantly more energy and exhibits a significantly higher protein content compared to the short-winged form. Carbohydrate and lipid content do not differ. The males have higher protein content and consume more energy than females, providing males with the energy needed to search for females.

Color Morphs – Thermoregulation or Camouflage?

Many grasshoppers exhibit color morphs (Nabours 1929; Rowell 1971; Holst 1986; Forsman 1999, 2000). *Tetrix subulata* is able to exhibit a variety of morphs (Figure 6, Figure 10-Figure 11) even within a single clutch (Forsman 2000). *Tetrix subulata* occurs in damp places on the soil surface where it eats mosses, algae, and humus (Forsman 1999) and is widespread in Europe (Holst 1986). This species exhibits discontinuous color morphs that could affect body temperature or protection from predation (Forsman 1997). Forsman (1997) found that black morphs had up to 49% higher **temperature excess** (difference between ambient and body temperature) compared to white morphs in the same external conditions. Forsman (2000) found that females preferred higher body temperatures than did males. Dark morphs both attain higher temperatures and prefer higher temperatures compared to paler morphs.



Figure 10. *Tetrix subulata* as a dark variant, with somewhat shortened wings. Photo from Biopix, through Creative Commons.



Figure 11. *Tetrix subulata* as a grey variant, with long wings. Photo from Biopix, through Creative Commons.

Gause's Law and Bryophyte Dwellers

When multiple species in the same genus occupy the same area, one must ask what keeps the species from competing – and out-competing (**Gause's Law**)? Gause (1934) described this "law" and experiments to support it in his "Struggle for Existence." This "law" has become known as the **competitive exclusion principle**. Based on many plant experiments, Gause put forth the principle that competition begins due to the reaction when plants are spaced in such a way that the reaction of one affects the response of the other by **limiting** it. He used this base to suggest that animal experiments are needed, demonstrating that when there is growth a number of individuals of a first and a second species will compete for common food. "At a certain moment food will have been consumed, or toxic waste products will have accumulated, and as a result growth of the population will cease. Competition will take place for utilization of a certain **limited** amount of energy." I have emphasized "limited" because this part of Gause's argument is often ignored. If food and space are unlimited or in excess, competitive exclusion need not apply.

Gause built his famous law upon the work of many other ecologists. In his comprehensive treatment of competitive exclusion (Gause's Law), Gause again emphasized the importance of experiment, providing guidance on the types of experiments needed. Levin (1970) presented it somewhat differently: "No stable equilibrium can be attained in an ecological community in which some r of the components are limited by less than r limiting factors. The limiting factors are thus put forward as those aspects of the niche crucial in the determination of whether species can coexist." If each species is limited by an independent combination of predation and resource limitation, it is possible for them to coexist. "If the two have comparable threshold values, which is certainly possible, any equilibrium reached between the two will be highly variable, and no stable equilibrium situation will result."

Here is where proving the competitive exclusion principle gets messy. Two species may co-exist because the environment is constant and advantages for survival may shift as the weather shifts. As a result of this and other problems with the complex relationship, Gause's law has come under close scrutiny, with many researchers providing examples that appear to disprove it. For example, Simberloff (1982) stated that it "has not helped us to understand how nature works. It has generated predictions that are either practically untestable, by virtue of immeasurable parameters or unrealizable assumptions, or trivially true."

Simberloff (1982) recognized the inherent problems with our use of Gause's law and offered an explanation. "When species do compete with one another, effects are usually moderated by other factors (*e.g.*, weather, predators, pathogens) that keep populations below levels at which exclusion would occur, or else each competitor is favored in a different set of times and/or places and this fact combined with normal individual movements keep all species in the system."..."Chance plays a major role in many potentially competitive interactions, and there is good evidence that many species that do compete with one another do so rarely or intermittently, and at most times their population dynamics are governed by other forces."

While this explains why closely related species are able to co-exist, it does not disprove Gause's law.

But in many of the examples that seem to refute Gause's law, the requirement of competition for a limiting resource or being preyed upon by a common predator is often missing because neither population has reached a limiting state for the needed resource. Levin (1970) attempted to improve upon our understanding of the "law" by suggesting three considerations:

1. Eliminate the restriction that all species are resource-limited, a restriction persistent in the literature.
2. The results relate in general to periodic equilibria rather than to constant equilibria.
3. The nature of the proof relates to the crucial question of the behavior of trajectories near the proposed equilibrium, and provides insight into the behavior of the system when there is an insufficient number of limiting factors.

Vance (1978) added further to the explanation of seeming exceptions. He took the position that one means by which two closely related species can co-exist is by having "suitable differences in spatial refuges from the predator, differences in appearance and/or location which induce frequency-dependent predation, and a difference in energy allocation between competitive and predatory defense." Vance concluded that "Gause's Law is just as true when predators are common and important as when they are absent. Most of those prey in nature whose coexistence is known to depend on predation differ in resource use; *i.e.*, these prey appear to partition environmental resources just as is expected of coexisting species in predator-free systems. A large proportion of cases of coexistence of similar species in nature probably results not from resource partitioning alone or from predation alone but from both mechanisms operating simultaneously."

Hanski (1983) carries this argument somewhat farther to include the role of a patchy environment. He concludes that two possible outcomes of regional competition are (1) a decrease in the fraction of habitat patches occupied by the competing species and (2) an increase in the proportion of regionally rare species, some of which may ultimately go extinct. This study has implications for bryophytes as a habitat because of the often patchy nature of their distribution within a habitat. This patchiness can especially affect invertebrate species that have limited dispersal ability.

Caesar *et al.* (2010) examined the application of Gause's Law within the moss-dwelling pygmy grasshopper genus *Tetrix*. According to Gause's Law, if two species are in the same genus, then their niches are likely to be similar, but one might be expected to be better in that niche, out-competing the other. An often overlooked part of this law is the part "if any factor is limiting."

Tetrix subulata (Figure 6) not only differs within the species by differences in color pattern, but also in form, behavior, and physiology (Caesar *et al.* 2010). Caesar and coworkers tested the interactions of these factors, using the moss *Polytrichum* sp. (Figure 12) as food. Individuals climbed the moss to feed and to find the best combination of moisture, light, and temperature. Survival is higher in low density of mothers than in high density. In high

density, the intermediate color morphs survived best, but survival was independent of color diversity at low densities, presumably due to less intense competition. Mixed siblings had higher survival than mixes of non-siblings, suggesting some competitive advantage. The mosses in their natural habitat therefore provided not only food, but permitted the various morphs to find locations suitable to their temperature, moisture, and light needs as well as being the safest place for particular morphs.



Figure 12. *Polytrichum juniperinum*, an acceptable food source for *Tetrix subulata* (Figure 4). Photo by Janice Glime.

To demonstrate the advantages of certain color patterns against predators in grasshoppers, Forsman and Appelqvist (1998) likewise experimented with *Tetrix subulata* (Figure 6). By manipulating color patterns and exposing these pygmy grasshoppers to predation from domestic chickens they could determine prey advantages (Figure 13). They painted some black and others striped. The striped individuals experienced enhanced survival when reaction distance was short and jumping performance was poor, but when the reaction required a long distance jump with high performance, their survival decreased compared to those individuals painted black. The advantage to the multiple color patterns seems to differ with circumstances, resulting in each morph surviving at different times and circumstances. The differences in form, behavior, and physiology make their specific habitat needs differ, hence defining different niches.

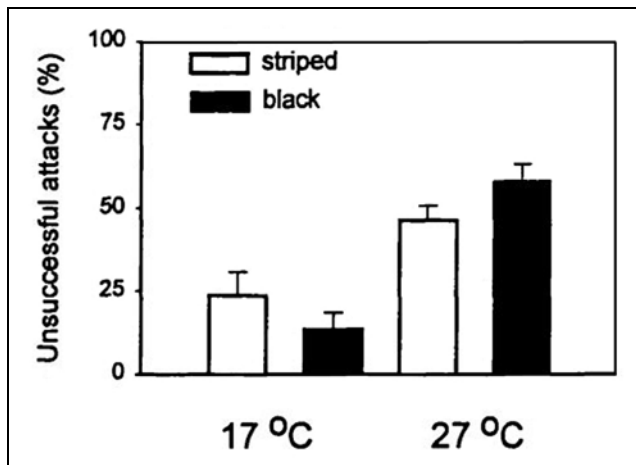


Figure 13. Comparison of *Tetrix subulata* (Figure 6) painted solid black and with stripes to determine the success of chickens preying upon them. Modified from Forsman & Appelqvist 1998.

Discotettix

One species, *Discotettix belzebuth* (= *Tetrix belzebuth*; Figure 14), occurs on mossy tree trunks in the orient (Gen & Rahman n.d.). Rather than having its own cryptic coloration, this species is sometimes bedecked with small plants of bryophytes or algae (I was unable to independently verify this). This enables them to move about undetected while they eat the epiphytic mosses, plants, and detritus on the tree trunks. However, when I searched for a picture to demonstrate this, all representatives were clean. Nevertheless, as you can see in Figure 14, the species is well suited for culturing bryophytes and algae. Its surface has pits where they can cling and become established, and the "thorns" could even help to hold larger bryophytes in place. These same pits and thorns provide disruptive coloration that helps to camouflage the uninhabited ones.



Figure 14. *Discotettix belzebuth* showing the pits in the exoskeleton and the thorns, both of which could aid in establishment of mosses. Photo by Bernard Dupont, through Creative Commons.

Vibration Sites

It seems a bit odd that females rest on mosses, but males do not call from mosses. But there is a very sound reason for that (pun intended!). Males attract females for mating by using vibrations (Kočárek 2010). But for vibrations to be effective, the hopper must be sitting on a suitable substrate, and that is not a moss. Moss, instead, can effectively absorb sounds. Rather, the males sit on bare ground, especially when exhibiting mating behavior. Sand is especially good at transmitting the sound, especially in the hearing range of frequencies between 300 and 400 Hz. And this is a choice mating substrate for males of *Tetrix ceperoi* (Figure 5), despite the increased risk of predation compared to resting on mosses or other vegetation. These vibrations are important in mate recognition in this species (Kočárek 2010).

Elias *et al.* (2004) examined the effectiveness of sound transmission from several substrates in their study of a jumping spider, *Habronattus dosseus*. They found that both rocks and sand quickly attenuated the sound, and that leaf litter was the most effective of the three for sound transmission. Furthermore, there is great variability among rock types. But mosses are more like a sponge, whereas

leaf litter has a large, nearly flat surface that can reflect and direct sound. I would hypothesize that at least some mosses would make effective sound-proofing. And different organisms make sounds with different tones and frequencies, so more study is needed to determine if mosses are good or bad for carrying mating sounds to females of any particular species. (See *Troglophilus neglectus* below.)

Reproduction

Competition isn't the only problem for closely related species living together. Reproductive barriers are likewise needed to maintain species differences. These are especially important for **sympatric** (having overlapping distributions) species such as members of *Tetrix*. To be an effective barrier, there must be an isolating mechanism such as behavior, timing, habitat, morphology, or genetics.

Reproduction is energetically costly. It typically carries a cost in future ability to reproduce, growth, or survival (Forsman 2001). Age is important in determining **clutch** size [number of eggs deposited in single reproductive bout (Godfray 1994)], with **clutch** size decreasing progressively from the first to the third clutch (Forsman 2001). Furthermore, larger first clutches correlate with greater reduction in the size of the next clutch and increase the time to the next clutch.

Reproduction in **ectothermic** (temperature controlled by external environment) animals, including insects, can be modified by body temperature. Temperature in grasshoppers affects both activity levels and physiological performance. Forsman (2001) compared four different color morphs under two different temperatures in *Tetrix subulata* (Figure 6). Different colors absorb different amounts of heat, whereas white reflects it. Warmer females were more likely to oviposit, had earlier first clutches, produced more clutches, and had decreased intervals between clutches compared to females kept at cooler temperatures. Some color morphs produced larger clutches with fewer clutches per unit time. No differences in relative fat content existed between dark and pale individuals in either sun or shade exposures. The data suggest that the differences in color morphs were advantageous in camouflage against predators rather than providing any reproductive advantage.

Forsman (1999) examined reproductive performance in five of these morphs, noting variation in body size and reproductive life-history characteristics. These lived in an area characterized by bare rocks and boulders, with bryophytes [*Ceratodon purpureus* (Figure 15), *Pohlia nutans* (Figure 16-Figure 17), *Polytrichum commune* (Figure 18), *P. juniperinum* (Figure 12)] and some tussock sedges (*Carex* spp.) dominating the vegetation. Season played a major role, with number of females with eggs declining significantly as the season progressed from mid-May (100%) to mid-June (40%). However, seasons had no effect on body size, clutch size, or egg size. On the other hand, morphs differed from each other in body size, and these size differences accounted for differences in clutch and egg size.



Figure 15. *Ceratodon purpureus* on bare rock, home for *Tetrix subulata* in Norway. Photo by Michael Lüth, with permission.



Figure 16. *Pohlia nutans* on expanse of rocks, forming a suitable habitat for *Tetrix subulata*. Photo by Michael Lüth, with permission.



Figure 17. *Pohlia nutans* bare rocks, a suitable habitat for *Tetrix subulata*. Photo by Michael Lüth, with permission.



Figure 18. *Polytrichum commune*, home and probably food for *Tetrix subulata* on rocks. Photo by David T. Holyoak, with permission.

The ratio of egg size to clutch size also differed among the morphs (Forsman 1999). These factors suggest that different color morphs may have different reproductive strategies. The color differences may be responsible for variation in thermoregulation, but they also most likely affect the ability to avoid predation due to cryptic coloration. This implies that predation would differ among the morphs.

Food Consumption

Most grasshoppers are not moss consumers. In Bavaria, all tested grasshoppers except *Tetrix* (Figure 1, Figure 11, Figure 30-Figure 31, Figure 34) rejected mosses, but in 80% of the fecal pellets of *Tetrix* there were leaves of the moss *Hypnum* (Figure 19) and rhizoids and protonemata of a variety of mosses (Verdcourt 1947). Kaufman (1965) likewise found that *Tetrix* sp. fed on mosses, whereas other grasshopper genera in that study fed on **forbs** (non-grass herbaceous flowering plants).



Figure 19. *Hypnum cupressiforme* with young sporophytes. Fecal pellets of *Tetrix* contained leaves from this genus. Photo by Dick Haaksma, with permission.

Tetrix ceperoi (Figure 5) is among the moss consumers in the **Tetrigidae** (Kočárek *et al.* 2008a, b). Kočárek and coworkers examined the gut of 21 males and 18 females of this species. Of the nine mosses [*Amblystegium serpens* (Figure 20), *Barbula convoluta* (Figure 21), *Brachythecium albicans* (Figure 22), *B. velutinum* (Figure 23), *Bryum argenteum* (Figure 24), *B. caespitium* (Figure 25), *Ceratodon purpureus* (Figure 15), *Funaria hygrometrica* (Figure 26), *Plagiomnium undulatum* (Figure 27)] in their sandy habitat, all nine appeared in at least one gut. The most frequent species was *Bryum argenteum* (in 81% of specimens). At least one fragment of moss occurred in 92% of the specimens, *i.e.* only 8% had not consumed mosses. **Tracheophytes** (in this case grasses) were in 20%, all females, and algae were in 25%. The average number of species of mosses per gut was three, but some contained as many as six. Hence, mosses appeared to be the preferred food, but there seemed to be only limited preference for any particular moss.



Figure 20. *Amblystegium serpens*, a species found in the guts of *Tetrix ceperoi* (Figure 5). Photo by David T. Holyoak, with permission.



Figure 21. *Barbula convoluta*, a moss found in the guts of *Tetrix ceperoi* (Figure 5). Photo by Janice Glime.



Figure 22. *Brachythecium albicans*, food for *Tetrix ceperoi* (Figure 5) in Europe. Photo by Michael Lüth, with permission.



Figure 25. *Bryum caespiticiun* males, a species eaten by *Tetrix ceperoi* (Figure 5) in Europe. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 23. *Brachythecium velutinum*, a species eaten by *Tetrix ceperoi* (Figure 5) in Europe. Photo by Michael Lüth, with permission.



Figure 26. *Funaria hygrometrica* young female plants, a species eaten by *Tetrix ceperoi* (Figure 5). Photo by Janice Glime.



Figure 24. *Bryum argenteum*, a species eaten by *Tetrix ceperoi* (Figure 5) in Europe. Photo by Dick Haaksma, with permission.



Figure 27. *Plagiommium undulatum*, a species eaten by *Tetrix ceperoi* (Figure 5). Photo by Michael Lüth, with permission.

Based on the gut analysis of *Tetrix ceperoi* (Figure 5), Kočárek *et al.* (2008c) found its "favorite" to be *Bryum caespiticium* (Figure 25), but this was also the most common moss in the area with a 70% cover (Table 1). Other commonly consumed mosses included *Bryum argenteum* (Figure 24), *Ceratodon purpureus* (Figure 15), and *Barbula convoluta* (Figure 21) and/or *B. unguiculata* (Figure 28). Only the females had grasses in their diet, whereas 94% of females and 86% of males had at least one fragment of moss in the gut. Males had an average of 1.5 moss species and females had an average of 2, whereas the maximum number of species in any gut was 4 (Figure 29). It was not unusual to find three species in the crop at one time. Kočárek and coworkers offer three explanations for this behavior:

1. A mixed diet promotes better health, development, and survival for grasshoppers than a single-food diet (Chapman & Sword 1997).
2. Mosses often contain toxic secondary compounds (Zinsmeister *et al.* 1991; Becker 1994; Markham *et al.* 2006) and must thus be consumed only in small quantities.
3. The multiple species indicate that the grasshoppers move around a lot and are able to sample the high diversity of mosses present in the area.

Table 1. Frequency of moss species in guts of 39 specimens of *Tetrix ceperoi* (Figure 5). From Kočárek *et al.* 2008c.

Moss species	T. ceperoi specimens					
	♂(ind.)	♂(%)	♀(ind.)	♀(%)	Σ(ind.)	Σ(%)
Barbula sp. (B. convoluta or/and B. unguiculata)	6	31.6	6	35.3	12	33.3
Bryum argenteum	4	21.1	6	35.3	10	27.8
Bryum caespiticium	15	78.9	17	100	32	88.9
Ceratodon purpureus	6	31.6	7	41.2	13	36.1



Figure 28. *Barbula unguiculata*, a moss present in the gut of *Tetrix ceperoi* (Figure 5). Photo by Michael Lüth, with permission.

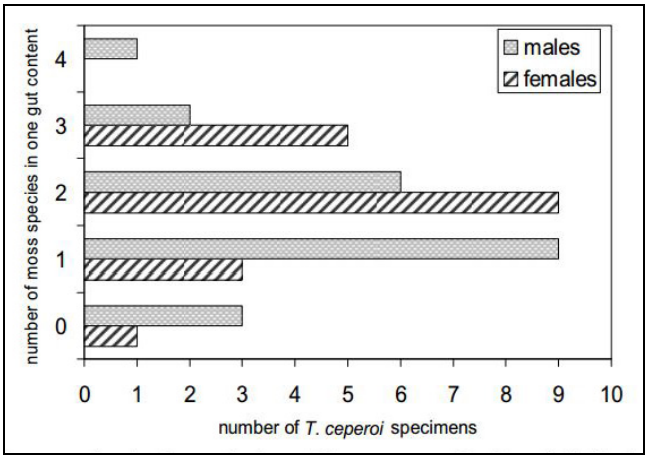


Figure 29. Comparison of mosses in guts of one individual in males and females of *Tetrix ceperoi* (Figure 5). Modified from Kočárek *et al.* 2008c.

Like the aforementioned species of *Tetrix*, *T. bolivari* (Figure 30) eats primarily detritus and mosses (Kočárek 2011). The main mosses consumed in this European study were *Bryum caespiticium* (Figure 25) and *B. argenteum* (Figure 24), but at least eight different species were consumed. Like the other species, these were sensitive to temperature and were most active at warmer temperatures. However, their activities were negatively correlated with humidity, suggesting that mosses were most likely not important in maintaining a humid environment for them.



Figure 30. *Tetrix bolivari*, a moss eater. Photo by Petr Kočárek, with permission.

The moss eater *Tetrix undulata* (Figure 31) eats mosses throughout its life (Hodgson 1963). As it gets older, it is able to eat coarser food. Both young and old eat mosses, humus, lichens, and algae, but adults add **tracheophytes** (lignified vascular plants) such as grass to their diet.



Figure 31. *Tetrix undulata*, a moss eater on moss. Photo by Gilles San Martin, through Creative Commons.

Paranjape (1985) compared the diets of three subfamilies of the **Tetrigidae** and found that not only mosses, but also liverworts and hornworts are consumed (Figure 32).

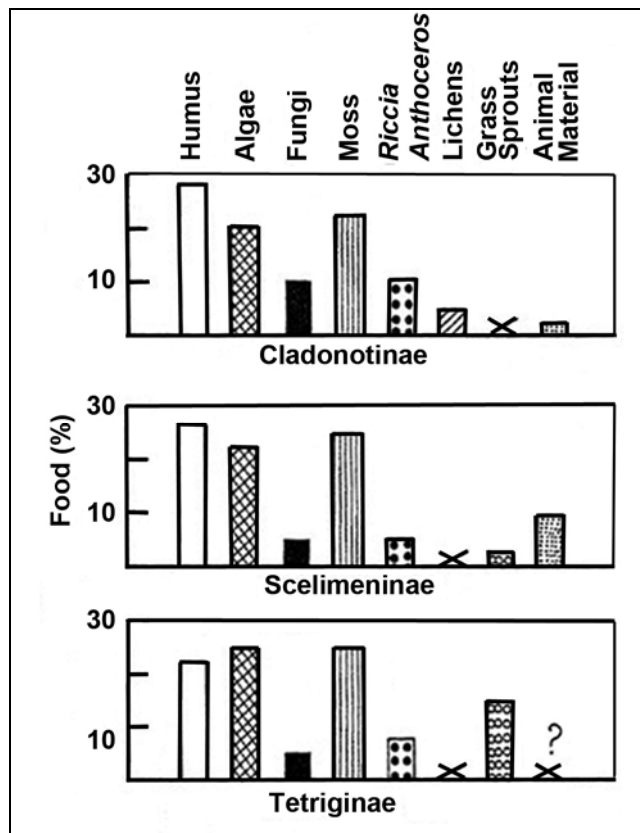


Figure 32. Diet of three subfamilies of **Tetrigidae**. Note that in addition to mosses, they consume the liverwort *Riccia* and the hornwort *Anthoceros*. Modified from Paranjape 1985.

Age and Seasonal Differences

Tough foods require strong mandibles and teeth to break through the lignin in vascular tissue. The strength can change as the nymphs age, so diets can change or expand as the organism matures. Similarly, moss tissues can change with the seasons, becoming tough when dry and soft when wet. These factors can affect the diet of the consumers.

Tetrix tenuicornis specializes on mosses and detritus (Kuřavová & Kočárek 2015). This species maintains its moss diet throughout the growing/feeding season. But the moss species change. More moss species occur in the alimentary tract in spring and summer compared to autumn. Females eat more food than males, and the diet changes with developmental stage. Furthermore, the rate of consuming detritus is affected by ambient temperature (most at 19-21°C), whereas the rate of moss consumption is primarily affected by relative humidity (lowest at 67-72%, highest at 90% or higher). Detrital consumption increases as body size increases.

These groundhoppers do not seem to specialize on any part of the mosses, consuming leaves, gemmae, and rhizoids (but apparently not stems) (Kuřavová & Kočárek 2015). Furthermore, they show little preference for moss species, consuming all of those present except *Pohlia nutans* (Figure 16-Figure 17) and *Bryoerythrophyllum recurvirostrum* (Figure 33). Nevertheless, an individual never contained more than 3 moss species, with the average being 1.9. Moss consumption was considerably less than that of detritus, with one population having 12% moss in the gut and the other only 3%. The amount of moss consumption is linearly related to the amount of moss available. Kuřavová and Kočárek suggest that keeping the moss consumption low prevents poisoning by secondary compounds produced by mosses. A reduction in moss consumption near the end of the growing season supports this hypothesis. Mosses increase their production of secondary compounds in autumn in preparation for the freezing conditions of winter (Cornelissen *et al.* 2007).



Figure 33. *Bryoerythrophyllum recurvirostrum*, a moss that seems to be avoided as food by *Tetrix*. Photo by Hermann Schachner, through Creative Commons.

It is also possible (probable?) that the choice of food is more a choice of habitat as the environmental conditions change. Low or high temperatures could drive the groundhoppers to the more stable conditions of the moss cushions. Furthermore, unfavorable conditions most likely reduce activity, resulting in lower consumption.

Mandibular Abrasion

Tetrix tenuicornis (Figure 34) avoids eating grasses, instead eating mosses [16.3%; *Barbula convoluta* (Figure 21), *Brachythecium albicans* (Figure 22), *Bryum caespitium* (Figure 25), *Campylopus introflexus* (Figure 54), and *Ceratodon purpureus* (Figure 15)] and detritus (83.7%) (Kuřavová *et al.* 2014). But it still exhibits

increased mandible abrasion with age, with females showing more age-related abrasion than males, perhaps due to greater frequency of feeding. On the other hand, Hence, even detritus and bryophytes cause wear on groundhopper mandibles.



Figure 34. *Tetrix tenuicornis*, a species whose mandibles show wear from eating bryophytes. Photo by B. J. Schoenmakers, through Creative Commons.

It is interesting that the diet of males and females may differ. Hochkirch *et al.* (2000) found that *Tetrix subulata* (Figure 6) males fed exclusively on algae and mosses, but females consumed grasses and forbs as well, perhaps accounting for the greater mandibular abrasion in females of *T. tenuicornis* observed by Kuřavová *et al.* (2014). Temperature also plays a major role in feeding, with only 1% feeding on a cool day but 24.7% feeding on the warmest day of the study (Hochkirch *et al.* 2000). When not feeding, the grasshoppers preferred sitting on the more open, warmer locations. These resting locations differed significantly from the feeding locations, which included mosses, suggesting that a color morph might be at a disadvantage in one of those locations.

Potua sabulosa

This pygmy grasshopper (Figure 35) is also a moss consumer, having mosses, especially *Funaria* (Figure 26), as its preferred food (Bhalerao *et al.* 1987). It lacks the molar dentes that are used for eating tracheophyte leaves, making it difficult to eat these foods as an alternative food source. For example, female adults fed on only "paddy" sprouts died within 5-6 days. The species overwinters as an adult. During the cold winters and hot, dry periods in summer it does not eat.



Figure 35. *Potua sabulosa*, a moss consumer that lacks polar dentes. Its roughened body helps it to blend with its surroundings. Photo by Jason Weintraub, through Creative Commons.

These tiny grasshoppers can jump 25-35 cm (Paranjape & Bhalerao 1985). In southwest India they hang out among mosses, being protected by their cryptic coloration. They also eat the mosses, as well as humus, and are capable of making an entire clump of moss disappear (Paranjape 1985). In the summer they survive the heat and drought by burrowing into soil, where they can remain for at least two months without food (Paranjape & Bhalerao 1985). When it is time for egg laying, the females dig a small burrow (~2 mm) in the soil or between the dense moss tufts, using their ovipositors. Their 23-25 eggs are laid in a loose cluster, hatching 10-12 days later at 23-25°C.

Acrididae – Grasshoppers

Akris is the Greek word for locust and is the basis for the name of the family that contains them (Acrididae 2015). More than 10,000 species comprise this family. The species are medium to large, as grasshoppers go. They are **diurnal** (day-active) and typically travel by jumping in their preferred open habitats. They often have cryptic coloration, but some are brightly colored. And many prefer "mossy" habitats.

"Three years ago there was a grasshopper 'explosion' in some central British Columbia grassland sites" (Terry McIntosh, pers. comm. 6 September 2013). "In the Gilpin Grasslands, they completely cleaned up most of the broad-leaved herbaceous plants (and ignored the grasses by the way), then started browsing on some shrubs, including, at one site, poison ivy! Later that day, I noticed a peculiar *Grimmia* on an outcrop. On closer inspection, the reason it look odd was because the whole moss face (mainly *G. ovalis*) had been grazed by the 'hoppers.' Not one plant in some 10 square meters had any leaf tips left." And the capsules were eaten too. (See discussion of other moss eaters under Food below.)



Figure 36. *Grimmia ovalis* growing on a rock outcrop where it may serve as food for grasshoppers during outbreaks. Photo by Michael Lüth, with permission.



Figure 38. *Melanoplus islandicus* male, a shoreline inhabitant where there are short grasses and mosses. Photo by David Kleiman, through Creative Commons.

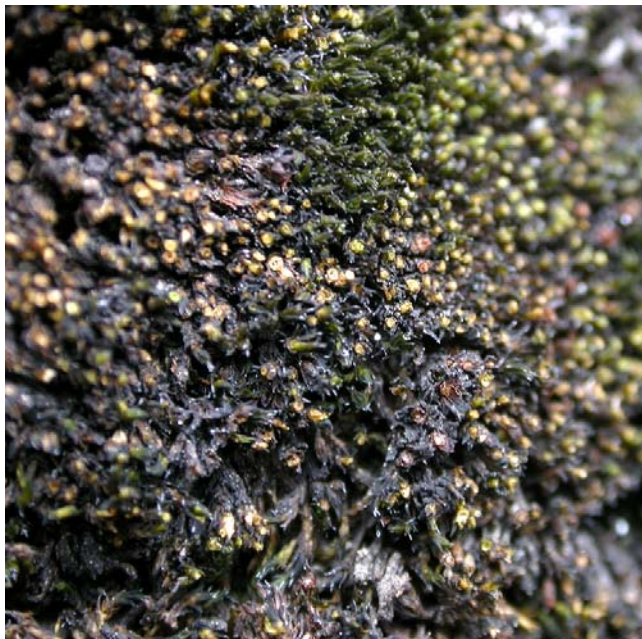


Figure 37. *Grimmia ovalis* grazed by grasshoppers. Note the absence of white tips on the leaves. Photo courtesy of Terry McIntosh.

Melanoplus

Although this genus (Figure 38-Figure 44) does not exhibit the close food association exhibited by the **Tetrigidae**, at least several members prefer mossy habitats. *Melanoplus lovetti* lives in damp mossy ground, avoiding taller grasses (Fulton 1930). *Melanoplus islandicus* (Figure 38) in Michigan, USA, occurs along damp shorelines of pools where vegetation includes short grasses and sedges as well as mosses and organic debris (Bland 1989).

Melanoplus borealis (Figure 39) is well camouflaged among the mosses near Fairbanks, Alaska, USA. Kaufmann (1971) recounts seeing an adult that jumped/flew away from the approaching human. Once it landed, it became invisible among the moss-covered field where its color pattern blended with both the colors and spongy texture of the mosses. This species, like others in the genus, avoided areas of tall grass, apparently requiring areas where they could rest in the sun.



Figure 39. *Melanoplus borealis* male, a species well camouflaged among the Arctic mosses. Photo by Denis Doucet, with permission.

This genus has a variety of feeding strategies. Kaufmann (1968) found that *Melanoplus differentialis* (Figure 40) in Maryland, USA, prefers *Taraxacum officinale* (dandelion), but will also feed on grasses. They also eat dried plants, even when fresh ones are present. Kaufman found that the habitat was more important in the

choice of food (light, temperature, plant orientation) than the foods themselves. The mandibles are typical of grasshoppers that eat forbs, but the maxillae are similar to the moss feeders in the genus *Tetrix*.



Figure 40. *Melanoplus differentialis*, a grasshopper that eats mostly forbs but has maxillae similar to those of moss feeders. Photo by Rob Curtis, through Creative Commons.

Melanoplus femurrubrum (Figure 41-Figure 43), like many of the grasshoppers, has many color forms (Figure 41-Figure 43). This species has been studied to determine the effect of food absence on survival. As you may know, grasshoppers will eat their own appendages when starved for days. Bland (1981) found that nymphs survived up to 113 hours with no food. But hatchlings required food within 48 hours to insure their continued survival and growth. This species tends to eat the first suitable food it encounters, using olfactory senses to find it.



Figure 41. *Melanoplus femurrubrum* in Zion National Park, showing an olive-green form. Photo by Leyo, through Creative Commons.



Figure 42. *Melanoplus femurrubrum* grayish green color form. Photo by Sheryl Pollock <www.discoverlife.org>, with permission.



Figure 43. *Melanoplus femurrubrum* reddish form. Photo by Sheryl Pollock <www.discoverlife.org>, with permission.

It appears that members of this genus have not been tested for sensitivity to secondary compounds in mosses. In tests of compounds in tracheophytes on nymphs of *Melanoplus sanguinipes* (Figure 44), a species that does not typically eat mosses, many elicited no response, but several compounds caused a reduction in mean weight (Westcott *et al.* 1992). Saponin decreased survival and seven compounds significantly decreased both survival and mean weight. Vanillic acid significantly increased mean weight. This leaves the intriguing question of the effects of secondary compounds of bryophytes. Investigations into the chewing apparatus and digestive response to bryophytes compared to preferred foods may help us to understand why some insects choose bryophytes while others avoid them.



Figure 44. *Melanoplus sanguinipes* female, a forb feeder that benefits from vanillic acid in forbs. Photo by Lynette Schimming, through Creative Commons.

Not only do populations of *Melanoplus* (Figure 40-Figure 44) differ in coloration, but their physiology can differ as well. Fielding (2006) demonstrated **facultative diapause** (resting period that can change based on conditions) in the widely distributed *Melanoplus sanguinipes*. In an Idaho population, diapause in this species was facultative, with pre-diapause embryos averting diapause when held at 5°C for 90 days. On the other hand, this same population entered diapause in the late stage of development if held at 22°C for 30 days or more (Figure 45). The subarctic Alaskan populations had obligate diapause and entered diapause in a late stage of development. Chilling in the pre-diapause stages had no effect on diapause. These differences in life cycle strategies permit this species to occupy its wide distribution and are likely to be important for some of the moss-dwelling species as well.

Chorthippus

Langmaack (1997) found that mosses were important in the reproduction of some grasshoppers. *Chorthippus montanus* (Water-meadow Grasshopper; Figure 46) and *C. parallelus* (Figure 47) (*Acrididae*), both flightless, clearly selected moist mosses for depositing their egg pods.

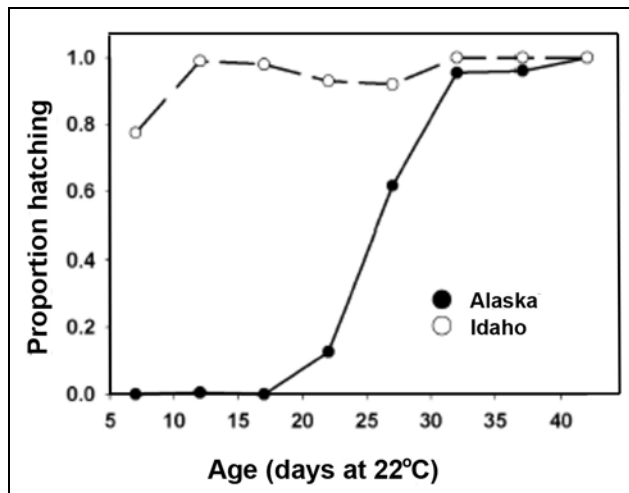


Figure 45. Comparison of proportion of eggs from Alaska and Idaho populations of *Melanoplus sanguinipes* that hatched after exposure to 5°C for 90-100 days following incubation at 22°C for different times. $n > 200$ observations at each point. Modified from Fielding 2006.



Figure 46. *Chorthippus montanus*, a flightless grasshopper that selects moist mosses for egg deposition. Photo by Gilles San Martin, through Wikimedia Commons.



Figure 47. *Chorthippus parallelus* male, a flightless grasshopper that selects moist mosses for egg deposition. Photo by Atlasroutier, through Wikimedia Commons

Chorthippus montanus (Figure 46) is a flightless wetland species and therefore it is likely to become rarer because its habitat is disappearing. Using a mark-recapture technique, Weyer *et al.* (2012) found that this species travels on average only 23.5 m, with a maximum of 104 m. This is not sufficient to permit its dispersal among widely fragmented wetland landscapes, and even the requirement to replace a drained wetland with another (somewhere else) will not solve this dispersal problem. Even if it could travel farther, it has restricted habitat requirements and is unable to traverse unsuitable habitats.

Based on fecal analyses, *Chorthippus pullus* (Figure 48) has a varied diet that includes dicotyledons, monocotyledons, and bryophytes (Steiner & Zettel 2006). The bean *Astragalus onobrychis* was the most consumed food in the Steiner and Zettel study. Moss consumption, including the moss *Dicranoweisia crispula* (Figure 49), formed a greater part of the diet in seasons and locations when other herbs were less abundant, despite having mandibles adapted for eating grasses. At one location *D. crispula* comprised 45% of the diet. Contrary to the suggestion of Uvarov (1977) that grasshoppers eat mosses for their water content, the water content of this moss was the lowest among the top four foods consumed, suggesting that the grasshoppers derived some other value from eating it.



Figure 48. *Chorthippus pullus*, a species that lays its eggs in moss **polsters** (cushions) in Austria. Photo by Gabriele Kothe-Heinrich, through Creative Commons.



Figure 49. *Dicranoweisia crispula*, a species that can form as much as 45% of the diet of *Chorthippus pullus* (Figure 48). Photo by Michael Lüth, with permission.

In the Lake Salzburg area of Austria, *Chorthippus pullus* (Figure 48) lays its eggs in June and July as an ootheca (egg case; Figure 50) in sand or moss polsters (Schwarz-Waubke 2001). This species deposits an average of 75 eggs during its lifetime. Each ootheca contains an average of 6.1 eggs. These moss polsters are especially important in rocky areas where they supply protection in an otherwise hostile environment.



Figure 50. Insect ootheca. Photo by Gilles San Martin, through Creative Commons.

Nicarchus

The genus *Nicarchus* (Figure 51) is flightless and lives on tree trunks (Rowell 2009). These grasshoppers are adapted to their habitat by having a wider thorax with reduced sternal lobes, the latter correlating with the reduced wings and flightless condition. This reduction in wing muscle provides additional space for a larger than typical crop (part of digestive system in which food is stored before digestion). Like other members of this group of tree trunk orthopterans (*Ommatolampinae*), their adaptations include cryptic coloration that mimics mosses, lichens, or bark; roughened cuticle or spines, again mimicking their substrate; strongly protuberant eyes; pronotum with bumpy projections; widely separated metasternal lobes; nodular antennae; 7 external spines on hind tibia; all but *Sciaphilacris* (Figure 52) flightless. They live on the trunks and major branches of tropical forest trees in the Amazon basin and in Central America. Among this group, only *Nicarchus* is known to feed on mosses, a habit that is probably favored by the enlarged crop.



Figure 51. *Nicarchus erinaceus*, a species that lives among mosses on tree trunks and branches in the tropical forest and feeds on mosses. Photo by Frank through What's that Bug <<http://www.whatsthatbug.com/2014/01/19/orthopteran-costa-rica/>>.

Sciaphilacris – Moss and Lichen Mimics

Sciaphilacris (Figure 52) lacks many of the modifications noted for *Nicarchus* and is the only member of *Ommatolampinae* that is not flightless (Rowell 2009). Nevertheless, despite having somewhat reduced wings, it rarely flies. Little seems to be known about it – it lives in South and Central America and most likely spends part of its time among the mosses, blending well.



Figure 52. *Sciaphilacris alata*, a good moss mimic. Photo by Arthur Anker, with permission.

Myrmeleotettix maculatus

Interactions with mosses is not always positive, and *Myrmeleotettix maculatus* (Figure 53) would most likely agree. In Europe it is a species of acidic coastal dunes. However, these dunes are being invaded by the exotic moss *Campylopus introflexus* (Figure 54). In a comparison of invaded dunes vs non-invaded dunes, Schirmel (2010) found that the mean number of captures of this species in non-invaded (native) plots was significantly higher than that in the invaded plots. Schirmel suggested that this difference may have been due to the higher proportion of grasses as food, more appropriate shelter, or more favorable microclimate in the native plots, leading to a higher mortality in the invaded plots. On the other hand, the mean number of young and older nymphs did not differ between the two habitats, suggesting that the invaded sites were suitable for oviposition but in some way detrimental to adults.



Figure 53. *Myrmeleotettix maculatus* female, a species that is disappearing in European coastal dunes due to the invasion of the moss *Campylopus introflexus* (Figure 54). Photo by Brian Eversham, with permission.



Figure 54. *Campylopus introflexus*, an invasive moss that may destroy grasshopper habitat in Europe. Photo by Michael Lüth, with permission.

Food

Kaufman (1965) found that the feeding rate of *Acrididae* grasshoppers in Bolivia increased greatly with temperature. Feeding habits seem to correspond with mandibles and maxillary laciniae. These mouth parts can be divided into the graminivorous (grass) type, the forb-feeding type, and the moss-feeding type. Even the gastric caeca can be divided into four types based on diet preference. Nevertheless, experiments with *Euthystira brachyptera* (Figure 55) suggest that feeding on several different species, in this case of grasses, improves mortality, longevity, fecundity, and body weight.



Figure 55. *Euthystira brachyptera* female, a species that feeds on grasses but thrives best on mixed species. Photo by Gilles San Martin, through Creative Commons.

Position of the food can be important (Kaufman 1965). *Chorthippus parallelus* (Figure 47) prefers to feed on vertical grass blades. Passage time for the food in the alimentary tract differs not only in different species, but also depends on food plant, individual differences, and developmental stage. And males seem to assimilate more of the food they eat than do females.

Patterson (1984) demonstrated differences in shape and arrangement of dentes resulting in different mandibular ratios among members of the *Acrididae* with different feeding choices. Patterson (1984) and Kaufman (1965) pointed out the need for comparative studies among the moss-feeding species. Some of the species in this family are *stenophagous* (having narrow range of suitable foods) (Philippe 1991). For example, whereas *Trimerotropis saxatilis* (Figure 56-Figure 57) is specialized on eating mosses, *Boottettix punctatus* (Figure 58) specializes on *Larrea tridentata*, an evergreen shrub.



Figure 56. *Trimerotropis saxatilis* nymph well camouflaged among the grey lichens. Photo by Ted C. MacRae <beetlesinthebush.wordpress.com>, with permission.



Figure 57. *Trimerotropis saxatilis*, a specialist for eating mosses, is conspicuous here on mosses. Photo by Ted C. MacRae <beetlesinthebush.wordpress.com>, with permission.



Figure 58. *Bootettix argentatus*, a specialist on the shrub *Larrea tridentata*. Photo by Margarethe Brummermann, through Creative Commons.

In the southeastern United States lichen grasshoppers, also known as rock grasshoppers (*Trimerotropis saxatilis*; Figure 56-Figure 57), are important consumers in desert-like rock outcrops (Duke & Crossley 1975). This small species consumes 27.25 mg of the moss *Grimmia laevigata* (Figure 59), an **apparent** (conspicuous) moss, per day, totalling 391 mg m⁻² per year in this harsh habitat. This grasshopper species has a variety of color patterns that help it blend with its lichen and moss environment (Morse 1907). Although Morse says that *T. saxatilis* is restricted to bare rock surfaces, as its name implies, it has to eat somewhere, and it is a vegetarian. Do the math!



Figure 59. *Grimmia laevigata* on a rock outcrop, common habitat for *Trimerotropis saxatilis* (Figure 56-Figure 57). Photo by Michael Lüth, with permission.

Oviposition

Knowing that some grasshoppers eat mosses, it is not hard to imagine that they also lay their eggs among mosses. *Chorthippus pullus* (Figure 48), in Salzburg, Austria, is endangered in Europe (Schwarz-Waubke 2001). Despite this rarity, in the proper habitat of wild river landscape near Taugl it is a **eudominant** [>10% (Bick 1989)] among 12 other members of the **Saltatoria** (suborder of **Orthoptera**

including grasshoppers, crickets, and related forms). This species lays its eggs as an ootheca (Figure 50) in sand or moss clumps during June and July.

Some species of *Chorthippus* seem to have an inexplicable combination of oviposition habitats. For example, *C. albomarginatus* (Figure 60), *C. montanus* (Figure 46), and *C. parallelus* (Figure 47) prefer vertical plant surfaces for oviposition (Langmaack 1997). But *C. parallelus* and *C. montanus* also use moist mosses for egg deposition, a quite different type of structure. Rather than structure, it seems that height is important, with *C. albomarginatus* preferring 2-6 cm, *C. montanus* 0.5-2 cm, and *C. parallelus* 0-0.5 cm. Langmaack suggested that these preferences may indicate different requirements for moisture and temperature during development. *Chorthippus albomarginatus*, the species ovipositing at the greatest height, has the greatest desiccation resistance and highest temperature requirement for its eggs. Eggs of both *C. parallelus* and *C. montanus* have low desiccation resistance and a low temperature requirement.



Figure 60. *Chorthippus albomarginatus* female, a species that prefers higher positions of 2-6 cm above the ground for its egg deposition, including moss locations. Photo by Gilles San Martin, through Creative Commons.

Gryllidae – Crickets

The common names of the families of "crickets" have been hopelessly confused among the continents (Alexander *et al.* 1972), and me, so I will stay with only scientific names for most of these. The males are the callers in these groups, but in some the female may also call. The crickets make their well known chirps by rubbing together the leathery forewings. These chirps increase in frequency as the temperature increases. Overlapping species may have "songs" that we cannot distinguish, but they can be distinguished by instrumentation – and other crickets. Females are attracted to the calls and go to the males for mating. We know that frogs use mosses to modulate their calls, so it is appropriate to ask how grasshoppers might use them.

Alexander *et al.* (1972) report *Eunemobius melodius* singing in a *Sphagnum* bog (Figure 61) in Michigan, USA. Strang (2015) states that the sphagnum ground cricket (*Neonemobius palustris*; Figure 62-Figure 64) is not found outside of *Sphagnum* bogs. Some crickets make nests in *Sphagnum* (Vickery 1969). Crickets don't seem to be commonly known from mosses, but in captivity with

predators like frogs and lizards they will typically hide among the mosses. Does that happen in nature as well?



Figure 61. *Sphagnum* blanket bog where one might hear the song of *Eunemobius melodius*. Photo through Creative Commons.



Figure 62. *Neonemobius palustris* male (sphagnum ground cricket) on *Sphagnum*, its only known home. Photo by Brandon Woo, with permission.



Figure 63. *Neonemobius palustris* female on *Sphagnum*, its only known home. Photo by Brandon Woo, with permission.



Figure 64. *Neonemobius palustris* nestled among *Sphagnum* of bog. Photo by Carl Strang, with permission.

Rhaphidophoridae – Camel Crickets, Wetas

These **Rhaphidophoridae** like it dark, living in forests, caves, animal burrows, under stones, in wood, and in cellars (Rhaphidophoridae 2015). They occur on all seven continents, where they are usually active at night and rely on their sense of touch to identify things in their environment. Wetas are characterized by lack of wings, lack of auditory organs, long, compressed tarsi with no pads, small bodies, and long hind legs and antennae (Richards 1961). They are primarily scavengers, often eating plant debris that is washed into the cave and left stranded on the cave walls, but they also eat bryophytes.

Johns and Cook (2014) found the new genus and species *Maotoweta virescens* (Figure 65-Figure 66) hidden in a moss forest in New Zealand. This mottled green weta is inconspicuous among the mosses; *maoto* is the Maori word for fresh green. Johns and Cook reported the difficulty of finding this weta on the mossy tree trunks during their night-time activity; it required 16 person hours for them to locate only 5 individuals. The only female collected was in copulation – on a moss.



Figure 65. *Maotoweta virescens* on bryophytes, a recently described weta that is well camouflaged among bryophytes. Photo by Tony Jewell, with permission.



Figure 66. Green weta (cf. *Maotoweta virescens*) in its mossy habitat. Photo by George Gibbs, with permission.

In the caves of New Zealand, one might find *Pallidoplectron turneri* feeding on the thallose liverwort *Marchantia* that grows near the electric lights, but I cannot verify the reference and my new Zealand colleagues and I suspect it was really fern prothalli being eaten.

Troglophilus (Figure 67-Figure 69) species exhibit cryptic coloring with shades of marble brown, green, or grey (Karaman *et al.* 2011). These color patterns blend well with the forest background and the lichen and moss-covered rocks where they hide during the day.

One consideration for crickets of all kinds is the need to call in order to connect with a mate. But all calls are not equal (Stritih & Čokl 2012). The surroundings modify the calls, and mosses have a different resonance than that of grasses or bushes. The *sympatric* (occupying overlapping distributions) *Troglophilus neglectus* (Figure 67-Figure 68) and *T. cavicola* (Figure 69-Figure 70) use vibratory signalling to distinguish the opposite sex of their own species. *Troglophilus neglectus* uses abdominal vibrations, whereas this behavior is absent in *T. cavicola*. Both species use whole-body vibrations after copulation. Although they most frequently use bark for both signalling and mating, mosses are often used as well. The signalling frequency depended on the substrate. On rocks, the intensity of *T. neglectus* is below the detection range for this species and therefore could not be heard if they signal from within a cave. The frequency extends up to 600 Hz on mosses, whereas its highest frequency on stone was below 250-300 Hz. This difference explains the movement from the caves to bark, or less often moss, for mating calls, with mosses and litter providing suitable vibratory substrate (Magal *et al.* 2000; Elias *et al.* 2004).



Figure 67. *Troglophilus neglectus* female in cave. Photo by Florin Rutschmanni, through Creative Commons at <www.orthoptera.ch>.



Figure 68. *Troglophilus neglectus* female with green and brown cryptic coloration. Photo by František Chládek, with permission.



Figure 69. *Troglophilus cavicola* male with marbled brown coloration that blends with mosses and litter. Photo by Walter P. Pfliegler, with permission.



Figure 70. *Troglophilus cavicola* on moss. Photo by Stefan Pluess, through Creative Commons.

Tettigoniidae – Katydids

Katydids can be abundant and diverse. At only three collecting sites in Loreto Province, Peru, Nickle and Castner (1995) found more than 370 species of Tettigoniidae.

Many katydid males offer a large gelatinous spermatophore to the female during mating (Del Castillo & Gwynne 2007). This is energy expensive and the larger the

reward offered, the less calling is done, another energy expensive activity. Size of the spermatophore and of the male do not seem to play any role in mate selection, but larger females seem to be favored over smaller ones.

Bogs seem to be the most common place for moss-associated katydids. The bog bush cricket *Metrioptera brachyptera* (Figure 71-Figure 72) is frequent in southern England heaths and bogs, but in northern England it is rare and in Scotland it has been found only once (Aucheninnes 2011). *Neonemobius palustris* (Figure 62-Figure 64) in Canada is rare, confined to *Sphagnum* (Figure 61) bogs (Johnstone & Vickery 1970; Kevan 1979), and feeds on the *Sphagnum* (Kevan 1979). Not only are the various *N. palustris* populations distinct genetically, but their **phenotypes** (sets of observable characteristics of individuals resulting from interaction of genes with environment) differ as well because interbreeding is rare if not non-existent between populations in different locations. Both *Neonemobius palustris* and *Allonemobius fasciatus* (Figure 73) lay their eggs on *Sphagnum* (Gerson 1969). Only these two species are considered to be characteristic peatland species in Canada (Marshall & Finnamore 1999).



Figure 71. *Metrioptera brachyptera*, a green bog bush cricket. Photo by Gilles San Martin, through Creative Commons.



Figure 72. *Metrioptera brachyptera* female, a black bog bush cricket. Photo by Robert Vlk, through Creative Commons.



Figure 73. *Allonemobius fasciatus*, a cricket that lays its eggs on *Sphagnum*. Photo through Creative Commons.

Camouflage

Like the previous **Orthoptera**, katydids exhibit cryptic coloration. *Haemodiasma tessellata* (Figure 74-Figure 75), known as a moss mimic katydid, exhibits a mix of brown and green with a roughened light and dark surface (Thorman 2008) that helps it blend not only with mosses but also with leaf litter. But *Steiroxys strepens* (Figure 76), with a nearly solid green coloration, was sitting on damp mossy ground where it most likely blended better with the short grasses there (Fulton 1930).



Figure 74. This katydid (*Haemodiasma tessellata*) from Costa Rica was billed as a moss mimic katydid (Thorman 2008), but it seems to resemble a tracheophyte leaf more than it does a moss. It does have markings that would blend with epiphyllous bryophytes. Photos by Mary Thorman, permission pending.



Figure 75. *Haemodiasma tessellata* showing its cryptic coloration that could blend with leaves or bryophytes. Photo by Bernard Dupont, through Creative Commons.



Figure 76. *Steiroxys strepens* male, illustrating the solid colors typical of most katydids. Photo by Jim Johnson, with permission.

Nickle and Castner (1995) summarized the strategies used by katydids in the rainforests of northeastern Peru to protect themselves against daytime predators. These included primary defenses – camouflage, concealment within leaf parts or litter, territoriality by defending roosting sites against other katydids; secondary defenses used when making contact with predators – colorful displays by distasteful species (Figure 77), aggressive counterattacks, **aposematic** (serving to warn or repel) wasp mimicry, visual or acoustical alarm displays. They seem to return to the same daytime locations, suggesting they may be aware of their camouflage in those surroundings. Of the 378 species, 71.4% had general color patterns of green (208 spp.), brown (46 spp.), and both green and brown (19 spp.). Another 13.8% were more specific, mimicking wasps, bark, twigs, leaves, or lichens. Another 4.8% hid from view within vegetation or litter. Nickle and Castner did not distinguish any as having bryophyte camouflage, but some patterns that work well among leaf litter also work well among bryophytes (Figure 75).



Figure 77. *Acanthodis* sp. female showing startle display in Campana Highlands, Panama. Photo by Arthur Anker, with permission.

In Columbia, *Championica bicuspidata* (Figure 79) feeds on mosses and mimics them (Cardona Granda 2012). This genus has a number of moss mimics, including *C. pallida* (Figure 78-Figure 80). *Acanthodis curvidens* (see Figure 77) is also a moss mimic and rests prostrate to avoid detection (Robinson 1991). In addition to its camouflage, on Barro Colorado Island, Panama, this katydid avoids predation by bats when it is calling by maintaining a low frequency of calls (Belwood 1988). Bats locate katydids that produce frequent calls in about 26 seconds, immediately flying directly from their perch to the singing insect. In contrast, bats require nearly 34 minutes to locate the katydids (*Acanthodis curvidens*) that call less often (about once per minute), typically flying about seemingly randomly.



Figure 78. *Championica pilata* blending with a leaf and its epiphylls. Photo by Arthur Anker, with permission.



Figure 79. *Championica* sp. in Ecuadorian Amazon, illustrating its cryptic coloration that hides it on mosses. Photo by Geoff Gallice, through Creative Commons.



Figure 80. *Championica pilata* blending with a dead leaf. Photo by Arthur Anker, with permission.

Paraphidnia

Paraphidnia (Figure 81-Figure 85) is known as the moss katydid. Its markings look like leafy liverworts and lichens, making it blend well with its rainforest habitat, where it lives among and eats mosses and lichens (Ferrari 2015).



Figure 81. *Paraphidnia* sp. (lichen katydid) with markings that resemble leafy liverworts. Photo by Andreas Kay, through Creative Commons.



Figure 82. *Paraphidnia* sp. (lichen katydid) mimicking a stick that has bryophytes and lichens. Photo by Andreas Kay, through Creative Commons.



Figure 83. *Paraphidnia* sp. (mossy katydid) mimicking a stick with leafy liverworts. Photo by Arthur Anker, with permission.



Figure 84. *Paraphidnia* sp (mossy katydid) on bryophytes, mimicking a stick with leafy liverworts. Photo by Arthur Anker, with permission.



Figure 86. *Balboana tibialis* male with mosses on a branch covered with lichens. Photo by Arthur Anker, with permission.



Figure 85. *Paraphidnia* sp. from Ecuador, mimicking a stick with leafy liverworts. Photo by Arthur Anker, with permission.

Balboana tibialis

Like many tropical species, little seems to be known about *Balboana tibialis* (Figure 86-Figure 87). And like many katydids, it most likely benefits from its cryptic coloration.



Figure 87. *Balboana tibialis* in Gamboa, showing camouflage markings suitable for living on bryophytes. Photo by Arthur Anker, with permission.

***Arachnacris tenuipes* – Emperor Bush Cricket**

A big thank you to Nick Garbutt for allowing me to use his image to show *Arachnacris tenuipes* (Figure 88) eating a moss. This is a species that may reach 12 cm (Hincks 1956), and it has the largest wingspan (27.4 cm) in the **Orthoptera** s.s. (Cowardine 2008). Its size is limited by temperature (Makarieva *et al.* 2005). Because of increases in metabolism with increasing temperature, the maximum length increases approximately twofold for each 10°C increase in ambient temperature. Hence, larger **poikilotherms** (those with temperature controlled by the environment) occur farther north, with smaller individuals in the tropics. *Arachnacris tenuipes* (syn. *Macrolyrstes imperator*) is known from Malaysia and Indonesia, but its distribution may be wider. This may be the first report that it eats mosses.



Figure 88. *Arachnacris tenuipes*, an emperor bush cricket (katydid) eating moss. Photo by Nick Garbutt, with permission.

"Endless forms most hidden." Thus is the title of an article by Kikuchi *et al.* (2017) in *Ecology* regarding katydids that mimic mosses. A katydid, *Adeclus* cf. *trispinosus* (Cadena-Castaneda 2011), was discovered as a short-winged adult male, presenting a wing pattern and coloration with legs and other parts that made it resemble a moss (Kikuchi *et al.* 2017). The katydid that became famous in *Ecology* uses three strategies of concealment: background matching, disruptive coloration, and masquerade. A member of the **Pleminiini**, it joins many other species that resemble mosses. Other moss mimics in the **Tettigoniidae** include *Panacanthus varius* (Figure 89) and *P. intensus* (Montealegre-Z & Morris 2004). This type of mimicry seems to have evolved multiple times in the **Orthoptera** (Mugleston *et al.* 2013).



Figure 89. *Panacanthus varius*, a moss mimic. Photo by Andreas Kay, through Creative Commons.

PHASMIDA – Walking Sticks

The common name of walking stick indicates that the **Phasmida** is a group of mimics. While looking like a stick is cool, looking like a hanging moss is awesome! And some members in the rainforests do just that (Figure 90), resembling pendent mosses in both color and appearance (Robinson 1969). The genus *Acanthoclonia* (**Pseudophasmatidae**) exhibits this moss-mimicking appearance (Gutiérrez & Bacca 2014).



Figure 90. Moss mimic walking stick. This one moves with a swaying, vibrating motion that mimics the movement of moss branches in the wind. Photo by Neil Bell, permission pending.

This kind of camouflage has been named in different ways, including **Batesian mimicry** and **crypsis**. But these terms may both be misleading conceptually (Skelhorn *et al.* 2010). Rather, the term **masquerade** has been applied to them (Figure 91). One problem in naming and understanding this phenomenon is the paucity of evolutionary studies on it, perhaps because its greatest representation is in the tropics where our level of understanding the systematics is much less than in other parts of the world. The term **masquerade** was introduced to describe those organisms that cause misidentification by other organisms.



Figure 91. A walking stick in Peru that looks like a twig with mosses growing on it. Photo by Arthur Anker, with permission.

Trychopeplus laciniatus

An incredible insect, *Trychopeplus laciniatus* (**Diapheromeridae**; Figure 92-Figure 98), is a montane Neotropical rainforest walking stick that looks like strands of mosses and leafy liverworts. Its range includes the mountainous forests of Costa Rica, Nicaragua, Panama, and Colombia. It "sways" its way through its mossy habitat, a behavior scientists have suggested resembles the moving of mosses in the wind. Regarding its presence in Monte Verde, Costa Rica, Ryan Burrows (Bryonet 14 April 2010) states that it "would be a perfect match to the habitat there." This phenomenal insect bears such resemblance to the mosses on the cloud forest tree trunks that it is virtually

undetectable to an untrained eye. It is flightless and slow moving, and has no means of defense (Simon 2015). Hence, this invisibility is its only means of protection.



Figure 92. An immature walking stick, *Trychopeplus laciniatus*, from Nectandra Cloud Forest Garden in Balsa, Costa Rica. Photo by Diane Lucas, with permission.



Figure 93. *Trychopeplus laciniatus* in Costa Rica. Photo by Dorothy Allard, with permission.



Figure 94. Bryophytes in Monte Verde, Costa Rica, Nectandra cloud forest where *Trychopeplus laciniatus* lives. Photo by Diane Lucas, with permission.



Figure 95. *Trychopeplus laciniatus*, a walking stick that mimics bryophytes, on twig in Costa Rica. Photo by David Meagher.



Figure 96. Bryophytes in Monte Verde, Costa Rica, Nectandra cloud forest where *Trychopeplus laciniatus* lives. Photo by Diane Lucas, with permission.



Figure 97. *Trychopeplus laciniatus* on bark. Photo by Dan Doucette through Project Noah, with permission.



Figure 98. *Trychopeplus laciniatus*, clearly masquerading as a bryophyte. Photo by Dan Doucette through Project Noah, with permission.

Another observer (Anonymous 2015) describes the mating in more detail. *Trychopeplus laciniatus* is a herbivore and uses its mossy appearance to hide among the mosses while it feeds. Instead of laying its eggs in a cluster like most mantids, it lays them singly and loosely on the trees. The eggs subsequently fall to the forest floor where the nymphs hatch and develop.

Ng (2015) reports a moss mimic stick insect that laid eggs among mosses in the Botanical Garden of the Kinabalu Park, Malaysia (film is available on website). In China, *Pericentrus* (Phasmatidae; possibly synonym of *Trychopeplus laciniatus*, Error! Reference source not found.-Figure 98) has coloration of green and brown that makes it look like mosses and lichens (Hennemann *et al.* 2008). It moved its body back and forth from side to side as it laid the eggs, occasionally releasing the ovipositor and re-inserting. It is likely that variants of these mimics exist in many locations in the tropics. Some may have been transported along with mosses, but their lack of wings would limit their distribution once they arrived. This kind of isolation promotes the formation of new species through the **founder principle** and **genetic drift**. For example, Belt figured one of these masqueraders in 1888 (Figure 99). But Tilgner (2002) disagrees with this explanation, suggesting instead that the multiple locations of such masquerading phasmids is the result of **convergent evolution**.

In Puerto Rico, *Lamponius nebulosus* (Pseudophasmatidae; Figure 100), a spiny green and brown mantid, represents the mimics (Nico Franz & Ines Sastre-de Jesus, Bryonet 15 April 2010). Those moss "leaves" you see are the spiny cuticle projections. This species is endemic to the cloud forest in the Luquillo Experimental Forest (Tilgner *et al.* 2000; Tilgner 2002) and has only been known for a short time. Its host plants include *Miconia* sp. and *Guzmania*, both likely to have associated mosses where it can rest undetected. In this group, activity is typically restricted to only certain times of day; when they are resting they are well camouflaged (Willig *et al.* 1993; Basset 2000; Berger 2004). But this species has two backup plans if it is discovered – it can exhibit **catalepsy** (trance state) or regurgitate fluid from its mouth.

T. Belt 1888

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related genus (*Pterochroza*), imitate leaves in every stage of decay, some being faded-green, blotched with yellow; others, as in the species figured, resemble a brown withered leaf, the resemblance being increased by a transparent hole through both wings that looks like a piece taken out of the leaf. In many butterflies that resemble leaves on the under side of their wings, the wings being raised and closed together when at rest so as to hide the bright colours of the upper surface, there are similar transparent spots that imitate holes; and



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others again are jagged at the edge, as if pieces had been taken out of them. Many chrysalides also have mirror-like spots that resemble holes; and one that I found hanging from the under side of a leaf had a real hole through it, formed by a horn that projected from the thorax and doubled back to the body, leaving a space between. Another insect, of which I only found two specimens, had a wonderful resemblance to a piece of moss, amongst which it concealed itself in the daytime, and was not to be distinguished except when accidentally shaken out. It is the larval stage of a species of *Phasma*.

Figure 99. "Moss insect" from Nicaragua as illustrated in "The Naturalist in Nicaragua" by Thomas Belt 1888. Photo by Rob Gradstein, with permission.



Figure 100. *Lamponius nebulosus*, a moss mimic. Photo courtesy of Alfredo D. Colon Archilla <alfredocolon.zenfolio.com>.

Even egg shape may contribute to adaptations for living among bryophytes (see Hennemann 2008). *Parasthenobea foliculata* (Diapheromeridae) has many

irregular pale green, straw, or brown markings and speckles that give it good camouflage among lichens and mosses. *Parastheneboea exotica* (Figure 101) and *P. imponens* (Figure 102-Figure 103) have elongate, cylindrical, bullet-shaped eggs with conical polar ends. The **operculum** (lid) is surrounded by a collar of **setae** (hairs). This egg shape is usually associated with taxa having an appendicular ovipositor that is suitable for laying eggs into soil, moss, and bark crevices.



Figure 101. *Parastheneboea exotica*, a species with good camouflage among lichens and mosses. Photo by Albert Kang through Project Noah, permission pending.



Figure 102. *Parastheneboea imponens*, a moss and lichen mimic. Photo by Albert Kang through Project Noah, permission pending.



Figure 103. *Parastheneboea imponens* is blending here among the mosses. Photo by Albert Kang through Project Noah, permission pending.

In *Cnipsus rachis* (Phasmatidae; Figure 104) the thorn pads consist of a single pair (Buckley *et al.* 2010). Projections along the body resemble moss leaves. Some of the New Caledonian species prefer ferns for food, but it seems that New Zealand species do not feed on ferns.



Figure 104. Mantid *Cnipsus rachis* from Costa Rica – and New Caledonia. Photo by Louis Thouvenot, with permission.

Neoclides laceratus

Neoclides laceratus is a stick insect from Sumatra, Kalimantan, and Sarawak (Meagher 2022). In the swampy forests of Borneo it resembles creeping moss or the liverwort *Jungermannia* (Figure 106) with the insect's olive-green color and leaf-like projections.



Figure 105. *Neoclides laceratus* camouflaged perfectly among bryophytes on wood in Costa Rica. Photo by David Meagher.



Figure 106. *Jungermannia atrovirens*, in a liverwort genus that is mimicked by the stick insect *Neoclides laceratus*. Hermann Schachner, through Creative Commons.

***Antongilia laciniata* (Bacillidae)**

The moss mimic stick insect *Antongilia laciniata* (Figure 107) blends well with mosses in its aerial habitat. Although there are several images of this mimic online, there seems to be little information about its life.



Figure 107. *Antongilia laciniata* showing its moss-like camouflage in Madagascar. Photo by Frank Vassen, through Creative Commons.

***Phanocles* (Diapheromeridae)**

The genus *Phanocles* (Figure 108) is distributed in Central and South America (Gutiérrez & Bacca 2014) where it blends in with the epiphytic and epiphyllous bryophytes due to its markings and its shape like a twig.



Figure 108. *Phanocles* sp. nymph resembling a twin with adnate mosses, liverworts, and lichens in Panama. Photo by Arthur Anker, with permission.

MANTODEA – Preying Mantids

This group of mantids are predators, hence the name preying mantis, but they also look like they are praying, so you will see the name spelled both ways. I still recall seeing my first mantid as a child. I thought at first someone had dropped a pocket knife, then realized it was the largest insect I had ever seen. These insects usually are safely camouflaged while at rest (Figure 109), but when they are searching for food or attacking prey they become more visible (Figure 110). Some are able to secrete a nasty spray that can blind the predators ("Steve" on Fellowship of the Minds 6 May 2013).



Figure 109. Mantid moss mimic among mosses on tree trunk. Photo by Nick Garbutt <www.nickgarbutt.com>, with permission.



Figure 110. *Polytrichum strictum* capsules with a mantid. Photo by Michael Lüth, with permission.

But they are not all so large – Zborowski (1993), in *Animals in Disguise*, illustrates mantids from Borneo that are no more than a cm long. Coyne (2013) discusses *Pogonogaster tristani* (Thespidae; Figure 111-Figure 112), described in 1918 but reported only a few times since. Others in this genus are present in Colombia (Gutiérrez & Bacca 2014). This is one of the minute preying mantids that mimics mosses.



Figure 111. *Pogonogaster tristani*, one of the many moss mimics in this genus. Photo by Oscar Blanco, through Creative Commons.



Figure 112. Mantid that resembles mosses. Photo by Evelyne Lennette.

Not all camouflage involves morphology of the insect. Some mantids carry their own flora around with them. Two species of the shield mantis, *Choeradodis rhombicollis* (Figure 113) and *C. rhomboidea* (Figure 114-Figure 115) (Mantidae) in Costa Rica have epizoic (growing on animals) leafy liverworts and lichens growing on them (Lücking *et al.* 2010). Of the 84 individuals Lücking and coworkers examined in the lowland rainforests, 60 of them had epizootes, comprised of five liverwort species, 23 lichen species, and several unidentified fungi (Figure 116). These epizootes grew mainly on the enlarged pronotum, but some also grew on the forewings. The liverworts were all in the family

Lejeuneaceae and were all species typical as epiphylls on leaves, especially *Leptolejeunea elliptica* (Figure 117). These pronotal inhabitants were more pronounced in *C. rhombicollis* than in *C. rhomboidea*, and more in females than in males (Figure 116). One female of *C. rhombicollis* also had the leafy liverworts *Diplasiolejeunea brunnea* (Figure 118), *Cololejeunea gracilis* (Figure 119), *C. camillii* (Figure 121), and *Colura tortifolia* (Figure 120). The researchers suggested that the longer life span of females may account for the greater development of liverworts there. This camouflage permits these large mantids to rest undetected among the leaves with their own flora of "epiphylls."



Figure 113. *Choeradodis rhombicollis* showing the large hood that resembles a leaf. Photo by Andreas Kay, through Wikipedia Commons.



Figure 114. *Choeradodis rhomboidea* carrying a flora on its back like the leaves it inhabits. Photo by Andreas Kay, through Creative Commons.



Figure 115. *Choeradodis rhomboidea* showing its hood thorax (=enlarged pronotum) that resembles a leaf – in this case a damaged one. Photo by Andreas Kay, through Creative Commons.

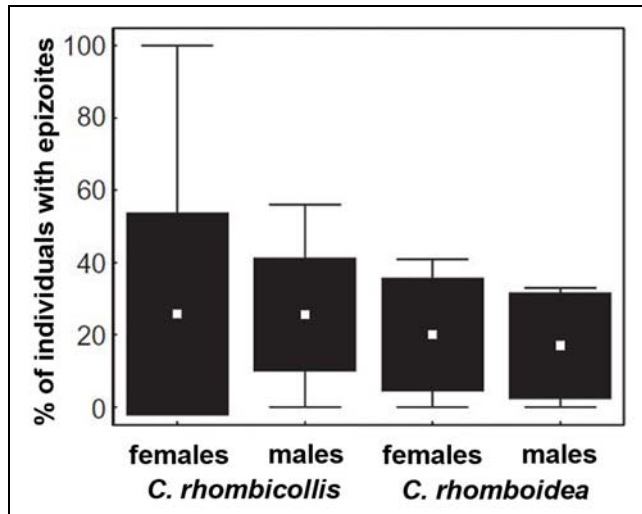


Figure 116. Comparison of males and females of two *Choeradodis* species showing percentage with liverwort, lichen, and fungus epizoids. Modified from Lücking *et al.* 2010.



Figure 117. *Leptolejeunea elliptica* epiphylls. Photo by Yan Jia-dang, through Creative Commons.



Figure 118. *Diplasiolejeunea brunnea* on leaf in Ecuador. Photo courtesy of Tamás Pócs.

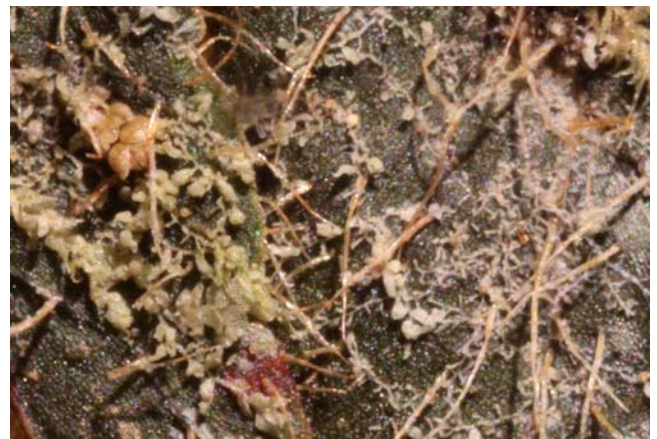


Figure 119. *Cololejeunea gracilis* var. *linearifolia*, a tiny liverwort that can grow on larger liverworts as well as leaves of evergreen plants. Photo courtesy of Tamás Pócs.



Figure 120. *Colura tortifolia*, an occasional epizoite on *Choeradodis rhombicollis*. Photo by Michaela Sonnleitner, with permission.



Figure 121. *Cololejeunea camillii* on leaf in Panama. Photo courtesy of Tamás Pócs.

Liturgusidae

Members of the genus *Majangella* can even resemble liverworts – a common group of bryophytes in the tropics. *Majangella moultoni* (Figure 122) has a green and brown patterned coloration with various protuberances that give it good camouflage when it is among mosses and liverworts. This species is tropical southeast Asian from Borneo, Indonesia, Malaysia, and Sumatra where it is inconspicuous in its rainforest habitat (Svenson & Vollmer 2014).



Figure 122. *Majangella moultoni* closely resembling the bryophytes beneath it. Photo by Hee Jenn Wei, with permission.

Mating

The mantids are well known for their mating behavior (Figure 123). The male is smaller than the female, and the female needs to be well fed before producing her egg case with eggs (Figure 124). Perhaps this is why the katydid males have evolved to offer a gelatinous spermatophore before mating. In short, it isn't safe to be the male mantid – you might get eaten! The predatory females see the smaller males as food (Figure 125), so males must make their moves carefully.



Figure 123. *Mantis religiosa* couple mating. Note that the smaller, brown mantid is the male. Photo by Zwentibold, through Creative Commons.



Figure 124. *Mantis religiosa* egg case. Photo by Hans Hillewaert, through Creative Commons.



Figure 125. *Polyspilota* sp female chewing on the head of the male while mating with him. Photo by Arthur Anker, with permission.

BLATTODEA – Cockroaches and Termites

You would most likely prefer not to think of cockroaches and termites as moss dwellers. If so, it may please you to know that the Australian wood-boring cockroach *Panesthia australis* (Blaberidae; Figure 126) prefers odors of individual tracheophyte species over the odor-neutral *Sphagnum* (Figure 61) (Billingham *et al.* 2009).



Figure 126. *Panesthia australis*, a cockroach that avoids mosses as a food item. Photo by Toby Hudson, through Creative Commons.

But the tables can be turned. Bernard Dupont photographed the ootheca (Figure 127) of a cockroach that was deposited on bryophytes and that had leafy liverworts growing up onto the ootheca. And Chatervedi sent me a picture of a cockroach that was hiding under the thallose liverwort *Dumortiera hirsuta* (Figure 129).



Figure 127. Cockroach ootheca with leafy liverworts growing on it. Photo by Bernard Dupont, through Creative Commons.



Figure 128. Cockroach on ventral surface of *Dumortiera hirsuta*. Photo courtesy of Chatervedi.



Figure 129. *Dumortiera hirsuta*, a hiding place for cockroaches. Photo by David T. Holyoak, with permission.

ISOPTERA – Termites

Termites have lost their status as an order and are now included as an infraorder within the **Blattodea**. Termites have a division of labor much like that of the ants.

There are some bizarre habitats occupied by bryophytes, and these include termite mounds (Figure 131-Figure 133). One of these is the preferential occurrence of four species of *Fissidens* (*F. gymnostomus*, *F. hornschurchii*, *F. scariosus*, and *F. subulatus*) on termite structures in the Amazon (Reese & Pursell 2002). In one case, *F. allionii* co-occurred with *F. subulatus* on mounds in Amazonian Brazil. In another *F. pellucidus* var. *pellucidus* (Figure 130) and *F. prionodes* both occurred on one mound.



Figure 130. *Fissidens pellucidus* var. *pellucidus*, a termite mound colonizer. Photo by Scott Zona, with permission.



Figure 131. Termite mounds in the Bungle Bungle Range in Western Australia. Photo by Ouderkraal, through Creative Commons.



Figure 132. *Nasutitermes triodiae* in Northern Territory, Australia. Photo by J. Brew, through Creative Commons.

These organically enriched structures may benefit from the mosses through erosion control, while the mosses benefit from enrichment by feces, saliva, and other substances (Reese & Pursell 2002). The raised mounds serve in the same way as tree roots and soil banks by elevating the substrate above the leaf litter accumulation. Nevertheless, few other mosses and liverworts seem able to live in this habitat.

It appears that *Fissidens* may actually help the termites (Reese & Pursell 2002). One can observe fishbone-like patterns on some kinds of termite nests, and *Fissidens* provides such a pattern on nests it occupies. This pattern most likely facilitates drainage of rainfall. Furthermore, the mosses can serve to bind the particles that comprise the nest as well as softening the blow as raindrops strike.

Fissidens termitarum in Bolivia and Brazil occurs almost exclusively on termite structures (Reese & Pursell 2002). In the Amazon Churchill (1998) recorded 13 of the

38 *Fissidens* taxa on termite structures, but none were found there exclusively. In Rondônia, Brazil, Lisboa (1993) found 7 of the 15 *Fissidens* taxa associated with termite nests.



Figure 133. Termite mound with mosses at base. Photo by Izuchukwu Ezukanma, with permission.

Fissidens is also known from termite mounds in Africa (Potier de la Varde 1928, 1936; Bizot & Pócs 1979; Bizot *et al.* 1990; Bruggeman-Nannenga 1993). Likewise, Catcheside and Stone (1988) reported this genus from termite mounds in northern Australia. Even Mitten (1869) referred to *Fissidens pellucidus* (Figure 130) on "ant mounds," but Reese and Pursell (2002) considered that these were most likely termite mounds.

Other species of mosses are rare on the termite structures. Reese (2001) reported several species of *Calymperaceae* on termite structures. Churchill (1998) has the largest number of collections noted, including *Calymperaceae*: *Syrrhopodon cryptocarpus* (Figure 138), *S. ligulatus*, *S. xanthophyllus*; *Pilotrichaceae*: *Brymela parkeriana*; *Stereophyllaceae*: *Pilosium chlorophyllum*. Reese and Pursell (2002) found *Phyllocladus falcifolium* (*Phyllocladaceae*) with *Fissidens* on one termite structure in the Amazon. Nevertheless, none of these non-*Fissidens* species seems to frequent the nests. Ezukanma (in prep) found 5 species (none included above) on termite nests in the Eastern Nigeria highlands: *Campylopus savannarum* (Figure 134), *Daltonia angustifolia* var. *angustifolia* (Figure 135), *Philonotis hastata* (Figure 136), *Rhachitheciopsis tisserantii*, and *Sematophyllum brachytheciiforme*.



Figure 134. *Campylopus savannarum*, a species that occurs on termite nests in the Eastern Nigeria highlands. Photo by A. J. Ramalho, through Creative Commons.



Figure 135. *Daltonia angustifolia*, a species known from Nigerian termite mounds, shown here growing on the weevil *Gymnopholus reticulatus*. Photo courtesy of Rob Gradstein.

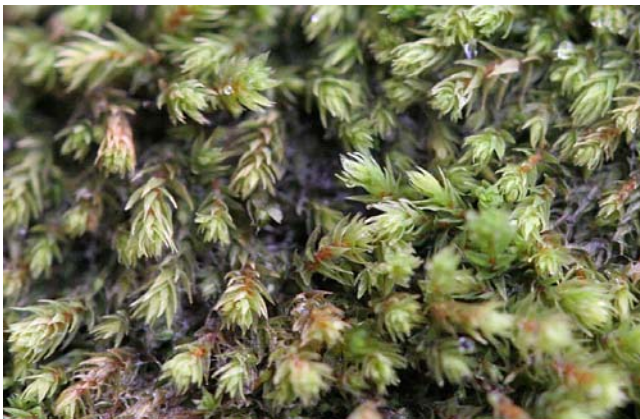


Figure 136. *Philonotis hastata*, a species known from Nigerian termite mounds. Photo by Michael Lüth, with permission.

Termites are generally unable to digest mosses (Bush 2015). Their guts have protozoa that facilitate their digestion of cellulose and lignin, hence their ability to eat wooden houses. Some people have considered termites to actually be a deterrent to mosses. Bush (2015) refers to a study in Ontario, Canada, that compared various types of

mulch on termite mortality. When used as the only source of food, peat moss starved the termites to death. Another study showed that subterranean termites tended to avoid travelling through peat, but only if the peat was moist. Dry peat seemed to have no effect.

Nevertheless, *Hospitalitermes umbrinus* (Termitidae; Figure 137) has "food balls" that contain bryophytes, but it prefers lichens (Collins 1979). This species forms foraging parties of roughly 500,000 soldiers and workers that leave the nest in the evening and return in the morning carrying these food balls.



Figure 137. *Hospitalitermes umbrinus*, a species that makes food balls containing bryophytes. Photo by Budak, through Creative Commons.

Termite mounds are an interesting ecosystem engineering feat. The termites actually benefit the ecosystem. The structure of these mounds cause more water to be absorbed into the soil and thus provide oases where green plants are able to subsist, preventing desertification (Bonachela *et al.* 2015; Hance 2015).



Figure 138. *Syrrhopodon* sp. Several species in this genus are known from termite mounds. Photo by Blanka Shaw, with permission.

EMBIOPTERA - Webspinners

This is a little-known order of tropical and subtropical net spinners. The name *embio* refers to the fluttery wings (*ptera*) of the first one described (Meyer 2009). One must wonder why one net spinner was collected from a moss cushion in Israel (Gerson 1982), but the image (Figure 139) below from Brazil supports it.



Figure 139. **Embioptera** from Brazil with net on mosses. Photo by Arthur Anker, with permission.

Summary

The **Orthopteroidea** include grasshoppers, pygmy grasshoppers, crickets, wetas, katydids, walking sticks, preying mantids, cockroaches, ice crawlers, and **Embioptera**. Among this group are many forms of camouflage and mimicry, and some of these are adaptations to living among bryophytes.

The pygmy grasshoppers (**Tetrigidae**) include many species that live among bryophytes and eat them. Some species have multiple morphs, permitting the species to occupy a variety of habitats. Many in this family also lay eggs there, as do many members of the **Acrididae**, a family that also includes bryophyte feeders. *Discotettix beelzebuth* has bryophytes growing on it, providing camouflage.

Mosses contribute a variety of patchy habitats that enable grasshoppers to remain separated spatially, supporting **Gause's** law by coexisting in the same environment but failing to compete due to the spatial separation.

Gryllidae (crickets) are rare among bryophytes, with bogs being the primary bryophyte habitat for them. Wetas are often found with bryophytes in caves or among them on tree trunks.

Rhaphidophoridae (camel crickets and wetas) include cave dwellers and other species that have color patterns blending with bryophytes. Some of the cave crickets also eat bryophytes.

Tettigoniidae (katydids) are good leaf mimics and some blend well with bryophytes by having a more broken color pattern. Some feed on *Sphagnum* and some lay their eggs there.

Walking sticks (**Phasmida**) are the master of disguise, mimicking pendent mosses in their rainforest homes. This type of mimicry, in which the insect can be mistaken for a hanging moss, may more

appropriately be termed **masquerading**. This type of mimicry has recently been termed masquerading. Some of these seem to have egg shapes adapted for oviposition among bryophytes.

The mantids (**Mantodea**) can have bryophyte camouflage and blend well, but their broad bodies prevent them from being mimics of pendent bryophytes. However, some do an excellent job of mimicking leaves with epiphylls living on them, including liverwort epiphylls, by having their own garden of bryophytic epizoots.

Cockroaches (**Blattodea**) seem to avoid mossy habitats, but one image shows the **ootheca** on bryophytes with liverworts growing onto the ootheca. Termites, formerly **Isoptera**, are members of the **Blattodea**. They often build mounds, especially in Australia, Africa, and the Amazon. These mounds are suitable habitats for a number of species of *Fissidens*, some of which seem to prefer that habitat. Few other bryophyte species occupy the mounds.

The **Embioptera** are probably not moss dwellers, although they were reported among mosses once.

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CHAPTER 12-5 TERRESTRIAL INSECTS: HEMIMETABOLA – NOTOPTERA AND PSOCOPTERA

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CHAPTER 12-5

TERRESTRIAL INSECTS:

HEMIMETABOLA – NOTOPTERA AND PSOCOPTERA



Figure 1. Example of **Mantophasmatodea**, a subgroup of the **Notoptera**. Photo by Michael F. Schöntzer through Creative Commons.

NOTOPTERA

The order **Notoptera** perhaps deserves its own chapter simply because the smallest chapter is appropriate for the smallest order (<30 species) of insects (Ando & Machida 1987). But alas, for practical reasons, I have included the **Psocoptera** here as well, a much larger order but rare among bryophytes. The order **Notoptera** is poorly known and has limited, but widespread, distribution. Nevertheless, it is important in our understanding of insect evolution (Vrsansky *et al.* 2001). And mosses seem to play a role for at least some of their lives.

The order **Notoptera** is **relict** (survived from an earlier time period) (Vrsansky *et al.* 2001; Schoville & Kim 2011) and in addition to the two living families, it is known from fossils in middle Eocene (Lutetian) Baltic amber (Ariño & Engel 2006) and the Lower Permian (Aristov 2004), suggesting that it has been widespread in time and space. The living **Notoptera** are known only from Canada (Walker 1914), western United States (Caudell & King 1924; Kamp 1963, 1970), Russia (Bey-Bienko 1951; Kevan 1979), Korea (Storozhenko & Park 2002; Kim &

Lee 2007), China (Wang 1987), and northern Japan (Schoville 2010). Genetic isolation in parts of Asia may have resulted from geologic events in which islands fragmented and collided, causing mountain uplifts in Japan (Schoville *et al.* 2013). The remaining taxa appear to be a "poorly dispersing, cold-adapted terrestrial insect lineage" that occupies Japan, Korea, and Russia. The island fragmentation events have created a number of endemic species. In the western US, several *Grylloblattidae* and *Gryllacrididae* returned to the devastated Mt. St. Helens within three years after its eruption in 1980 (Sugg & Edwards 1998), suggestion that it has some means of dispersal.

The order **Notoptera** was named in 1915 but was largely overlooked (Wikipedia 2016a). More recently, it was somewhat resurrected and joined with the *Grylloblattodea*, placing both of them in the order **Notoptera**.

These insects resemble mantids, but never have wings (Ando & Machida 1987). They live under stones and in

caves in the alpine areas (Schoville & Kim 2011). They are well adapted to cold conditions (Pritchard & Scholefield 1978; Kevan 1979; Jarvis & Whiting 2006). Many retreat deep below the surface to escape surface temperatures ranging -35 to +45°C (Kevan 1979).

Grylloblattodea – Ice Crawlers

The **Grylloblattodea** are predominately nocturnal and feed on detritus (Wikipedia 2015). They are wingless and have either reduced eyes or no eyes (Figure 2). There is only one family and it is comprised of only 5 genera and 34 species that live mostly in leaf litter and under stones of extremely cold environments of higher elevations.



Figure 2. Member of **Grylloblattidae** on snow, a small family that may lay eggs in mosses. Photo by Alex Wild through Creative Commons.

When temperatures are cold enough for ice crystals to form in the body, the **Grylloblattidae** retreat under the snow pack near the soil (Grimaldi & Engel 2005). They feed mostly on arthropod carcasses, but if these are insufficient they rely on plant material (Wikipedia 2015). At least one member deposits its eggs among mosses (Richards & Davies 1977).

Grylloblattidae – Ice Crawlers

The North American ice crawlers are known for their adaptations to cold, whereas the Asian members are the most diverse (Jarvis 2005; Jarvis & Whiting 2006). They are rarely encountered, but this may be due to their seclusive habit of going underground or hiding among mosses. Bai *et al.* (2010) suggested that they lost their wings and became adapted to living under rocks or hidden in mosses in cold areas.

Most members of this family are carrion feeders, but they will also eat plant material, fungi, and detritus (Bai *et al.* 2010).

The modern (extant) members of this family are 14-34 mm long, pale, wingless, and avoid light (nocturnal or living in caves) (Bai *et al.* 2010).

Galloisiana

Galloisiana nipponensis (Figure 3) was first described by Caudell and King in 1924 from Japan. This was the introduction of a new genus and new family, the **Grylloblattidae**. This species occurs on the ground under stones and in moss (Memim Encyclopedia 2015). To date, no eggs have been found among mosses in **G. nipponensis** (Rentz & Ingrisch 2009).



Figure 3. **Galloisiana nipponensis**, an extant member of the **Notoptera** in northern Japan. Photo by Obsidian Soul through Creative Commons, with modified background.

Three quarters of a century later, **Galloisiana olgae** is a recently described species occurring in a small area on the banks of the Vasilkovka River in southeastern Russia (Vrsansky *et al.* 2001). The genus has also spread to Korea (Schoville & Kim 2011) and China (Wang 1987). It inhabits wet soil and is found under rocks that are covered with mosses. This raises an interesting question. What is the importance of the mosses on those rocks. I venture a guess. This and all members of the order are omnivores, often feeding on carcasses of other arthropods (Wikipedia 2015). Rocks with mosses provide easy access for these wingless insects to hunt for food among the mosses at night (or whenever they feed).

Grylloblatta

In North America, 13 species of **Grylloblatta** (Figure 4) have been described, but Schoville and Graening (2013) considered that another 16 are awaiting description and publication. Its known distribution in western North America (Caudell & King 1924) includes California, USA (Caudell 1923; Schoville & Roderick 2010; Schoville 2012), to British Columbia, Canada (Gregson 1938; Kamp 1979; Huggard & Klenner 2003). This is a genus with high endemism and small species ranges.

Bai *et al.* (2010) considered temperature to be the primary limiting factors in their distributions. This does not bode well for them in the face of global warming. A species of **Grylloblatta** (Figure 4) on Mt. Rainier, Washington, USA, is active on the snow in summer, where it forages at night (Edwards 1982). But they have behavioral strategies that enable them to avoid freezing, as seen in this **Grylloblatta**. This species lacks the usual means to survive freezing (cryoprotectants, supercooling) and dies at a mere -6.5°C (Edwards 1987). On the other hand, it experiences heat convulsions at temperatures of 14°C. Morrissey and Edwards (1979) similarly found that the Mt. Rainier species suffers lethal heat convulsions at 15-20°C and speculated that unsaturated fatty acids might be important in their low-temperature adaptations. Could it

be that arachidonic acid, a polyunsaturated fatty acid in mosses, might contribute to this cold tolerance? Nevertheless, it migrates downward to overwinter among the rocks under deep snow where it is assured of temperatures above its -6.5°C lethal temperature (Edwards 1987). Henson (1957) was able to maintain nymphs of *Grylloblatta campodeiformis* (Figure 4) at 4.5°C for six months.



Figure 4. *Grylloblatta campodeiformis*, a cold climate species that lays eggs on mosses. Photo through NSF public domain.

Huggard and Klenner (2003) collected 147 specimens of *Grylloblatta campodeiformis* (Figure 4) in British Columbia, Canada, in pitfall traps in the subalpine spruce-fir forest and lower elevation cedar-hemlock forest. Many were associated with mossy old-growth forests. They suggested that the moss layer was important for this species and that forest management practices might be reducing suitable habitat by affecting microclimate and snow accumulation – and moss cover.

When the female is about one year old, she will deposit black eggs singly among mosses or in soil (Kamp 1963, 1970; Ramel 2015). These eggs require another year to incubate, and the nymphal instars require about 5 years (8 instars) to become adults.

Grylloblatta campodeiformis (Figure 4) is a predaceous species that feeds on other arthropods (Pritchard & Scholefield 1978). Pritchard and Scholefield collected this species in the Rocky Mountains in Alberta, Canada at 1300 asl. Beamer (1933) found *G. campodeiformis* var. *occidentalis* in Mt. Baker in Washington.

The gut contents contained arthropods and little else, with a crane fly in the Tipulidae being the most common food. Both the *Grylloblatta campodeiformis* (Figure 4) and the tipulid are typical of cold, montane habitats. The *G. campodeiformis* eat only live or recently killed animal prey and both larvae and adults fail to develop or grow without animal food. To detect their prey, they use their antennae. Both the antennae and palpi (mouth parts) have sensitive hairs that most likely help in prey identification. The prey are seized by the mandibles.

I would expect to find some of them living among mosses or going there to feed because there are several species of crane fly larvae that live among the mosses. It could explain their association with the moss layer in old-growth forests. One cannot expect a wingless species to travel very far for food.

Members of *Grylloblatta* (Figure 4) possess **sensilla** (McIver & Sutcliffe 1982), a series of branched hairs protected by cuticle near the tip of the mandibles. Baker (1982) suggests they may be used to sense the pressure being exerted on the mandible tips, perhaps avoiding damage to the muscles.

Grylloblattella

Grylloblattella cheni was described as the second species in this genus, occurring in China (Bai *et al.* 2010). It is known from only one specimen, collected in the primary boreal coniferous forest near a lake. It was under the bark of a log near the summer snow line. This and other extant species have a shorter meso- and metathorax than prothorax, the opposite of the fossil species where the prothorax is shorter. They suggest this may be due to the loss of wings in the extant species.

PSOCOPTERA – Booklice, Barklice, Barkflies

This order is considered the most primitive of hemipteroids (Wikipedia 2016b). These are small insects (1-10 mm long). The barklice are harmless to the trees where they live, eating mostly algae and lichens. Their small size apparently makes scraping their food somewhat hazardous; their chewing mandibles are accompanied by a slender rod modified from the central lobe of the maxilla. This modified rod is used to brace them while they scrape their food with their mandibles. Some can spin silk, covering large areas of the bark (Hoell *et al.* 1998).

Most of the **Psocoptera** feed on detritus, epiphytes, fungi, and some on leaves (Baz 2008). They have a thin cuticle and thus are susceptible to desiccation. They are able to take up moisture from the atmosphere and obtain some of their water from food, but rarely by drinking.

Bryopsocus (**Bryopsocidae**) is associated with trees and mosses in wet forests (New & Lienhard 2007). This genus is endemic to New Zealand. Only two species occur there, both associated with mosses: *Bryopsocus angulatus* and *B. townsendi*, ranging 2-3 mm long (Bess & Johnson 2009). Likewise in New Zealand, *Echmepteryx madagascariensis* (**Lepidopsocidae**; Figure 5) lives on mosses that grow on the horizontal trunks of *Metrosideros* (Figure 6) (Smithers 1973). Smithers (1974) also collected *Spilopsocus avius* (**Elipsocidae**) from mosses in the subAntarctic islands of New Zealand.



Figure 5. *Echmepteryx madagascariensis*, a species that lives among mosses on horizontal trunks of *Metrosideros*. Photo by Sean McCann through Creative Commons.



Figure 6. *Metrosideros umbellata* (rata) showing horizontal trunks with mosses where one might find *Echmepteryx madagascariensis*. Photo by John Barkla, with permission.

Evidence of members of **Psocoptera** eating bryophytes is limited. Valle *et al.* (1977) reported one that feeds on mosses and lichens growing on citrus in Cuba.

Lucking (2000) pointed out that the **Psocoptera** are among the insects that feed on epiphyllous bryophytes, as well as other organisms (algae, fungi, lichens) that grow on the leaves. Unlike the **Lepidoptera** feeding there, the **Psocoptera** are generalists, eating whatever is available on the leaf. They typically lay their eggs on the lower leaf surfaces. The young juveniles are protected by their mothers. Lucking concluded that although they did considerable damage to the leaf habitat, they positively influenced the diversity of the lichen and bryophyte community.

Schmidt and New (2008) recorded other **Psocoptera** in association with mosses in Tasmania. *Lepinotus patruelis* (**Trogiidae**; Figure 7) was among mosses on a log; *Liposcelis* (**Liposcelidae**; Figure 8) occurs among mosses on logs and living trees.



Figure 7. *Lepinotus patruelis*, a moss dweller on logs and trees in Tasmania. Photo from <www.aphotofauna.com>, with permission.



Figure 8. *Liposcelis* sp. hiding under bark. Photo by Peter J. Bryant, with permission.

Some members of this order are known from mossy forests, but the role of the mosses is unclear. García Aldrete (2009) reported several species from this habitat in Argentina: *Polypsocus jujuyensis*, *Polypsocus selenius* (**Amphisocidae**), *Lachesilla dividiproctus*, *Lachesilla peckorum*, and *Lachesilla cuala* (**Lachesillidae**). On the other hand, Thornton (1985) found that the numbers and diversity of **Psocoptera** decreased on mountain tops with wet conditions and epiphytic mosses in many areas of the Pacific.

Some **Psocoptera** are restricted to caves. The **neotenous** (retaining juvenile characteristics in adults) *Cyptophania pakaratii* (Figure 9) seems to be limited to the fern-moss "gardens" in the cave entrances (Figure 10) in the Pacific basin (Mockford & Wynne 2013). These habitats serve as relict habitats of the last glacial maximum, supporting species that are restricted to the conditions they offer (Benedict 1979; Northup & Welbourn 1997; Wynne 2013; Wynne *et al.* 2014).



Figure 9. *Cyptophania pakaratii*, a species apparently restricted to the fern-moss patches in cave entrances. Photo by Jut Wynne, with permission.

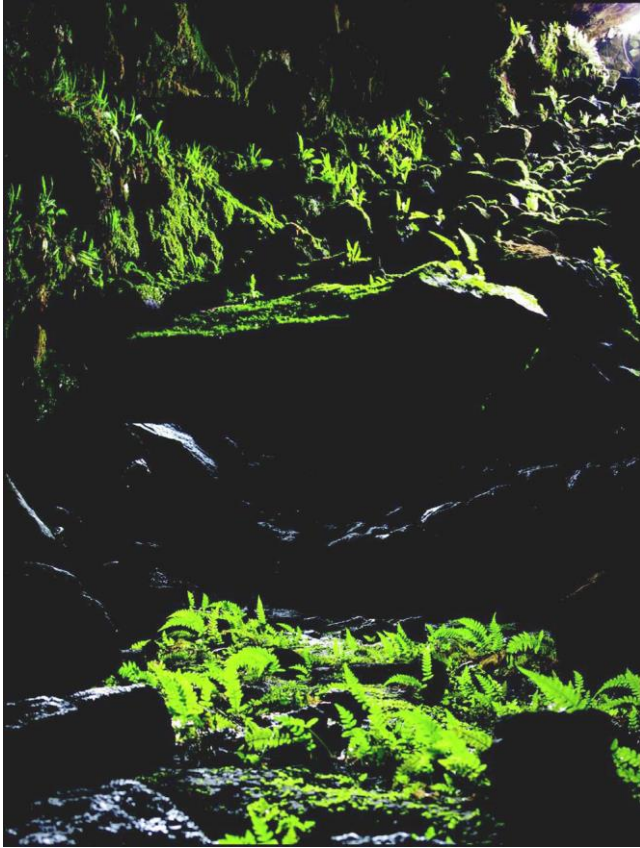


Figure 10. Relict fern-moss garden in cave at Rapa Nui National Park, Easter Island, Chile. Photo by Jut Wynne, with permission.

Summary

The **Notoptera** is a small order of relict insects, due in part to absence of wings and dispersal limitations. The **Grylloblattodea** (ice crawlers) are mostly nocturnal detritus feeders. Some can use mosses for oviposition. Members of **Grylloblattidae** may live under mosses in cold regions. **Grylloblatta campodeiformis** is often associated with mossy old-growth forests and deposits her eggs on the mosses.

Few species of **Psocoptera** are moss inhabitants, but their small size permits some of them to live there. The genus **Bryopsocus** is known only from mossy habitats in New Zealand. Some may feed on bryophytes, including epiphyllous bryophytes. Some are restricted to cave entrances where they live among mosses and ferns.

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Thank you to Wikipedia as a free source of basic information on so many taxa. Those who have placed their images in the public domain or given me permission have made this chapter more interesting for the readers.

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CHAPTER 12-6

TERRESTRIAL INSECTS: HEMIMETABOLA – HEMIPTERA (HETEROPTERA)

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CHAPTER 12-6

TERRESTRIAL INSECTS:

HEMIMETABOLA – HEMIPTERA

(HETEROPTERA)



Figure 1. Lacebug (**Tingidae**) with moss *Tortula papillosa* and lichen *Candelaria concolor*. Photo by Robert Klips, with permission.

HEMIPTERA – True Bugs

While many people call all insects bugs, there is only one order that officially carries that name. Their scientific name of **Hemiptera** revealed their most unique character, wings that are "half" membranous and "half" chitinized. But recent classification has added other groups to the **Hemiptera** that do not have this character, and some have no wings at all. The order is now divided, including the traditional "bugs" in the suborder **Heteroptera**. The **Hemiptera** are **hemimetabolous**, having a life cycle of eggs, nymphs, and adults. The overwintering stage depends on the species and may be spent among mosses.

Although most bugs feed on tracheophyte (mostly flowering plant) leaves, often specializing on one species, for many the bryophytes are important alternate hosts when the tracheophyte leaves are no longer available or no longer hospitable. But Rédei *et al.* (2003) considered the ground fauna to be under-sampled relative to the pest species that

occurred above ground on plants. Using Berlese funnels for extraction (without specifying sample size) they found that the assemblages of **Hemiptera** from mosses were similar to those from soil and could occur "in great numbers" (Table 1). In fact, moss samples had higher numbers per sample than soil samples, although it is hard to know the appropriate base (weight, area, volume, *etc.*) on which to compare them. To sample **Hemiptera** among bryophytes, Marie-Claude Larivière uses a sieve technique (Figure 2).

As an example of moss hemipteran diversity, the communities among various moss species in Hungary differ little from each other, with the exception of those on *Sphagnum* (Figure 3; Table 1) (Rédei *et al.* 2003). On the other hand, the **Hemiptera** communities on bryophytes differ significantly ($p < 0.05$) from those of tussocks and those of soil, leaf litter, and debris (Figure 4). An important factor among the bryophyte habitats is the moisture level. Mosses on the ground retain water longer

than those on tree trunks, with those on rocks retaining the least water and providing the driest habitats. Consequently, **Hemiptera** species preferring humid conditions are common among bryophytes on the ground and some tree trunk conditions but do not occur among the drier rock dwellers.

Table 1. Comparison of Hemiptera in bryological samples and non-bryological samples on the ground. From Rédei *et al.* 2003.

substrate	number of samples	number of specimens	number per sample
mosses on tree trunks	225	725	3.2
mosses on stones and rocks	292	1240	4.2
mosses on ground	259	520	2.0
other mosses	117	221	1.9
<i>Sphagnum</i>	94	107	1.1
soil	390	159	0.4
leaf litter, debris	795	586	0.7
tussocks, tufts of sedges	287	209	0.7



Figure 2. Marie-Claude Larivière sifting moss and leaf litter in NZ to find **Hemiptera**. Photo by André Larochelle, with permission.



Figure 3. *Sphagnum* becoming established on *Potentilla fruticosa* as a fen becomes more moist and acidified. The fen and bog locations typically have both flowering plants and mosses, providing the two alternative hosts needed by many **Hemiptera** species. Photo by Janice Glime.

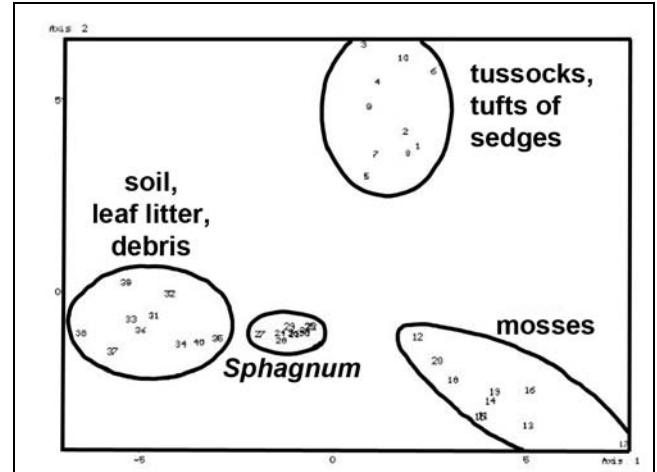


Figure 4. Similarity pattern of communities associated with the four major substrata groupings of Hungarian hemipteran ground fauna. Redrawn from Rédei *et al.* 2003.

True bugs are affected by the nutrients available to mosses. Richardson *et al.* (2002) found that moss-feeding true bugs in fertilized plots in Scandinavia diminished in number to as little as 6% of those in the unfertilized controls. The **Homoptera** on grasses, on the other hand, were more than 400% more abundant, indicating that fertilization was detrimental to the moss communities. Such a reduction could be the result of nutritional changes in the mosses or a reduction in mosses, reducing both food and cover for bryophyte-adapted bugs.

Adaptations

Most of the bugs that live among bryophytes are tiny, often only 1-2 mm in length. Their biggest adaptation is that many of the moss dwellers are able to eat mosses. This ability not only may involve differences in mouthparts, but at least sometimes requires the presence of **endosymbiotic** bacteria to help in digestion (Kuechler *et al.* 2013). But it seems that few other adaptations exist. Their coloration is often brown, and I find that the common moss-dwelling lace bugs often resemble seeds, not mosses. That's not a bad appearance if you are hiding from carnivores, but it doesn't make you invisible. Instead, the coloration of most species is adaptive for the primary host. On the other hand, mosses provide a habitat where behavior is important. Many species are able to migrate vertically within the moss mat to find suitable temperature and humidity (Marie-Claude Larivière, pers. comm. 1 September 2015).

Nutrients

Among the factors that limit **Hemiptera**, nutrients in the plants can play an important role. This can be especially important for some adapted to Arctic and sub-Arctic habitats where nutrient turnover is slow. In a dwarf shrub heath community, Richardson *et al.* (2002) manipulated nutrients and temperatures to determine responses. Nutrient addition had a strong effect on the subordinate mosses and resulting changes in the abundance of the insect herbivores. These changes had a greater impact on the insect herbivore community than those of the shrub layer. Those **Hemiptera** (**Heteroptera**) on the fertilized plots reached an abundance only 6% that of the unfertilized controls. **Homoptera** (former classification),

on the other hand, were more than 400% more abundant. The grass-eating **Delphacidae** (plant hoppers) were only present in fertilized plots.

Habitats

Forests

Forests offer a variety of habitats for bryophyte-dwelling **Hemiptera** (Lattin & Moldenke 1990). In the woodland habitats of Hungary, Rédei *et al.* (2004) found *Acalypta carinata* (2.5 mm; **Tingidae**; Figure 5) among the *Sphagnum* (Figure 3) and the moss *Abietinella abietina* (Figure 6), living on tree trunks or the ground. This lace bug prefers humid, shady woodland habitats. *Acalypta musci* (2.5-2.8 mm; Figure 7) is typically a moss dweller, but it also occurs on fungi on tree trunks and among mosses at tree bases.



Figure 5. *Acalypta carinata* female on moss in Germany. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission



Figure 6. *Abietinella abietina*, a woodland home for *Acalypta carinata*. Photo by Janice Glime.



Figure 7. *Acalypta musci*, a species named for its association with mosses. Photo by Boris Loboda, with permission.

The mossy forests of the temperate and Antarctic rainforests of New Zealand (Figure 8) are home to the tiny **Peloridiidae** (2-4 mm) (Burckhardt 2010; Burckhardt *et al.* 2011; Harris 2011, 2014). The **Peloridiidae** also occur in temperate forests in Australia (Grozeva *et al.* 2014). The genus *Xenophyes* (2.18-3.23 mm; Figure 9), a member of **Peloridiidae**, is common in the rainforests throughout the southern hemisphere, including Chile, Argentina, New Zealand, New Caledonia, and Australia (Burckhardt *et al.* 2011). *Peloridium hammoniorum* (3.9-4.3 mm), the only member of the family with both winged and flightless forms, was recently described as a new species from Chilean secondary forests, living among mosses, primarily on *Polytrichadelphus magellanicus* (Figure 10) (Shcherbakov 2014).



Figure 8. Wet Rimu (*Dacrydium*) forest in New Zealand where **Heteroptera** live among mosses. Photo by Marie-Claude Larivière, with permission.



Figure 9. *Xenophyes rhachilophus*, member of a genus that is common among mosses in rainforests of the Southern Hemisphere. Photo by S.E. Thorpe, through Creative Commons.



Figure 10. *Polytrichadelphus magellanicus*, home of *Peloridium hammoniorum*. Photo by Juan Larrain, with permission.

Dikraneura aridella (5.6-6 mm; **Cicadellidae**; Figure 11) lives in moss-covered coniferous European forests, where it feeds on grasses (Söderman 2007). *Aguriahana pictilis* (~5 mm; **Cicadellidae**; Figure 12) likewise lives in moss-covered forests, but it feeds on blueberry (*Vaccinium myrtillus*) leaves. The importance of the mosses for these two species is unclear. Elsewhere, *Macrocixius emeljani* (0.51-0.64 mm; **Cixiidae**) and *M. oropilus* (0.69-0.70mm) live in high mountain mossy forests in Taiwan and Nepal (Orosz 2013). *Melanocoryphus albomaculatus* (~9 mm; **Lygaeidae**; Figure 13-Figure 14),

a critically endangered species in the Czech Republic, lives under lichens, moss, dry leaves, stones, etc. (Kment *et al.* 2013a). Its bright orange and black color patterns seem left over from some prior host of its relatives because they do not seem adaptive to mosses or to some of its host plants like *Senecio* (Chateau Moorhen 2015). And, oddly for a moss dweller, in France it likes hot, dry places!



Figure 11. *Dikraneura aridella*, a species that prefers moss-covered coniferous forests in Europe. Photo by Marko Mutanen, through Creative Commons.



Figure 12. *Aguriahana pictilis*, an inhabitant of moss-covered forests. Photo by Gernot Kunz, with permission.



Figure 13. *Melanocoryphus albomaculatus*, a critically endangered species in the Czech Republic, often living under mosses. Photo by Valter Jacinto, through Creative Commons.



Figure 14. *Melanocoryphus albomaculatus*, a moss dweller that does not have cryptic coloration for moss dwelling. Photo by Didier Descouens, through Creative Commons.

Larivière *et al.* (2011) reported *Oiophysa ablusa* (Peloridiidae; Figure 15) from montane *Nothofagus* forests in New Zealand where they lived among wet mosses and leaf litter. *Oiophysa cumberi* (Figure 16) is a more lowland species, living in broadleaf-podocarp and *Nothofagus* forests among both mosses and liverworts on the ground and on trees. *Oiophysa distincta* is likewise in the lowland to montane podocarp and *Nothofagus* forests where it lives among mosses on the ground and on trees as well as in litter. This species also occurs on the pendulous moss *Weymouthia* sp. (Figure 17).



Figure 15. *Oiophysa ablusa* on leafy liverwort. Photo by E. Wachmann through M.-C. Larivière, with permission.

Epiphytes

Tree-trunk bryophytes are typically drier than those growing on the ground and some species of *Lygaeidae* prefer to live among mosses in this habitat (Rédei *et al.* 2003). Members of *Peloridiidae* (Bechly & Szewdo 2007) and *Rhyparochromidae* (Rédei *et al.* 2003) are common on tree trunk mosses in Europe. Furthermore, the genus *Acalypta* (*Tingidae*) is represented there by a number of species, and *Piesma maculatum* (2-3 mm.; *Peismatidae*; Figure 18), *Myrmedobia exilis* (1.3-2.2 mm; *Microphysidae*; Figure 19), *Cryptostemma* (2.5-2.8 mm; *Dipsocoridae*; Figure 20), and *Ceratocombus coleoptratus* (1.5-2.0 mm; *Ceratocombidae*; Figure 21) also prefer this tree trunk habitat, as well as ground and other substrata.

Rédei *et al.* consider many terrestrial *Hebrus* (*Hebridae*; Figure 36-Figure 38) species, including young nymphal stages, to prefer moss on tree trunks, ground, and other surfaces. In Tasmania, *Xenophyes cascus* (2.48-3.10; *Peloridiidae*; Figure 22) occurs among bark mosses (Burckhardt *et al.* 2011).



Figure 16. *Oiophysa cumberi*, a moss inhabitant. Photo by George Gibbs, with permission.



Figure 17. *Weymouthia mollis*, home for some members of *Oiophysa distincta*. Photo by Phil Bendle, through Creative Commons.



Figure 18. *Piesma maculatum*, a hemipteran living among mosses on tree trunks. Photo by Joe Botting, with permission.



Figure 19. *Myrmedobia exilis*, a tree-trunk bryophyte dweller. Photo by Mardon Erbland, through Creative Commons.



Figure 20. *Cryptostemma* sp.; *Cryptostemma waltli* lives among mosses in shaded habitats. Photo by Michael F. Schönlitzer, through Creative Commons.



Figure 21. *Ceratocombus coleoptratus*, a tree-trunk and ground moss dweller. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission

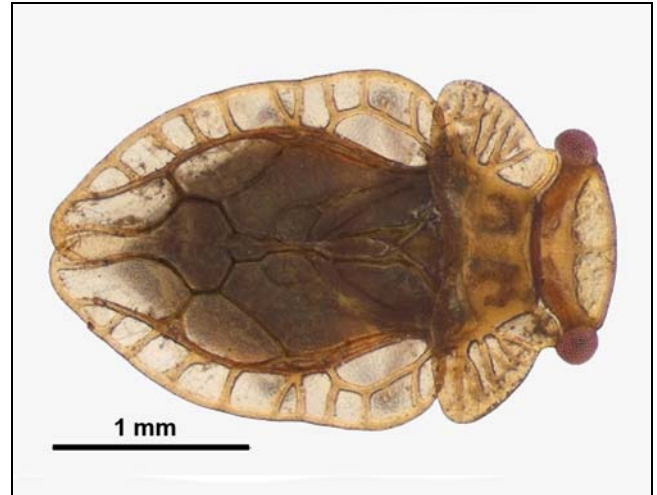


Figure 22. *Xenophyes cascus*, a species that lives among epiphytic mosses in epiphytes. Photo by Marie-Claude Larivière, with permission.

The **Saldidae** (shore bugs; Figure 24-Figure 23) include a range of habitats from the intertidal zone to terrestrial habitats. Among these habitats is the moss on the trunks of rainforest trees (Polhemus & Chapman (1979). *Lampracanthia crassicornis* (1 mm; Figure 23) and *Salda anthracina* (Figure 24) lay their eggs between the leaves of mosses (Hungerford 1918). *Salda anthracina* is much like the preying mantis in its mating behavior. But unlike the preying mantis, the male initially follows the female around, keeping a safe distance (Hungerford 1919). When he decides to mate (or the opportunity is right), he pounces upon her. He exits quickly at completion lest he too, like the preying mantis male, be eaten by his mate. And sometimes he is eaten.



Figure 23. *Lampracanthia crassicornis*, a species that lays its eggs on mosses. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons



Figure 24. *Salda anthracina*, a species that lays her eggs among moss leaves and will eat her mate if he doesn't leave fast enough. Photo by Tom Murray, through Creative Commons.

Sand Dunes

In dunes, bryophytes can offer respite from the dry sand. Spungis (2005) found that **Hemiptera** density was limited by available cover of mosses and lichens. Sand dunes are dry and inhospitable for insects that do not have desiccation protection. For some, that protection comes in surface waxes, hard chitin, and a reduced physiological need for water. For others, behavior is the most important adaptation, allowing the hemipterans to move to mosses when host plants become inhospitable. Spungis (2005) found that mosses provided a refuge for bugs in the coastal grey dunes (Figure 25) of Latvia. The number of species of **epigeic** (active at the soil surface) **Hemiptera** correlated with the moss-lichen cover in the dunes ($p < 0.01$). The density of ground-dwelling species was low and both population density and species diversity were limited by available cover of lichens and mosses. *Nysius thymi* (3.5-4.5 mm; **Lygaeidae**; Figure 26) and members of **Miridae** (jumping tree bugs; Figure 118-Figure 123) had high population densities and were dominant compared to the grass-dwelling hemipterans. *Sciocoris cursitans* (4.5-6.0 mm; Figure 27) in the **Pentatomidae** dominated the soil dwellers (41%), with a high correlation ($r = 0.81$; $p < 0.01$) with moss and lichen cover.



Figure 25. Coastal grey dunes in The Netherlands. Similar sites in Latvia have limited **Hemiptera**-moss associations, including mostly **Miridae**. Photo by Bas Kers, through Creative Commons.



Figure 26. *Nysius thymi* on thyme flower. This species is dominant in sandy areas of Latvia with dense moss and lichen cover. Photo by Tristan Bantock, with permission.



Figure 27. *Sciocoris cursitans* adult, a soil dweller with a high correlation with mosses and lichens. Photo by Tristan Bantock, with permission.

In Hungary, Rédei *et al.* (2004) found that *Acalypta gracilis* (2-2.8 mm; **Tingidae**; Figure 28) preferred the Pannonic dune open grassland patches (Figure 29) over the dune-slack (Figure 30) purple moor grass meadow. *Acalypta marginata* (2.0-3.0 mm; Figure 31-Figure 32) was present equally in the Pannonic dune open grassland and the Pannonic sand puszta patches (Figure 33), but likewise avoided the dune-slack purple moor grass meadow. Both species are moss dwellers.



Figure 28. *Acalypta gracilis*, a moss dweller that prefers dune open grassland in Hungary. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission.



Figure 29. Pannonic sand steppe, Hungary. Photo by Daniel Dítě in Šeffarová Stanová *et al.* 2008, with authorized reproduction.



Figure 30. Dune slack and meadow in UK, a habitat that seems to be avoided by moss dwelling *Acalypta* species in Hungary. Photo by David Hawgood, through Creative Commons.



Figure 31. *Acalypta marginata* with moss, a dweller among mosses in sandy areas, including dunes. Photo by Boris Loboda, with permission.



Figure 32. *Acalypta marginata* disappearing into the depths of a moss. Photo by Boris Loboda, with permission.



Figure 33. Pannonic sand puszta with draw well in Hungary. Photo by Andreas Poeschek, through Creative Commons.

Streamside and Wet Habitats

This habitat group includes bugs with high moisture requirements, but that are not truly aquatic. For example, *Macrovelia hornii* (4.2 mm; **Macroveliidae**; Figure 34) nymphs and adults live among mosses at the water's edge but are unable to live in the water or on its surface (Usinger 1974).



Figure 34. *Macrovelia hornii*, a moss inhabitant at water's edge. Photo by Jerry Wilson, with permission.

Hebrus concinnus (2.25-2.5 mm; **Hebridae**; Figure 35), from a genus that is dominant among **Hemiptera** in bogs and fens (see Chapter on aquatic Hemiptera in this volume), lays its eggs where they are partially concealed between moss leaves (Uisinger 1974). Schuh and Slater (1995) described them as living deep in moss mats, with *Hebrus ruficeps* (1.3-3.7 mm; Figure 36) overwintering frozen in ice among *Sphagnum* (Figure 37). *Hebrus pusillus* (1.6-2.1 mm; Figure 38) is associated with *Sphagnum* and other mosses (Howe 2004) and also reproduces among mosses at the edge of water (Münch 2013). Hebrids also often lay their eggs among mosses, suggesting that early instars may develop there.



Figure 35. *Hebrus concinnus*, a species that lays its eggs among mosses. Photo through Creative Commons.



Figure 36. *Hebrus ruficeps* on *Sphagnum*, a common bog dweller that overwinters in ice among *Sphagnum*. Photo by Ruth Ahlburg, with permission.



Figure 37. Frozen *Sphagnum fimbriatum* and ice habitat where *Hebrus ruficeps* is able to spend its winter in ice among the moss plants. Photo by Dick Haaksma, with permission.



Figure 38. *Hebrus pusillus*, among the dominant *Hebrus* species in bogs and fens. Photo by Joseph Botting, with permission.

Micracanthia schuhi (2.64-3.35; **Saldidae**; see Figure 39) is a moss dweller in Oregon, USA, where it lives beside a small stream on Mt. Hood among moist mosses (Lattin 1968, 1997). It moves up and down within the moss mat to achieve the best temperature level (Lattin 1968).



Figure 39. *Micracanthia marginalis*. *Micracanthia schuhi* lives among mosses on Mt. Hood, Oregon, USA. Photo by Jürgen Deckert, with permission.

Cryptostemma waltli (1.2-1.5 mm; **Dipsocoridae**; Figure 20) lives in shaded wet habitats where it inhabits the mosses *Sphagnum* (Figure 37), *Hypnum* (Figure 40), *Brachythecium* (Figure 41), and *Cratoneuron* (Figure 42) (Kment *et al.* 2013b).



Figure 40. *Hypnum lindbergii*, potential home for *Cryptostemma waltli* in wet, shaded habitats. Photo by Michael Lüth, with permission.



Figure 41. *Brachythecium rutabulum* with capsules, a genus that could be home to *Cryptostemma waltli* in shaded, wet habitats. Photo by Malcolm Storey through DiscoverLife.



Figure 42. *Cratoneuron filicinum*, one of the mosses that may house *Cryptostemma waltli* in shaded, wet habitats. Photo by J. C. Schou, with permission.

Peatlands

Peatlands are borderline between aquatic and terrestrial habitats. I have already discussed the more aquatic-leaning taxa in the chapter on Aquatic Insects, especially those living in bog pools. Here I will treat the species that use other (non-bryophyte) plants that live in the bogs, perhaps also using the mosses, but that require or benefit from the peatland habitat.

Rédei *et al.* (2003) found that the **Hemiptera** tussock community and species living among *Sphagnum* (Figure 3) species were comprised primarily of ubiquitous species that were able to occupy most kinds of mossy substrata. Like many other invertebrates, many of the species of **Hemiptera** are not restricted to bogs and tend to be widespread (Holzinger & Schlosser 2013).

Holzinger and Schlosser (2013) conducted a survey of the **Hemiptera** fauna of Austrian peat bogs in the Bohemian Forest. They found that the **Auchenorrhyncha** formed a considerable fauna, with 93 species among 7465 specimens in these bogs, making them one of the most abundant animal groups in peatlands (see also Holzinger 1995, 2000; Holzinger & Novotny 1998). Eleven of these species were either **tyrphobiontic** (peat bog specialist; restricted to bogs) or **tyrrophilous** (common in bogs but not restricted to them). Tyrphobiontic species in these bogs include *Sorhoanus xanthoneurus* (3.1-3.4 mm; **Cicadellidae**; Figure 43) and *Stroggylocephalus livens* (5-6.5 mm; **Cicadellidae**; Figure 44), *Kelisia vittipennis* (3-3.6 mm; **Delphacidae**; Figure 45), and *Cixius similis* (5 mm; **Cixiidae**; Figure 46) (see also Trivellone 2010). *Cixius similis* migrates from mosses to shrubs to feed and mate, then returns to the moss-covered ground to oviposit (Söderman 2007). Tyrrophilous species include the **Cicadellidae** *Sorhoanus assimilis* (often the most frequent hemipteran; 2-2.9 mm; Figure 47), *Cicadula saturata* (4-5.5 mm; Figure 48), and *Macrosteles ossiannilssoni* (Figure 49), and the **Delphacidae** *Paradelphacodes paludosa* (2.8-3 mm; Figure 50), *Kelisia ribauti* (3-4.5 mm; Figure 51), and *Oncodelphax pullula* (2-4 mm; Figure 52) (Holzinger & Schlosser 2013).



Figure 43. *Sorhoanus xanthoneurus*, a restricted bog dweller. Photo by Joe Botting, with permission.



Figure 44. *Stroggylocephalus livens*, a restricted bog species in Europe. Photo by Gernot Kunz, with permission.



Figure 45. *Kelisia vittipennis*, a species restricted to bogs. Photo by Joe Botting, with permission.



Figure 46. *Cixius similis*, a bog-restricted species that moves from mosses to shrubs to feed and back to mosses to oviposit. Photo by Joe Botting, with permission.



Figure 47. *Sorhoanus assimilis* adult, a bog-loving moss dweller. Photo by Gernot Kunz, with permission.



Figure 48. *Cicadula* sp. adult, a tyrphophilous species. Photo by Tristan Bantock, with permission.



Figure 49. *Macrosteles ossiannilssoni*, a tyrphophilous bog dweller. Photo by Marko Mutanen, through Creative Commons.



Figure 50. *Paradelphacodes paludosa* adult, a bog-loving moss dweller. Photo by Gernot Kunz, with permission.



Figure 51. *Kelisia ribauti*, a species that is common in bogs but that is not restricted to them. Photo by Gernot Kunz, with permission.



Figure 53. *Conomelus lorifer*, a bog dweller in Europe. Photo by Gernot Kunz, with permission.



Figure 52. *Oncodelphax pullula* on Cyanobacteria, a species that is common in bogs but not restricted to them. Photo by Joe Botting, with permission.



Figure 54. *Conomelus lorifer* adult, a bog dweller. Photo by Gernot Kunz, with permission.

Conomelus lorifer (Delphacidae; Figure 53-Figure 54) occurs in *Sphagnum-Carex* associations in Switzerland (Trivellone 2010) at higher altitudes (Ökteam 2012). *Conomelus anceps* (4 mm; Figure 55-Figure 56) is a lower altitude species and comprised 17% of the individuals in the Austrian peat bogs and was the most common species there (Holzinger & Schlosser 2013). This species was followed by *Muellerianella extrusa* (3.6-4.2 mm; Delphacidae; Figure 57) (9.2%), *Sorhoanus xanthoneurus* (Cicadellidae; Figure 43) (7.6%), *Jassargus pseudocellaris* (Cicadellidae; Figure 58) (5.5%), and *Macustus grisescens* (5-6 mm; Cicadellidae; Figure 59) (5.2%). Most of these species are **stenoeicous** (having a narrow habitat range) and specialize not only on the habitat, but also on their host plants (Nickel *et al.* 2002; Nickel 2003). The bogs have more **univoltine** (having one brood of offspring per year) **Auchenorrhyncha** species compared to other habitats in Austria and likewise more of their species in the bogs hibernate during their nymphal stage (Holzinger & Schlosser 2013). Densities of adults are low in spring (10-60 individuals per m²), rising to a high of 180 individuals per m² in July.



Figure 55. *Conomelus anceps* nymph, a bog dweller. Photo by James K. Lindsey, with permission.



Figure 56. *Conomelus anceps* adult, a bog dweller, with moss. Photo by Tim Faasen, with permission.



Figure 57. *Muellerianella extrusa*, a species associated with *Sphagnum* in Europe. Photo by Gernot Kunz, with permission.



Figure 58. *Jassargus pseudocellaris* adult, a species associated with *Sphagnum*. Photo by Tristan Bantock, with permission.



Figure 59. *Macustus grisescens*, a *Sphagnum* associate in Europe. Photo by Tristan Bantock, with permission.

In Austrian peatlands, life cycle stages of the **Auchenorrhyncha** represent different proportions than in the whole of the Austrian fauna (Figure 60) (Holzinger & Schlosser 2013). The number of generations tends to be fewer in peatlands than in the general fauna (Figure 60).

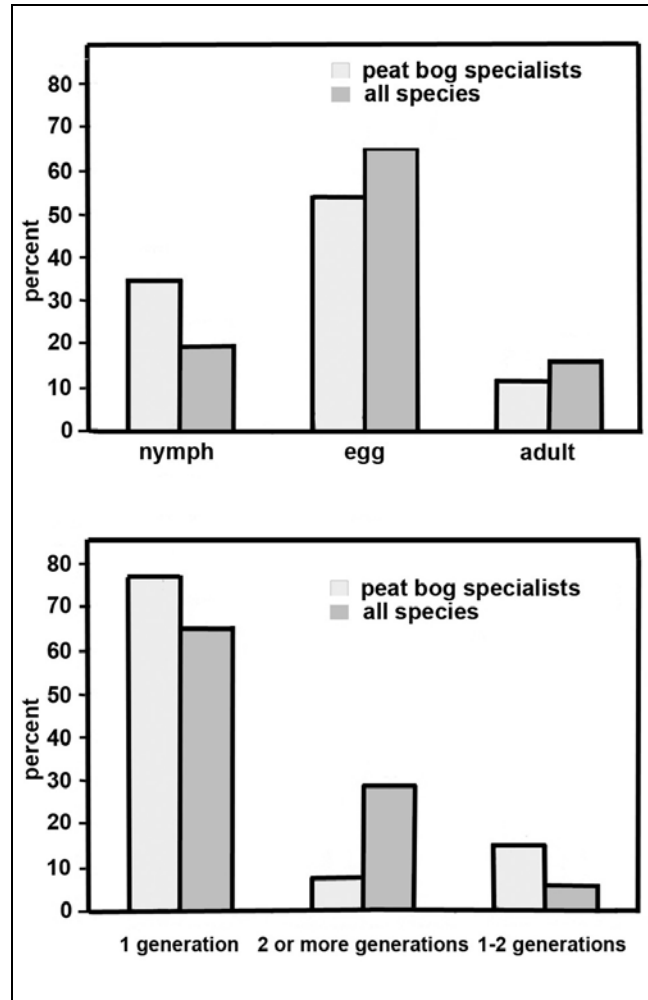


Figure 60. Comparison of generation stages and numbers of generations per year for species of **Auchenorrhyncha** in Bohemian forest peat bogs compared to those of the whole Austrian **Auchenorrhyncha** fauna. Redrawn from Holzinger & Schlosser 2013.

SUBORDER HETEROPTERA

(true, typical bugs)

PENTATOMOMORPHA – STINK BUGS, FLAT BUGS, AND SEED BUGS

Thyreocoridae – Ebony Bugs

One member of this family was collected among mosses of the Cheviot Hills, UK – *Corimelaena scarabaeoides* was common among mosses (Champion 1871). *Thyreocoris scarabaeoides* (Figure 61-Figure 63) is a common moss inhabitant, measuring only 3-4 mm (British Bugs 2015a). Its black color as an adult makes it difficult to notice in the depths of the moss. (I can't find confirmation of the nomenclature for *Corimeleana scarabaeoides*, so it may be a synonym of *Thyreocoris scarabaeoides*.)



Figure 61. *Thyreocoris scarabaeoides* mid-instar nymph, a common moss inhabitant in the UK. Photo by Tristan Bantock, with permission.



Figure 62. *Thyreocoris scarabaeoides* late-instar nymph. Photo by Tristan Bantock, with permission.



Figure 63. *Thyreocoris scarabaeoides* adult. Photo by Tristan Bantock, with permission.

Cydnidae – Burrowing Bugs, Shield Bugs

Burrowing bugs don't normally inhabit bryophytes, but there are some exceptions. These include the somewhat larger *Canthophorus impressus* (6-7 mm; Figure 64), a rare species (British Bugs 2015b) that hibernates in groups under mosses and leaves in winter (eImageSite.net 2013). Records for *Canthophorus dubius* (7mm; Figure 65) are often actually *C. impressus*, requiring dissection for certain identification (British Bugs 2015b).



Figure 64. *Canthophorus impressus*, a species that hibernates in groups under mosses. Photo by Tristan Bantock, with permission.



Figure 65. *Canthophorus dubius*, a winter moss inhabitant in the chalk downs of the UK. Photo by Dragiša Savić, with permission.

The shield bug *Adomerus biguttatus* (Figure 66-Figure 67) overwinters among bryophytes (Southwood & Leston 1959).



Figure 66. *Adomerus biguttatus* nymph on moss, its overwintering site. Photo by Tristan Bantok, with permission.



Figure 68. *Rhacognathus punctatus* nymph, a species that lives among mosses in heath in the UK. Photo by Tristan Bantok, with permission.



Figure 67. *Adomerus biguttatus* adult on moss, its overwintering site. Photo by Tristan Bantok, with permission.



Figure 69. *Rhacognathus punctatus* adult, a moss dweller. Photo by James K. Lindsey, with permission.

Pentatomidae – Stink Bugs and Shield Bugs

In Hungary this family is represented in great numbers in moss mats (Rédei *et al.* 2003). In the UK Champion (1871) reported *Rhacognathus punctatus* (7-9 mm; Figure 68-Figure 69) among mosses in heath (Figure 70) and *Zicrona caerulea* (5-7 mm; Figure 71-Figure 72) as a common bug among mosses on the chalk downs (Figure 73). *Sciocoris cursitans* (4.5-6 mm; Figure 27) dominated the epigeic Hemiptera at the coastal gray dunes in Latvia (Spungis 2005) and demonstrated a significant positive correlation with the amount of moss-lichen cover. This family seems to prefer mosses for cover in relatively exposed and dry habitats. Despite the statement by Rédei *et al.* (2003) that they occur in great numbers in moss mats, there seems to be little published about the role of these relationships.



Figure 70. Heathland where one might find *Rhacognathus punctatus* among mosses. Photo by James K. Lindsey, with permission.



Figure 71. *Zicrona caerulea* early instar, a moss inhabitant. Photo by Tristan Bantock, with permission.



Figure 72. *Zicrona caerulea* adult, a common bug among mosses in UK chalk grasslands. Photo from <www.entomart.be>, through Creative Commons.



Figure 73. Chalk downs at Chanctonbury Hill Chalk Pits, UK, home to *Zicrona caerulea* among mosses. Photo by Malcolm Oakley, with permission.

Berytidae – Stilt Bugs

The **Berytidae** are comprised of about 100 species (Encyclopædia Britannica 2015). They are delicate looking, with slender bodies, and despite their long legs they are slow moving. They are somewhat larger (5-9 mm) than most moss dwellers, but their brown color helps them to blend somewhat with at least some mosses. All members of the family are plant feeders and they

sometimes damage crop plants. A few are known moss dwellers.

Berytinus signoreti (4.5-6 mm; Figure 74-Figure 75), *Berytinus minor* (Figure 76), and *Neides tipularius* (10-11.5 mm; Figure 77) are all moss dwellers in the UK (Champion 1871). Woodroffe (1959) reported *Berytinus signoreti* occurring under the flower *Lotus corniculatus*, but also noted "scattered individuals" among mosses. *Berytinus minor* is common among mosses and grass roots in the UK (Douglas & Scott 1865). In Dorset, England, members of *Cymus* (2.5-5 mm; Figure 78-Figure 79) live in meadows and heathlands on rushes, but in winter this genus overwinters under moss or bark (Recording Dorset 2011).



Figure 74. *Berytinus signoreti*, a moss dweller in the UK. Photo by Tristan Bantock, with permission.



Figure 75. *Berytinus signoreti* adult, a moss dweller. Photo by Tristan Bantock, with permission.



Figure 76. *Berytinus minor*, a moss dweller in the UK. Photo by Miroslav Deml, through Creative Commons.



Figure 77. *Neides tipularius*, a moss dweller in the UK. Note the long legs. Photo by Tristan Bantock, with permission.



Figure 78. *Cymus glandicolor* nymph, a moss dweller. Photo by Tristan Bantock, with permission.



Figure 79. *Cymus glandicolor*, a species that overwinters under mosses or bark. Photo by Tristan Bantock, with permission.

Lygaeidae – Seed Bugs and Milkweed Bugs

Most of the members of this family are ill-suited for living among bryophytes. They typically feed on seeds, but

some are predatory, some feed on sap, and some feed on blood (TrekNature 2011). They often exhibit bright colors (Figure 80) and are too large to move easily among most kinds of mosses.



Figure 80. *Lygaeus creticus* on *Atrichum*, exhibiting a size and sharp color contrast that does not make this a safe environment. Photo by Dragiša Savić, with permission.

In Eastern Europe, Kment *et al.* (2013a) found *Melanocoryphus albomaculatus* (7-9.5 mm; Figure 13-Figure 14), a colorful bug, under lichens, mosses, dry leaves, and stones. They preferred sunny rocky hillsides and clearings. Perhaps its red and black warning colors are enough to scare away would-be predators, or it simply isn't seen when under the moss. *Taphropeltus hamulatus* (2.9-3.4 mm; Figure 81) lives in well-drained base-rich sites, particularly among the mosses in areas with loose rocks (Alexander 2008). At least its colors are less conspicuous. *Lamproplax picea* (4.0-5.0 mm; Figure 82) is a moss dweller in the UK and has similar dark coloration (Hallett 1916).



Figure 81. *Taphropeltus hamulatus*, a moss dweller in well-drained, base-rich sites. Photo by Tristan Bantock, with permission.



Figure 82. *Lamproplax picea*, a moss dweller in the UK. Photo by Joe Botting, with permission.

Piesmatidae – Ash-Grey Leaf Bugs

This is a small family of plant-eating bugs. Using the Berlese funnel to extract bugs from various substrata, Rédei *et al.* (2003) found that *Piesma maculatum* (2-3 mm; Figure 83) preferred to live among mosses on tree trunks, ground, and other substrata. Alexander (2008) likewise found it in moss litter in the UK. I have not found any other records for this family among bryophytes.



Figure 83. *Piesma maculatum*, a species that "prefers" living among mosses. Photo by Joe Botting, with permission.

Rhyparochromidae – Seed Bugs

I discovered a record of this family by accident as I was searching for harvestman pictures. Naturalist Graeme Lyons (2011) of Sussex, UK, reported "beating" a clump of *Thuidium tamariscinum* (Figure 84) to find invertebrates. With this activity, he was able to add a new species of **Hemiptera** to his list of finds: *Peritrechus nubilus* (5-6 mm; Figure 85). In New Zealand, this family occurs among mosses in the forest (Figure 86).



Figure 84. *Thuidium tamariscinum* with capsules, home to *Peritrechus nubilus*. Photo by Michael Lüth, with permission.



Figure 85. *Peritrechus nubilus*, a species found in the moss *Thuidium tamariscinum*. Photo by Tristan Bantock, with permission.



Figure 86. **Rhyparochromidae** habitat under moss in Arthur's Pass, NZ. Photo by Marie-Claude Larivière, with permission.

Early reports of bryophyte dwellers in this family date as far back as 1871 (Champion 1871). A species of *Peritrechus lundii* (4-5 mm; Figure 87) along with two *Drymus* (Figure 97-Figure 98) species, *Trapezonotus arenarius* (4-4.5 mm; Figure 88-Figure 89), and *Stygnocoris sabulosus* (2.5-3 mm; Figure 90-Figure 91), were most common among mosses in alder (*Alnus*) woods.



Figure 87. *Peritrechus lundii*, a moss dweller. Photo by Tristan Bantock, with permission.



Figure 88. *Trapezonotus arenarius* nymph, a common species among UK mosses in alder woods. Photo by Tristan Bantock, with permission.



Figure 89. *Trapezonotus arenarius* adult, a common species among alder woods in the UK. Photo by Tristan Bantock, with permission.



Figure 90. *Stygnocoris sabulosus*, a moss dweller. Photo by Tristan Bantock, with permission.



Figure 91. *Stygnocoris sabulosus* adult at Crowle Moors, UK. Photo by Brian Eversham, with permission.

Alexander (2008) reported that *Trapezonotus desertus* (4-5 mm; Figure 92) nymphs occurred among dry mosses and lichens. *Peritrechus geniculatus* (5-6 mm; Figure 93-Figure 94) is also known from mosses and leaves on light sandy and chalky soils in Dorset, England (Alexander 2008; Recording Dorset 2011). This species overwinters as an adult, protected by the mosses. *Eremocoris abietus* (6-7.5 mm; Figure 95) and *Stygnocoris rusticus* (3-4 mm; Figure 96) likewise occur among mosses elsewhere in the UK (Champion 1871).



Figure 92. *Trapezonotus desertus*, a species whose nymphs live among dry mosses and lichens. Photo by Tristan Bantock, with permission.



Figure 93. *Peritrechus geniculatus* nymph, an inhabitant of mosses and leaves on light sandy and chalky soils in the UK. Photo by Tristan Bantock, with permission.



Figure 94. *Peritrechus geniculatus* adult, a species that spends time among mosses in the UK. Photo by Tristan Bantock, with permission.



Figure 95. *Eremocoris abietis*, a moss dweller in Europe. Photo by R. Altenkamp, Berlin, through Creative Commons.



Figure 96. *Stygnocoris rusticus*, a species that lives among mosses in the UK. Photo by Tristan Bantock, with permission.

Drymus sylvaticus (Figure 97), *D. brunneus* (Figure 98), *Stygnocoris sabulosus* in a UK study occurred primarily among mosses in the alder woods. *Canthophorus dubius* (Cynidae; Figure 65) was more rare, overwintering among mosses under junipers of the chalk downs, a habitat where *Zicrona coerulea* (Pentatomidae; Figure 71-Figure 72) was common. *Drymus brunneus* (4-5 mm) occurs among mosses in damp, shady places; it is widespread and common (Stenhouse 2007) despite preferring damper soils than other species of *Drymus* (Alexander 2008). *Drymus sylvaticus* (4-5 mm) is one of the most common of the British ground bugs, often occurring among mosses on dry soil (Alexander 2008; Bury Wildlife 2014). This species becomes active at night, feeding on mosses and fungal hyphae (Southwood & Leston 1959; Alexander 2008). Champion (1871) reported both of these species from mosses near Cheviot Hills, UK. *Recording Dorset* (2011) reports *D. sylvaticus* as common, occurring in most dry habitats that have mosses. In the UK, the rare *Drymus pilicornis* (3.9 mm) lives mostly in moss clumps among grasses on calcareous or base-rich grassland (Alexander (2008). In France, the rare *Drymus pilipes* (~2 mm) lives among mosses and litter (Péricart 1999).



Figure 97. *Drymus sylvaticus* adult, a moss dweller on dry soil in the UK. Photo by Tristan Bantock, with permission.



Figure 98. *Drymus brunneus*, a moss dweller in damp, shady places in Europe. Photo by Tristan Bantock, with permission.

Pterotmetus staphyliniformis (5-5.5 mm; Figure 99) is a rare species in the UK, living on moss-covered boulders on cliffs (Alexander 2008). Both *Megalonotus praetextatus* (4-5 mm; Figure 100) and *M. sabulicola* (4.5-5.5 mm; Figure 101) live in dry areas, the former where it is warm and sunny, especially in dunes and quarries, but it also lives on cliffs with mosses on partly vegetated ledges and gentle slopes. *Megalonotus sabulicola* is mainly coastal and is a ground-dwelling species that is most easily found among mosses. *Megalonotus chiragra* attaches its eggs to moss stems (Southwood & Leston 1959; Gerson 1982).



Figure 99. *Pterotmetus staphyliniformis*, a rare species that lives on moss-covered boulders on cliffs. Photo by Gernot Kunz, with permission.



Figure 100. *Megalonotus praetextatus*, a species that lives on cliffs with mosses on partly vegetated ledges and gentle slopes. Photo by Tristan Bantock, with permission.



Figure 101. *Megalonotus sabulicola*, a coastal species found most easily among mosses. Photo by Tristan Bantock, with permission.

The *Recording Dorset* (2011) website notes that the tiny *Tropistethus holosericus* (2mm) (Figure 102) lives among the low vegetation and mosses over sand and chalk, overwintering there as adults.



Figure 102. *Tropistethus holosericus*, a species of low vegetation and mosses. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission.

Rédei *et al.* (2003) found this family "in great numbers" in moss mats in Hungary. Abundant species included *Plinthisus pusillus* (1.8 mm; Figure 103) and *Rhyparochromus vulgaris* (7-8 mm; Figure 104). Adult members of *Rhyparochromidae* preferred mosses on tree trunks, ground, and other substrata. The seed eaters in this family search mostly on the ground, where they live among the mosses. In Hungary Rédei *et al.* (2003) found that *Stygnocorini* young nymphs (a tribe in the *Rhyparochromidae*) preferred moss mats on rocks. Other members of the family *Rhyparochromidae* seemed to prefer mosses on tree trunks, ground, and other surfaces. Within these, humidity conditions typically determined the preference.



Figure 103. *Plinthisus pusillus*, an abundant species in moss mats in Hungary. Photo from Zoologische Staatssammlung Muenchen, SNSB, through Creative Commons.



Figure 104. *Rhyparochromus vulgaris* on moss, an abundant species there in Hungary. Photo by Tristan Bantock, with permission.

In Dorset, England, one can find *Scolopostethus puberulus* (4 mm; Figure 105) among mosses that reside with taller vegetation, especially at cliff bases and in marshy places (Champion 1871; Recording Dorset 2011). Alexander (2008) likewise found this species in damp, mossy places. The adults hibernate in mosses (Champion 1871). Other moss-dwelling members of this genus include overwintering *S. thomsoni* (3.5-4 mm; Figure 106) and commonly *S. affinis* (3.5-4.5 mm; Figure 107) (Torre-Bueon 1917).



Figure 105. *Scolopostethus puberulus*, an inhabitant of mosses at cliff bases and other mossy places. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission.



Figure 106. *Scolopostethus thomsoni*, a species that overwinters among mosses. Photo by Tom Murray, through Creative Commons.



Figure 107. *Scolopostethus affinis*, a common species among mosses. Photo by Tristan Bantock, with permission.

Englund (2003) found several new species of **Rhyparochromidae** in the Austral Islands. These were mostly located by fogging mosses in the rata (*Metrosideros*) forest (Figure 108). Englund commented that his habitat had been largely overlooked.

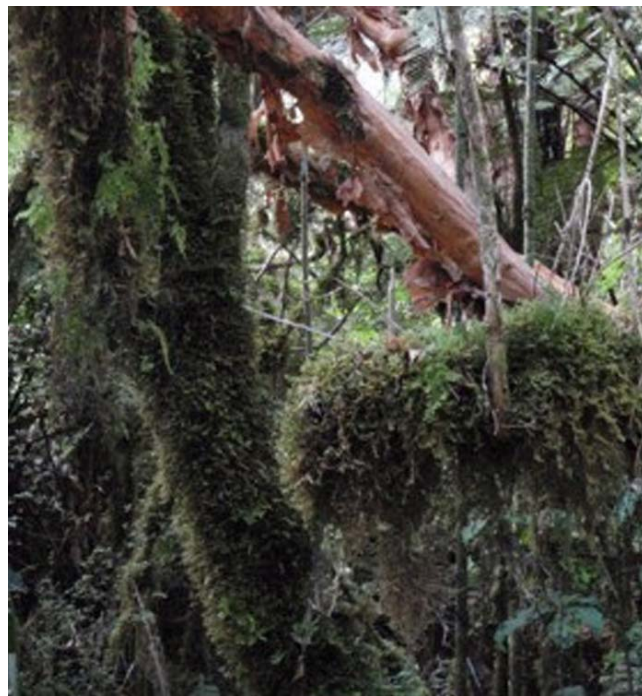


Figure 108. Rata (*Metrosideros*) forest near stream, home for Austral **Rhyparochromidae** in mosses. Photo by Marie-Claude Larivière, with permission.

Scutelleridae – Jewel Bugs

The **Scutelleridae** are rarely reported from mosses. Alexander (2008) reported the coastal species *Odontoscelis lineola* (4-5 mm; Figure 109), a warmth-loving species, on fairly stable sandy substrates, often with growth of mosses. This species is an active burrower. But the mosses may simply have been indicative of the habitat.



Figure 109. *Odontoscelis lineola*, a burrowing species that often occurs with mosses in coastal regions. Photo by Tristan Bantock, with permission.

CIMICOMORPHA – BED BUGS, BAT BUGS, ASSASSIN BUGS, AND PIRATE BUGS

Anthocoridae – Minute Pirate Bugs or Flower Bugs

These are predaceous bugs that suck fluids from their prey by cutting a hole in the prey, injecting enzymes, and drinking the contents (Wikipedia 2016). In Hungary Rédei *et al.* (2003) found the **Anthocoridae** (among others) represented in great numbers in moss mats by using Berlese funnel extraction, but it is possible he was referring to those previous members of the family treated herein as **Microphysidae**.

Nevertheless, *Anthocoris nemorum* (3-4 mm; Figure 110) builds a **hibernaculum** (winter shelter for dormant animal) in sheltered places under bark, in leaf litter, or among mosses (Hill 1957). *Temnostethus pusillus* (2.5-3.1 mm; Figure 111) often occurs on branches and trunks that are overgrown with mosses (Graff 2015). Fauvel (1999) suggests that mosses and lichens on trees may help members of the **Anthocoridae** to colonize that habitat.



Figure 110. *Anthocoris nemorum*, a species that uses mosses for its winter hibernaculum. Photo by Joe Botting, with permission.



Figure 111. *Temnostethus pusillus*, a species that lives on branches and tree trunks overgrown with mosses. Photo by Tuomo Vainio, through Creative Commons.

Microphysidae – Minute Bladder Bugs

This is a family of tiny insects (0.5-2.4 mm long) that emit a repugnant liquid to defend themselves (Watson & Dallwitz 2003). The family **Microphysidae** (Figure 112- Figure 113) finds its food among the bryophytes (Howe 2004). They feed on booklice, aphids, and other small creatures under bark and among those lichens and mosses growing on trees.



Figure 112. *Loricula* sp. female, member of the family **Microphysidae**. This predominately terrestrial family feeds on organisms living among mosses. Photo by Sarefo, through Creative Commons.



Figure 113. *Loricula* sp. male, a predator on moss-dwelling organisms. Photo by Sarefo, through Creative Commons.

Loricula ruficeps (lichen bugs) (1.5-1.6 mm; see Figure 112-Figure 113) in Hungary is numerous in moss mats (Rédei *et al.* 2003). *Myrmedobia exilis* (3 mm; Figure 19) lives among mosses on tree trunks, ground, and other substrata. It is often associated with *Polytrichum commune* (Figure 138) or *Rhytidiadelphus triquetrus* (Figure 114) (EOL 2015). The good news is that it is a predator on *Adelges* (see *Adelgidae* in next sub-chapter on Hemiptera). Nymphs of *Myrmedobia exilis* live among mosses in open clearings on acid or sandy soils, but the adult females move to conifers to feed on aphids (Alexander 2008). *Myrmedobia coleoptrata* (0.5 mm; Figure 115) usually grows beneath the bark of various trees, especially *Picea*, but it occasionally occurs in tufts of mosses at the tree base (Alexander 2008), as well as being associated with *Rhytidiadelphus triquetrus* and *Polytrichum commune* (EOL 2015). Douglas (1861) considered it a rare species that lives with ants. Moisture is important in determining which species occur in which locations (Rédei *et al.* 2003).



Figure 114. *Rhytidiadelphus triquetrus*, one of the homes of *Myrmedobia exilis* and *M. coleoptrata*. Photo by Janice Glime.



Figure 115. *Myrmedobia coleoptrata* with moss, a species that occasionally lives among mosses at tree bases. Photo by Rob Ryan, with permission.

Nabidae – Damsel Bugs

In Hungary Rédei *et al.* (2003) found the **Nabidae** (among others) represented in great numbers in moss mats by using Berlese funnel extraction. The **Nabidae** were mostly 5-10 mm long. *Nabis ferus* (8-8.5 mm; Figure 116) lives on mossy outcrops in the relict dry acid grassland of the UK (Alexander 2008).



Figure 116. *Nabis ferus*, a species living on mossy outcrops in dry acid grasslands in Europe. Photo by Joe Botting, with permission.

Miridae – Jumping Tree Bugs

Wheeler (2001) stated that mosses have been undocumented hosts for **Miridae** until recently. Using the Berlese funnel method, Rédei *et al.* (2003) found the **Miridae** (among others) represented in great numbers in moss mats. Humidity was important in determining locations and substrata.

Spungis (2005) found this family to have high population densities in the coastal grey dunes (Figure 25) of Latvia, dominating over grass-dwelling **Hemiptera**. These habitats suggest that these hemipterans may do best in somewhat dry habitats, but that they require the protective cover of mosses to survive there.

The predominantly North American genus *Bothynotus* (Figure 117) is relatively small (2.4-4.7 mm), typically brown, and densely pilose (Henry 1979), making it somewhat inconspicuous on soil or among mosses. Mosses may serve as the main habitat for the predatory *Bothynotus pilosus* (Figure 117) in Great Britain (Southwood & Leston 1959; Wheeler 2001). Bedwell (1930) found this species among *Sphagnum* and other mosses in Scotland. Later, Scudder (1995) found that it has a Nearctic distribution as well, occurring on the ground (probably among mosses) in the Yukon and British Columbia, Canada, and now it is known in China (Qi & Huo 2007). Henry (1979) considered that its association with conifers may actually be an association with the mosses that grow there, with few collectors actually finding them on the conifers. Nevertheless, the importance of bryophytes to this genus remains unknown, but ground level trapping records suggest that mosses may be an important habitat for it.



Figure 117. *Bothynotus pilosus*, a ground dweller that might live among mosses. Photo by Petri Parkko, through Creative Commons.

In another study in Great Britain, *Plagiognathus chrysanthemi* (Figure 118-Figure 120) and *Amblytulus delicatus* (see Figure 121) occurred among mosses (Woodroffe 1959).

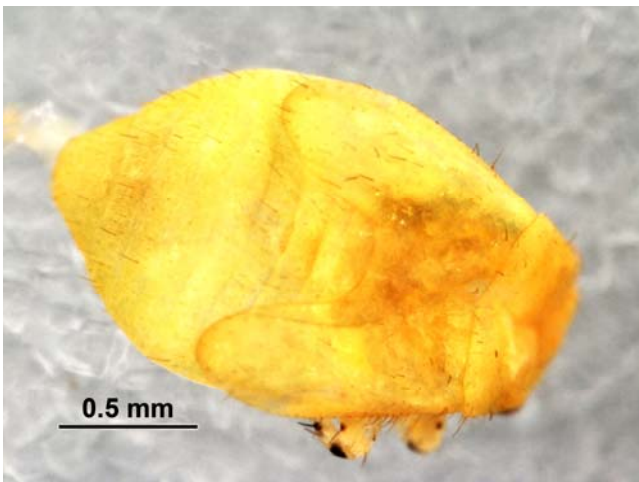


Figure 118. *Plagiognathus chrysanthemi* nymph, a moss dweller. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 119. *Plagiognathus chrysanthemi* adult, a moss dweller in Great Britain. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 120. *Plagiognathus chrysanthemi* adult, a moss dweller in Great Britain. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 121. *Amblytulus nasutus* adult; *A. delicatus* is a moss dweller in Great Britain. Photo by Ruth Ahlburg, with permission.

In Hawaii, the endemic species *Kamehameha lunalilo* (Figure 122) occurs on the mosses and ferns that cover trunks and branches of a number of tree species (Zimmerman 1948). Few of the moss dwellers have long legs and antennae like this species.



Figure 122. *Kamehameha lunalilo*, a moss dweller in Hawaii. Photo from American Museum of Natural History, through Public Domain.

Pseudoclerada (Figure 123), an endemic genus with only two species currently, is another Hawaiian **Miridae** (Asquith 1997). This genus lives in mid-elevation wet gulches and mid- to high-elevation mesic to wet forests. The species are usually solitary and live among the mosses covering tree branches.



Figure 123. *Pseudoclerada kilaueae*, a moss dweller on tree branches. Photo from American Museum of Natural History, through Public Domain.

Tingidae – Lace Bugs

This is a family of small to mid-sized bugs (2-10 mm) with lacy wings. The **Tingidae** are primarily associated with flowering plants, but *Acalypta* (Figure 124-Figure 125, Figure 133-Figure 136, Figure 139, Figure 146, Figure 149)

is most frequently collected from mosses (Froeschner 1976). In fact, it appears that mosses offer an alternative habitat housing a number of species.

The evolutionary history of *Acalypta* (Figure 124-Figure 125, Figure 133-Figure 136, Figure 139, Figure 146, Figure 149) is reflected in its occasional use of seed plants (Froeschner 1976). This seems to occur most commonly when the mosses are not in a favorable condition for lace bug development. Predictably, the genus is absent in the dry desert and plains states of the United States, but its absence along the Mississippi River is more difficult to explain. Its **brachypterous** (short) wings and recent geological history of the Mississippi flood plain may account for its continued absence there – it is dispersal limited.

Many species in *Acalypta* (Figure 124-Figure 125, Figure 133-Figure 136, Figure 139, Figure 146, Figure 149) live among the bryophytes (Michael Münch pers. comm. 30 October 2014). The bryophyte-dwelling members of the genus are tiny (~2 mm long) and have short (brachypterous) wings (British Bugs 2011). Some species, such as the widespread *Acalypta parvula* (~2 mm; Figure 124-Figure 125) (Hallett 1916), also have frequent macropterous (large or normal winged) forms. This species, the smallest of the *Acalypta* species, is common in the UK among short mosses, especially where soils are dry. It overwinters as an adult.



Figure 124. *Acalypta parvula* on moss in Germany. Photo by Michael Münch <www.insekten-sachsen.de> through GBIF, with permission.



Figure 125. *Acalypta parvula* amid mosses and soil. Photo by Tristan Bantock, with permission.

In the United Kingdom, five species of *Acalypta* feed on both capsules and vegetative parts of mosses (Howe 2004). Bailey (1951) likewise observed members of *Acalypta* feeding on the capsules of *Climacium* (Figure 126-Figure 128) after the calyptrae had fallen.



Figure 126. *Climacium dendroides* individuals, a species whose capsules and leaves are eaten by *Acalypta*. Photo by Michael Lüth, with permission.



Figure 127. *Climacium dendroides*; the capsules and leaves serve as food for *Acalypta*. Photo by Janice Glime.



Figure 128. Capsules of *Climacium americanum* that have shed their calyptrae and are suitable food for species of *Acalypta*. Photo by Janice Glime.

The substrate under the moss helps to determine which *Acalypta* species will occur there (Rédei *et al.* 2003). *Acalypta musci* (2.5-2.8 mm; Figure 7) prefers mosses on stones and rocks, along with most nymphs in the *Acalypta* genus. In addition to living among *Abietinella abietina* (Figure 6), often a rock dweller, *A. musci* also lives on typical soil moss species such as *Plagiomnium cuspidatum* (Figure 129) and *P. undulatum* (Figure 130) (Roshko 1969; Putshkov 1974; Rédei *et al.* 2004), and frequently occurs among mosses growing at the bases of trees (Singer 1952; Jordan 1963; Wagner 1967; Rédei *et al.* 2004). In the Bükk Mountains of Hungary, Varga (1992) found *Acalypta musci* and *A. gracilis* (Figure 28) living among the protected subalpine moss species *Plagiobryum zieri* (Figure 131) and *Saelania glaucescens* (Figure 132). Nearby road traffic polluted these mosses with lead, causing a poor bryofauna, and those invertebrates living there, including the two *Acalypta* species, contained high concentrations of lead. *Acalypta gracilis flaventis* occurs in the eastern and central Palearctic among mosses under *Ephedra* (Golub 1998). *Acalypta susanae* has been observed feeding on mosses (Allen *et al.* 1988). Whereas its typical habitat is among mosses, *Acalypta* can also occur on fungi growing on tree trunks (Rédei *et al.* 2004).



Figure 129. *Plagiomnium cuspidatum*, home for *Acalypta musci*. Photo by Michael Lüth, with permission.



Figure 130. *Plagiomnium undulatum*, home for *Acalypta musci*. Photo by Michael Lüth, with permission.



Figure 131. *Plagiobryum zierii*, mountain home for *Acalypta musci* and *A. gracilis*. Photo by Michael Lüth, with permission.



Figure 132. *Saelania glaucescens*, mountain home for *Acalypta musci* and *A. gracilis*. Photo by Michael Lüth, with permission.

Tree trunk mosses, ground, and other surfaces are preferred by *Acalypta carinata* (2.5 mm; Figure 5) and *A. platycheila* (Figure 133). *Acalypta carinata* occurs among *Sphagnum* (Figure 37), but also can be found in the drier habitat of the moss *Abietinella abietina* (Figure 6) in Hungary (Rédei *et al.* 2004). In southeast England, Kondorosy *et al.* (2010) found *Acalypta platycheila* feeding on mosses in apple orchards (Figure 134). The typical habitat of this species is humid, shady woodland.



Figure 133. *Acalypta platycheila*, a tree-trunk moss dweller. Photo by Boris Loboda, with permission.



Figure 134. Apple orchards at Leavenheath, UK. Photo by Jonathan Billinger, through Creative Commons.

Moss mats house numerous *Acalypta marginata* (Figure 31) in Eurosiberia and *A. platycheila* (Figure 133) in Hungary (Rédei *et al.* 2003). *Acalypta marginata* occurs in mosses such as *Rhytidiadelphus* sp. (Figure 135) as well as among tracheophytes (Roshko 1969; Rédei *et al.* 2004). In these habitats it occurs throughout the year, oviposits in the mosses and litter, and overwinters as adults or older larvae (Putshkov 1974; Rédei *et al.* 2004). *Acalypta platycheila* and *A. carinata* (Figure 5) also live among mosses in the *Dryopteridi-Alnetum* (ferns and alders) (Rédei *et al.* 2004), but Alexander (2008) considered them to have a preference for mosses on rotting logs in the UK. *Acalypta brunnea* is most likely to occur among mosses at tree bases or on decaying stumps (Alexander 2008). These substrate preferences of both the mosses and the species of *Acalypta* can be explained by differences in humidity.



Figure 135. *Rhytidiadelphus loreus*, home to *Acalypta marginata*. Photo by David T. Holyoak, with permission.

In Scotland, Corbet (2006) reported *Acalypta nigrina* (Figure 136) among mosses. Moss form may play a role in the choice of habitat by some hemipterans, but for *Acalypta nigrina* the selected mosses have diverse forms, including the horizontal-growing (pleurocarpous) *Hylocomium splendens* (Figure 137) and upright (acrocarpous)

Polytrichum sp. (Figure 138) among its Hungarian habitats (Rédei *et al.* 2004). However, both moss species form deep "mats" that provide a relatively wide moisture and light range that would permit the lace bug to seek the most suitable humidity level and temperature.



Figure 136. *Acalypta nigrina*, a moss dweller in Scotland. Photo by Johannes Skaftason, with permission.



Figure 137. *Hylocomium splendens*, one of the diverse forms of mosses inhabited by *Acalypta nigrina*. Photo by Michael Lüth, with permission.



Figure 138. *Polytrichum commune*, showing upright growth form, one of the forms occupied by *Acalypta nigrina* (Figure 136). Photo by Bob Klips, with permission.

Acalypta saundersi (Figure 139) does seem to have a moss form preference, selecting loose-growing bryophyte forms on fallen logs (Lattin 1997). It lives only in old-

growth western USA coniferous forests and its flightlessness, like that of other members of the genus, seems to correlate with its requirement for old growth (Lattin & Moldenke 1990), probably due to limited dispersal that causes a long colonization time. To find the lace bugs in this habitat, Lattin (1997) suggests gathering quantities of mosses and using a Tullgren funnel with heat and light to drive the bugs out of the moss. Sadly, this method is highly destructive if one wants to make a quantitative study and some slow-moving taxa simply die in place.



Figure 139. *Acalypta saundersi*, a species among loose-growing mosses on logs. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

In Hungary, Rédei *et al.* (2004) found only *A. marginata* (Figure 31) and *A. gracilis* (Figure 28) among the mosses of Kiskunság National Park, both in great numbers. *Acalypta gracilis* occurs in typical boreal forest mosses such as *Pleurozium schreberi* (Figure 140) and *Ptilium crista-castrensis* (Figure 141), as well as in the dry habitat of exposed sites among *Syntrichia ruralis* (Figure 142-Figure 143) (Péricart & Golub 1996).



Figure 140. *Pleurozium schreberi* on sand, home in the boreal forest for *Acalypta gracilis*. Photo by Janice Glime.



Figure 141. *Ptilium crista-castrensis*, home for *Acalypta gracilis* in the boreal forest. Photo by Li Zhang, with permission.



Figure 142. *Syntrichia ruralis* dry, home for *Acalypta gracilis*. Photo by Janice Glime.



Figure 143. *Syntrichia ruralis* wet, home for *Acalypta gracilis*. Photo by Janice Glime.

Although most of the species of *Acalypta* occur in relatively moist habitats, in the Upper Columbia River Basin, western North America, *Acalypta cooleyi* (Figure 144) lives at the bases of sagebrush (Figure 145) and other shrubs (Lattin 1995). There it finds refuge among the mosses, which it also eats.



Figure 144. *Acalypta cooleyi*, a species that finds refuge among mosses and eats them in sagebrush habitats. Photo by Bio Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 145. Sagebrush and moss, home for *Acalypta cooleyi* in western North America. Photo courtesy of Roger Rosentreter.

Acalypta barberi (1-2 mm; Figure 146) and *A. saundersi* (Figure 139) both feed and breed among the mosses (Drake & Lattin 1963). Interestingly, *A. barberi* feeds on mosses until they dry up. Then it shifts to hops (*Humulus lupulus*). Both adults and nymphs of *A. barberi* occurred on *Eurhynchium oregonum* (Figure 147) in Oregon and Washington, USA (Russell 1979). In the lab it subsisted for several weeks on this species. This widespread lace bug caused a shipment of nursery stock from Japan to be halted at quarantine in New York because of the danger of importing it among the mosses and introducing it where it can damage crops (Drake & Lattin 1963). In Arkansas, *A. susanae* (1.9 mm) was described as a new species from a log where it lived with mosses and slime molds (Allen *et al.* 1988). This species also eats mosses.



Figure 146. *Acalypta barberi*, a species that feeds on and breeds among mosses. Photo by Gary Griswold, with permission.



Figure 147. *Eurhynchium oregonum*, home and food for *Acalypta barberi*. Photo by Matt Goff, with permission.

Bryophytes are often used as packing material for house plants and garden plants. Froeschner (1991) suggested that the new species *Acalypta laurae* (2 mm) was almost introduced to the United States from Mexico in the mosses used for packing the house plant *Tillandsia inoantha* (Figure 148).



Figure 148. *Tillandsia ionantha*, a species that is packed in mosses for shipment. These mosses could introduce *Acalypta laurae* from Mexico to the US. Photo by Cliff, through Creative Commons.

Wheeler and Reeves (2004) searched for members of *Acalypta* in the southeastern United States. In North

Carolina they found one nymph and one adult of *Acalypta duryi* (Figure 149) associated with the moss *Dicranum scoparium* (an acrocarpous moss; Figure 150). In Tennessee they found both nymphs and one adult of this species associated with *Hylocomiastrum umbratum* (a pleurocarpous moss; Figure 151) and adults from *Anomodon rostratus* (a pleurocarpous moss; Figure 152). *Acalypta lillianis* (~2.2 mm; Figure 153) occurred with *Polytrichum commune* (acrocarpous; Figure 138) and *P. juniperinum* (Figure 154) in the southeastern states, including new records for Alabama and South Carolina. Bailey (1951) observed *A. lillianis* feeding on mosses. These tiny insects are hard to find and require destructive collecting techniques to be thorough. Both *Acalypta lillianis* and *A. mera* are bryophagous in northwestern USA.



Figure 149. *Acalypta duryi*, a species that has been found among several moss species in the southeastern United States. Photo by Nancy Lowe, through Discover Life.



Figure 150. *Dicranum scoparium* (acrocarpous), one of the several moss species where *Acalypta duryi* lives. Photo by Janice Glime.



Figure 151. *Hylocomiastrum umbratum* (pleurocarpous), one of the several moss species where *Acalypta duryi* lives. Photo by Michael Lüth, with permission.



Figure 152. *Anomodon rostratus*, one of the several moss species where *Acalypta duryi* lives. Photo by Bob Klips, with permission.

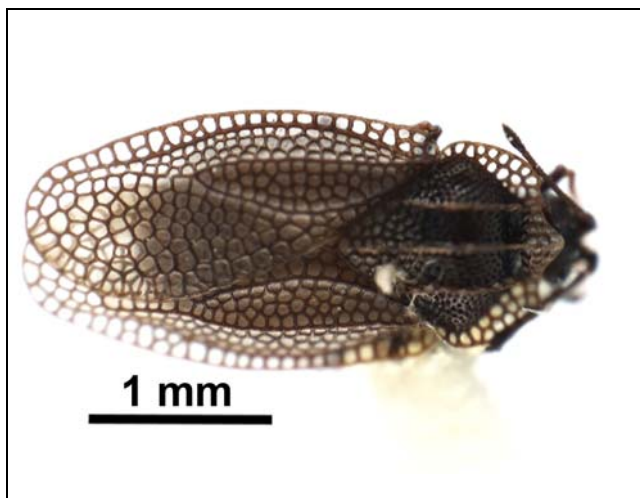


Figure 153. *Acalypta lillianis*, a moss-eating species in northern North America. Photo by Bio Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 154. *Polytrichum juniperinum*, one of the several moss species where *Acalypta lillianis* lives. Photo by Janice Glime.

But other genera of **Tingidae** do occur among mosses. Alexander (2008) described the habitat of *Campylosteira verna* (Figure 155) in the UK as one among mosses on hot, dry slopes, usually in calcareous grassland. *Campylosteira* and *Acalypta* (Figure 124-Figure 125, Figure 133-Figure 136, Figure 139, Figure 146, Figure 149) are **phytophagous** (plant-eating) bugs and subsist mostly on moss mats or stems of various herbaceous plants (Rédei *et al.* 2003). In their Hungarian study, Rédei *et al.* (2003) found more *Acalypta* species on mosses than on any other substrate. But for *Campylosteira verna*, only 16.2% were collected on moss, whereas 61.6% were collected among leaf litter. Based on their studies in Hungary, Rédei *et al.* considered members of *Acalypta* to be **musculolous** (growing best among mosses). The other **Tingidae** genera found among mosses seem to have wider preferences.



Figure 155. *Campylosteira verna*, a species that lives among mosses and elsewhere in hot, dry, calcareous grassland in the UK, often eating the mosses. Photo by Boris Loboda, with permission.

In West Virginia, USA, Torres-Miller (1995) found a different representative of this family. She was able to extract *Leptoypha mutica* (2.7-3.0 mm; Figure 156-Figure 157) from mosses with a Berlese funnel. *Derephysia foliacea* (foliaceous lace bug) (3-3.5 mm; Figure 158) hibernates as adults among mosses in the Ukraine

(Putshkov 1974; Lattin 2009). Thomas (1938) found that the uncommon species *Catoplatus fabricii* (3.8-4.5 mm; Figure 159) was located more easily among mosses, where it could even be abundant; Woodroffe (1959) reaffirmed that it was most frequently collected among mosses.



Figure 156. *Leptoypa mutica* nymph, a moss dweller in West Virginia, USA. Photo by Claude Pilon, with permission.



Figure 157. *Leptoypa mutica* adult, a moss dweller in West Virginia, USA. Photo by Tom Murray, through Creative Commons.



Figure 158. *Derephysia foliacea*, a foliaceous lace bug that hibernates among mosses in winter in the Ukraine. Photo by Tristan Bantock, with permission.

Drake and Buhoff (1959) reported a moss-feeding member of the **Tingidae** from Mexico. Lis (2000b) recently described *Paraphatnomella tamasi* (2.35 mm) as a new genus and species from India, likewise a moss dweller.



Figure 159. *Catoplatus fabricii* adult, a species found mostly among mosses in Great Britain. Photo by Boris Loboda, with permission.

Cantacaderidae

This family is a segregate of the **Tingidae**. And like some **Tingidae**, some members of **Cantacaderidae** are bryophyte eaters. Moir and Brennan (2007) point out that the more primitive bug families like these two feed on fungi, lichens, mosses, and underground roots. In Australia, *Carldrakeana tingalei* feeds on mosses and lichens (Hacker 1928). More recently, Lis (2000a) described a new Australian species, *C. pallida* (2.04-2.52 mm), also a moss feeder.

Reduviidae

There's always one! A beetle, a lizard, a mantid, and now a bug! These are all animals that cultivate bryophytes on their exterior. These are not just idle passengers using free transportation. The bryophytes actually grow on these animals. But unlike the other bryophyte gardeners, nymphs of *Reduvius personatus* (masked bug; Figure 160) actually place soil and various objects, sometimes including bryophytes (Figure 160), on their bodies as camouflage (Harz 1952; Weirauch 2006). Members of the genus *Reduvius* are only 9-14 mm in length (Wygodzinsky & Usinger 1964), so the kinds of plants that can grow on them are limited to those no bigger than bryophytes – small bryophytes.



Figure 160. *Reduvius personatus* with liverwort and insect camouflage. Photo compliments of Kurt (Hock Ping Guek) <orionmystery.blogspot.com>.

Reduvius personatus (Figure 160) builds two layers of camouflage. The first layer is made from soil, often called a **dust coat** (Brandt & Mahsberg 2002) or **natural camouflaging** (Figure 161) (Ambrose 1999). This was originally thought to be a product of dust in the habitat, but instead it is accumulated by an active process of kicking it there with the hind legs (Weber 1930; Immel 1955), using the **tarsal fan** (Weirauch 2006). This dust layer is present in all the reduviids that use this form of camouflage.



Figure 161. *Reduvius personatus* nymph with only the first layer of cover, the dust coat. Note the flatness typical of the nymph in spring. Photo by Whitney Cranshaw, through Creative Commons.

The second layer is more variable among the individuals. It typically contains coarser particles, including such objects as corpses of insects the reduviid nymph has eaten (Figure 161). This habit has earned this layer the name of **corpse camouflaging** (Ambrose 1999) or **backpack** (Brandt & Mahsberg 2002). It is this layer that sometimes has bryophytes in it (Figure 161). The question remains whether these bryophytes were placed there deliberately, or if they arrived as spores or fragments and grew there. I have seen pictures with protonemata growing on the soil layer. This entire camouflage apparatus must be replaced each time the insect molts. Nevertheless, I have seen pictures of liverworts with branches fully developed. Javahery (2013) reported that third instars were dormant during the first winter and the fifth instar was dormant during the second winter, with the life cycle being completed in two years. With the right climate and timing, this could permit the observed growth from a spore.

Reduvius personatus has multiple means of holding the soil particles there. Short setae help trap the dust and hold the first layer in place (Weirauch 2006). There are short-projection trichomes and long-projection trichomes that help to hold the outer layer. At least in some species, short-projection trichomes appear to be responsible for the fastening of the camouflaging layer close to the integument, whereas long-projection trichomes may hold the outer layer of camouflaging material in place. Both short-projection trichomes and long-projection trichomes, as well as grouped trichomes, secrete a sticky substance that helps to affix such items as smooth-bodied insect carcasses (Weirauch 2006; Javahery 2013).

The nymph becomes engorged before entering winter dormancy and does not eat during the entire winter (Readio 1931). By the time warm weather returns, the body is thin

and flat (Figure 161). Nevertheless, it has enough energy remaining to once again eat and be active. This dormancy behavior appears to be due to a biological clock and is not altered when the insect is maintained over winter in a warm environment with a supply of its normal food.

Other members of the **Reduviidae** in West Africa likewise adorn themselves with soil and the "backpack" materials. *Paredocla* and *Acanthaspis* (Figure 162) species add larger objects to the second layer, including prey corpses and plant parts (Brandt & Mahsberg 2002). In these species, the dust covering masks the chemical and tactile cues that are recognized by the worker ants that they often eat, making it easier for the reduviid nymphs to hunt. On the other hand, the second layer, the backpack, seems to play only a minor role in deterring the ants from approaching and being caught.

The predators on West African *Paredocla* and *Acanthaspis* (Figure 162) species include spiders, geckos, and centipedes (Brandt & Mahsberg 2002). In experiments using these three predators, the bug nymphs were more likely to survive with full camouflage than were the ones denuded of their covering. Not only did the backpack layer confuse the visually oriented predators, it also could be shed to distract the enemy while the reduviid nymph ran away, working much like the detached lizard's tail. In a different set of experiments in East Africa, Jackson and Pollard (2007) demonstrated that three species of the spider family **Salticidae** (*Hyllus* sp., *Plexippus* sp., and *Thyene* sp.) responded as predators to the naked *Acanthaspis petax* (Figure 162) (back packs removed) significantly more often than they responded to the masked bugs.



Figure 162. *Acanthaspis petax* nymph with ant carcass camouflage. This one is also eating an ant. Photo by Orionmystery, through Wikimedia Creative Commons.

DIPSOCOMORPHA

Dipsocoridae

Cryptostemma (Figure 20) in Hungary seems to prefer living among mosses on tree trunks, ground, and other surfaces (Rédei *et al.* 2003).

Ceratocombidae

Rédei *et al.* (2003) used Berlese funnels to assess the **epigeic** (ground-living) Hemiptera in Hungary. The

Ceratocombidae are not common among mosses, with only one species represented. *Ceratocombus coleoptratus* (1.5-2 mm; Figure 21) prefers mosses on tree trunks, ground, and other substrata as well as mosses in swampy meadows (Alexander 2008; Münch 2012). Edwards (1874) considered it to be rare in Norfolk, UK.

Ceratocombus vagans (3.8-4.5; Figure 163) is predaceous, eating such small arthropods as oribatid mites and springtails that frequently occur among bryophytes (Lattin 1997). In northern Michigan, USA, it lays its eggs at the end of the summer, inserting them into the tissues of *Sphagnum* (Figure 37) with its well-developed ovipositor.



Figure 163. *Ceratocombus vagans* nymph, a species that preys on small organisms among bryophytes and lays its eggs among *Sphagnum*. Photo by Jim McClarin, with permission.

Schizopteridae – Jumping Soil Bugs

This is a relatively small, mostly tropical family, but it has bryophyte dwellers among its species. Members of the family are suitable for moss-dwelling by their small size (0.5-2 mm). They eat small invertebrates, so bryophytes should provide suitable hunting grounds.

In New Zealand, *Hypselosoma acantheen* (Figure 164) lives mostly in forests among litter and mosses (Hill 1999). In New Caledonia, one can find *Hypselosoma rembaiensis*, another recently described species, among mosses (Hill 2013). In Australia, new species of *Kaimon* were described from mosses (*K. polysperes*, *K. thorntonensis*, *K. webbensis*) (Hill 2004).

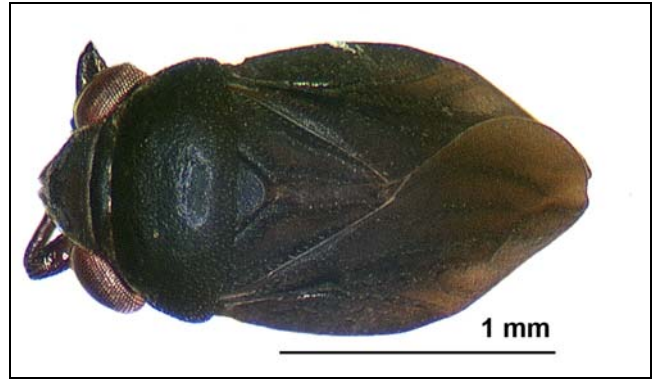


Figure 164. *Hypselosoma acantheen*, an inhabitant of forest mosses and litter. Photo by Marie-Claude Lariviere, through Landare Research, with permission.

India likewise has newly discovered moss dwellers in this family. Rédei (2008) described *Kikeshia stysi* from sifted mosses in West Bengal.

GERROMORPHA – SEMIAQUATIC BUGS OR SHORE-INHABITING BUGS

Hydrometridae

A few weeks ago I received an email from Eugenia Ron with an image of a strange object attached to the capsule of one (Figure 165) and seta of another (Figure 166) *Funaria hygrometrica* (Figure 167). This alien was unknown to both of us and was clearly not of bryophyte origin. We considered fungi, slime molds, and insects, so Eugenia sent the images to specialists in these groups. The fungal and slime mold experts said it wasn't one of theirs. Today Eugenia sent me an answer to the mystery.



Figure 165. *Hydrometra stagnorum* eggs on *Funaria hygrometrica* capsule courtesy of Tomas Sobota and Eugenia Ron.



Figure 166. *Hydrometra stagnorum* eggs on *Funaria hygrometrica* seta. Photo courtesy of Tomas Sobota and Eugenia Ron.



Figure 167. *Funaria hygrometrica* with maturing capsules. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Dr. Hernández de Miguel (Universidad Complutense, Madrid, Spain) identified it as the eggs of *Hydrometra stagnorum* (Figure 168), (Hemiptera, family Hydrometridae). Eugenia Ron has found additional eggs on both acrocarpous and pleurocarpous mosses and on leafy liverworts. The environments are always very humid near a river. This species uses its body like a kayak, rowing over the water surface of quiet streams or ponds to find food.



Figure 168. *Hydrometra stagnorum*, a species that often lays its eggs on bryophytes. Photo by alderash, through Creative Commons.

Mesoveliidae – Water Treaders

Although most of these species live on floating plants, some live in forest leaf litter and damp moss (DiTerlizzi 2004).

Gerridae

"Aquatic insects" are only aquatic for part of their lives, so many of the species discussed earlier as aquatic insects may also appear here as terrestrial insects. Among the amphibious species is *Gerris lacustris* (Figure 169). It skates on the water and does not live among mosses in the water, but when it hibernates it may seek out the protection and moisture of terrestrial mosses near its pond (Butler 1886).



Figure 169. *Gerris lacustris* adult in its aquatic, surface-dwelling stage. It may seek mosses on land to spend the winter. Photo by Jakub Rom, through EOL Public Domain.

NEPOMORPHA

Aphelocheiridae

I found only one record of this family associated with mosses. Alexander (2008) reported *Aphelocheirus aestivalis* (8.5-10.5 mm; Figure 170) among the UK fauna, living where there is overhanging vegetation or on moss-covered rocks.



Figure 170. *Aphelocheirus aestivalis*, a species one can find on moss-covered rocks. Photo by Niels Sloth, with permission.

Summary

Several orders of insects have been lumped into the current order **Hemiptera**. The suborder **Heteroptera** contains those members that were traditionally **Hemiptera**. Among these are a number of moss dwellers. The Hemiptera have a life cycle of egg – nymph – adult.

Some members of **Hemiptera** use bryophytes as a habitat, an egg-laying site, a food source, an overwintering site, and a hunting site. Most of the faithful species are tiny but seem to lack any special resemblance to bryophytes. They benefit from the moisture and protection while often finding food there among algae, slime molds, fungi, bryophyte leaves, and invertebrate fauna.

The most common habitats of moss dwellers include forest floor and epiphytic bryophytes, sand dunes, streamside and other wet mosses, and peatlands. Some aquatic bugs leave the water to spend the winter under mosses.

The most primitive **Hemiptera** are typically moss dwellers, especially the **Tingidae** and closely related families. Members of the genus *Acalypta* are typically moss dwellers, eat mosses, and have many species among mosses. Many of the species have limited distribution.

The **Miridae** most likely have bryophyte dwellers that are yet to be discovered, with evidence suggested by ground traps. In some parts of the world, **Rhyparochromidae** are common among mosses. A number of families have lesser representation than those just mentioned.

Some members of the **Reduviidae** include bryophytes among the camouflage items they carry on their backs. Such "back packs" are known to discourage would-be predators.

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CHAPTER 12-7

TERRESTRIAL INSECTS:

HEMIMETABOLA – HEMIPTERA (NON-HETEROPTERA) AND THYSANOPTERA

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CHAPTER 12-7

TERRESTRIAL INSECTS:

HEMIMETABOLA – HEMIPTERA (NON-HETEROPTERA) AND THYSANOPTERA



Figure 1. *Brachythecium buchananii* with capsules, overwintering home of *Schlechtendalia chinensis*, a gall aphid. Photo by Ivanov, with permission.

SUBORDER AUCHENORRHYNCHA

(Cicadas, Leafhoppers, Treehoppers, Planthoppers, and Spittlebugs)

Holzinger and Schlosser (2013) identified 93 species of **Auchenorrhyncha** fauna in Austrian peat bogs in the Bohemian Forest, indicating how common this group of **Hemiptera** is in bogs. Disturbance increases the number of species and densities in this group, but the number of species and densities of peatland specialists (**tyrphobionts**) decreases with disturbance.

CICADOMORPHA

Cicadellidae – Leaf Hoppers

Megophthalmus scanicus (3-4 mm; Figure 2) is among the few European **Cicadellidae** with a bryophyte association (Edwards 1874). This species overwinters among mosses. *Sorhoanus xanthoneurus* (3.1-3.4 mm; Figure 3), *Sorhoanus assimilis* (often the most frequent hemipteran; 2-2.9 mm; Figure 4), and *Stroggylocephalus livens* (5-6.5 mm; Figure 5) associate with *Sphagnum* (Figure 6) in bogs in Austria and seem to be true **tyrphobionts** (Holzinger & Schlosser 2013). Another

moderately common member of the family associated with *Sphagnum* is *Macustus grisescens* (5-6 mm; Figure 7).



Figure 2. *Megophthalmus scanicus*, a leaf hopper that overwinters among mosses in Europe. Photo by Tristan Bantock, with permission.



Figure 3. *Sorhoanus xanthoneurus*, a tyrphobiont associated with *Sphagnum* in Austria. Photo by Joe Botting, with permission.



Figure 4. *Sorhoanus assimilis* adult, a species commonly associated with *Sphagnum* in Austria. Photo by Gernot Kunz, with permission.



Figure 5. *Stroggylocephalus livens*, a tyrphobiont associated with *Sphagnum* in Austria. Photo by Gernot Kunz in Gallery, with permission.



Figure 6. *Sphagnum* blanket bog where several tyrphobionts in the *Cicadellidae* live. Photo through Creative Commons.



Figure 7. *Macustus grisescens*, a *Sphagnum* associate. Photo by Joe Botting, with permission.

Jassargus dentatus (Figure 8) occurs in association with *Sphagnum* in Slovenia and the Piedmont of Italy (Trivellone 2010). *Jassargus pseudocellaris* (Figure 9) is among the abundant hemipterans in Austrian bogs (Holzinger & Schlosser 2013).



Figure 8. *Jassargus dentatus*, a *Sphagnum* associate in parts of Europe. Photo by Gernot Kunz, with permission.



Figure 9. *Jassargus pseudocellaris*, a bog inhabitant in Austria. Photo by Tristan Bantock, with permission.

Paracephaleus curtus (Figure 10) lives on grass tufts of *Chionochloa rubra* (Figure 11) and mats of short plants, including mosses (Larivière *et al.* 2010).



Figure 10. *Paracephaleus curtus*, a species that sometimes lives among mosses. Photo by Marie-Claude Larivière, with permission.



Figure 11. *Chionochloa rubra* in New Zealand, home for *Paracephaleus curtus*. Photo by Ulrich Lange, through Creative Commons.

Spittlebugs are so-named for their production of a frothy medium that resembles human spit. This "spittle" provides them a place to hide from would-be predators, but it not only hides them, it has an acrid taste that deters the predators (Wikipedia 2015). It is good insulation against heat and cold, much like hiding in water, but with air spaces that make it an even better insulator. And it provides moisture, protecting the soft-bodied nymphs from dehydration. The nymphs are plant suckers, and it appears that bryophytes, at least *Polytrichum juniperinum*, are on the menu (Figure 12-Figure 13), as well as many tracheophyte species.



Figure 12. Spittlebug on *Polytrichum juniperinum*. Photo courtesy of Timea Deakova, with permission.



Figure 13. Spittlebug nymph. Photo by Diliff, through Creative Commons.

FULGOROMORPHA - PLANTHOPPERS

Delphacidae – Delphacid Planthoppers

The **Delphacidae** is a family of herbivores with a worldwide distribution. A sweep net revealed *Euconomelus lepidus* (1.8-3 mm; Figure 14) from mosses beside a lake in Scotland (Bratton 2012). This is one of the few species that seems to be associated with bryophytes.



Figure 14. *Euconomelus lepidus* lives in association with mosses near a lake in Scotland. Photo by Tristan Bantock, with permission.

Javesella opaca (see Figure 15, Figure 16) is a planthopper that feeds on mosses in the eastern United States (Wheeler 2003). Nymphs live on the upright leafy gametophytes of *Polytrichum commune* (Figure 17) and *Polytrichastrum alpinum* (Figure 18) where these mosses grow over flatrock areas. In South Carolina, USA, the late instars overwinter among *Polytrichum commune*, with adults developing by mid- to late March. Most of the adults are **brachypterous** (having short wings). It is interesting that these insects feed on the thick stems of the mosses, whereas in our experiments with pillbugs the stems were avoided in *Polytrichum* and only leaves were eaten. In Russia, *Javesella discolor* (Figure 19) lives in moss bogs, moist forests, and swamp meadows (Emeljanov 1988), where mosses play an important role in creating a suitable microclimate.



Figure 15. *Javesella pellucida*; *J. opaca* feeds on mosses in the eastern US. Photo by Tom Murray, through Creative Commons.



Figure 16. *Javesella opaca*, a moss feeder. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 17. *Polytrichum commune*, home for *Javesella opaca* in the eastern United States. Photo by Christopher Tracey, through Creative Commons.



Figure 18. *Polytrichastrum alpinum*, home and food for *Javesella opaca* in Europe. This species also overwinters here. Photo by Michael Lüth, with permission.



Figure 19. *Javesella discolor*, a species that lives in mossy bogs and other mossy habitats. Photo by Joe Botting, with permission.

Muellerianella extrusa (2.1-3.1 mm; Figure 20) occurs in association with *Sphagnum* in Austria (Holzinger & Schlosser 2013).



Figure 20. *Muellerianella extrusa*, a *Sphagnum* associate in Austria. Photo by Gernot Kunz, with permission.

Richardson *et al.* (2002) found that changes in subordinate plant species had a greater impact on the herbivorous insect community than on those living on the dominant dwarf shrubs. Moss-feeding bugs were reduced to as little as 65% of the controls when their plots were fertilized, whereas grass-feeding insect species showed a 400% increase. This benefitted the **Delphacidae**, a **graminivorous** (grass-eating) family, suggesting that for most of the species the mosses were not important.

Derbidae – Planthoppers

Wilson and Wheeler (2015) attempted to learn more about the life history of this little known family. They were able to rear *Cedusa hedusa* (Figure 21) successfully from fifth instars to adults. These were collected from populations of the moss *Polytrichum commune* (Figure 17) in Alabama, USA. Nevertheless, food of the nymphs remains unknown, as well as oviposition sites and food preferences of the adults.

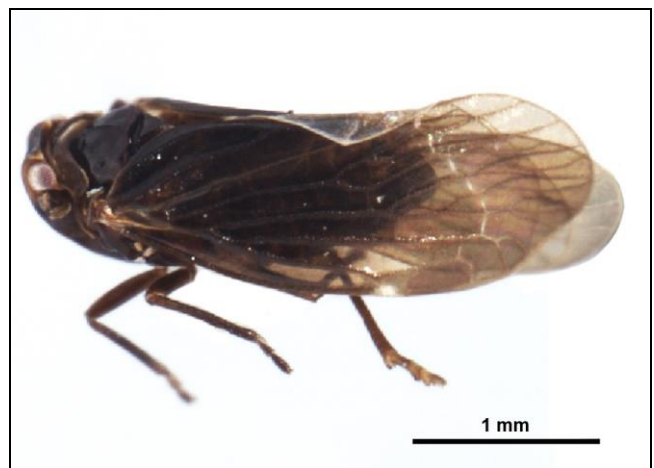


Figure 21. *Cedusa hedusa*, a species that lives on the moss *Polytrichum commune* in Alabama, USA. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Issidae – Planthoppers

Issus coleoptratus (3-4 mm; Figure 22-Figure 23) seems to spend most of its nymphal time among mosses (undocumented comment from Flickr). *Issus muscaeformis* (1.9-3.6 mm; Figure 24) has a name that suggests it has some relationship with mosses, but I can find no reference that places it in such a habitat. Consulted references include those that describe mosses as habitats for other insects.



Figure 22. *Issus coleoptratus* nymphal instar, a stage that lives among mosses. Photo through Creative Commons.



Figure 23. *Issus coleoptratus* adult, a moss-dwelling species. Photo by Sarefo, through Creative Commons.



Figure 24. *Issus muscaeformis* adult, a likely moss dweller. Photo by Roger S. Key, with permission.

The genus *Issus* (Figure 22-Figure 25) has an unusual means of locomotion (Burrows & Sutton 2013). It uses gears that intermesh, rotating like mechanical gears (Figure 25). These are located on the hind legs at the trochanter and rub together to propel the insect when it jumps. They insure that both legs have the same velocities and are synchronized. But as strange and unique as these are, they exist only in the nymphs, disappearing at the last molt. The adults must move like other insects.

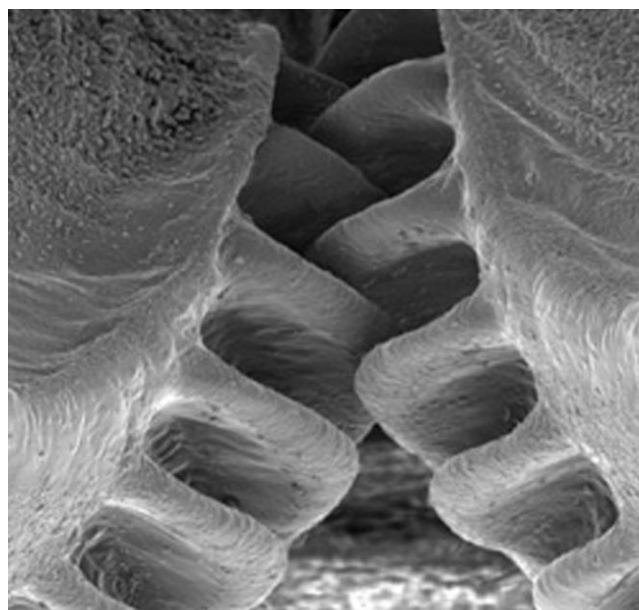


Figure 25. *Issus coleoptratus* interactive gears in the hind legs. Photo by Malcolm Burrows & Gregory Sutton, through Creative Commons.

SUBORDER STERNORRHYNCHA

(aphids, whiteflies, and scale insects)

Anyone who has kept a greenhouse will probably cringe at the mention of these insects. All are pests in that environment. And you might just introduce some of them with mosses you bring in.

Eriococcidae – Scale Insects

One of these greenhouse horrors is the scale insect (Figure 26). These seem like unlikely moss inhabitants, but Henderson (2007) considered mosses and ferns to be the most likely candidates as host plants for *Affeldococcus kathrinae* (0.4-0.65 mm). This very tiny species lacks a specific host tree, but lives in the high canopy epiphyte mat of the rata (*Metrosideros* spp.; Figure 27) in New Zealand. This led Henderson to conclude the epiphytic bryophytes and/or ferns might be the hosts.



Figure 26. *Eriococcus coriaceus* on *Eucalyptus* in Australia, representing a family with one known species of moss dwellers (*Affeldococcus kathrinae*). Photo by Arthur Chapman, through Creative Commons.



Figure 27. Rata forest (*Metrosideros umbellata*), Enderby Island, New Zealand. These forests have mostly mosses and ferns as ground cover and provide a suitable home for *Affeldococcus kathrinae*. Photo by John Barkla, with permission.

Aphididae (including Pemphigidae) - Aphids

Although incidences of **bryophagy** (eating bryophytes) are not well known among aphids, there are actually species that specialize on bryophytes, and others that eat them for special purposes (Hille Ris Lambers 1954; Müller 1973; Smith & Knowlton 1975; Stekol'Shchikov & Shaposhnikov 1994). Moss aphids pierce the cells, then

suck the contents from the cells (Thomas & Lombard 1991; Longton 1992). Aphids are common enough among mosses that there is a whole group known as the moss aphids (Müller 1973; Smith & Knowlton 1975).

Aphids are not common moss inhabitants, with the exception of the gall aphids, but perhaps we aren't looking in the right places. Recently Robin Stevenson found *Sphagnum* forming sleeves around young saplings of *Pinus sylvestris* and *Betula* spp. (Stevenson & Masson 2015). He pursued these strange sleeves, determining that they were formed by ants (*Lasius platythorax*). But why? Upon tearing them apart, he found lots of aphids (*Symydobius oblongus*; Figure 28-Figure 29) were running about. Ants are well known for tending aphids, using the "honey dew" excreted from two tubercles at the ends of the alimentary (digestive) canals (Figure 28). See Chapter 12-10 on Hymenoptera for more details on this relationship.



Figure 28. *Symydobius oblongus* nymph, a species that lives in *Sphagnum* sleeves created by ants on young birch and pine saplings in bogs. Note the two tiny white tubercles near the end of the abdomen where ants are able to harvest honey dew. Photo from <www.influentialpoints.com>, through Creative Commons.



Figure 29. *Symydobius oblongus* adult, a species that lives in *Sphagnum* sleeves created by ants on young birch and pine saplings in bogs. Photo from <www.aphotofauna.com>, with permission.

Gall Aphids

Some moss aphids form galls (Figure 85-Figure 86), but not on the mosses. Instead, the mosses act as alternate hosts (Chiuh 1976). One of the few remaining agricultural uses of mosses is the culturing of mosses as the winter host for Chinese gall aphids (Li *et al.* 1988, 1999; Liu & Li 1992, 1993; Liu *et al.* 1994). This has led to studies on the effects of temperature and water content on the vitality of these host mosses in winter (Liu *et al.* 1994) and on the physioecology of these mosses (Liu 2000).

Liu and coworkers (Liu 2000; Liu *et al.* 2000) studied the hosts *Plagiomnium acutum* (Figure 30), *P. maximoviczii* (Figure 41), *Thuidium cymbifolium* (Figure 31), and *Chrysocladium retrorsum* (Figure 32), hoping to cultivate them at optimal conditions. These mosses are able to maintain a net photosynthetic gain at temperatures as low as -15 to -10°C. The optimum temperatures for *T. cymbifolium* and *C. retrorsum* were in the range of 25-36°C in spring, dropping to 20-30°C in winter.



Figure 30. *Plagiomnium acutum*, overwintering host for gall aphids in China. Photo through Creative Commons.



Figure 31. *Thuidium cymbifolium* with capsules, a host plant for gall aphids, including *Schlechtendalia elongallis*. Photo by Li Zhang, with permission.



Figure 32. *Chrysocladium retrorsum*, a host plant for gall aphids. Photo by Yao Kuiyu, through Creative Commons.

Li *et al.* (1999) compared photosynthetic capacity in the two gall aphid hosts *Plagiomnium acutum* and *Herpetineuron toccoeae*. *Plagiomnium acutum* had lower photosynthesis on sunny days and higher on cloudy and rainy days compared to that of *H. toccoeae*. Consistent with its preferred bright days, *H. toccoeae* also had lower transpiration rates than did *P. acutum*, permitting the former to tolerate high temperatures and dry environments.

There are at least 24 known species of moss hosts in China, and their cultivation is critical to the production of the gall nuts (Li 1990). In China, the gall aphid species are generally highly specialized on only a few winter moss hosts (Chiuh 1976; Li *et al.* 1988). Among those used are *Mnium lycopodioides* (Figure 33), *M. thomsonii* (Figure 34), *Orthomnion dilatatum*, *Plagiomnium rhynchophorum*, *Brachythecium albicans* (Figure 35), *B. buchananii* (Figure 1), *B. velutinum* (Figure 36), *B. rutabulum* (Figure 37), *Homalothecium leucodonticaule* (Figure 38), *Hypnum callichroum* (Figure 39), and *Erythrodontium julaceum* (Figure 40). The first four of these are winter hosts of the Chinese gall aphid *Schlechtendalia chinensis* (Aphididae; Figure 42). The virus-carrying *Melaphidini* (Pemphigidae, a segregate from Aphididae) species shift their habitat between *Rhus* (sumac; Figure 85) and bryophytes (Eastop 1977).



Figure 33. *Mnium lycopodioides*, a winter host of the Chinese gall aphid *Schlechtendalia chinensis*. Photo by Michael Lüth, with permission.



Figure 34. *Mnium thomsonii*, a winter host of the Chinese gall aphid *Schlechtendalia chinensis* (Figure 42). Photo by Hermann Schachner, through Creative Commons.



Figure 37. *Brachythecium rutabulum* with capsules, an alternate host for gall aphids in China. Photo by Malcolm Storey from DiscoverLife, through Creative Commons.



Figure 35. *Brachythecium albicans*, an alternate host for gall aphids in China. Photo by Janice Glime.



Figure 38. *Homalothecium leucodonticaule* (= *Homalothecium laevisetum*), a species used by Chinese gall aphids. Photo through Creative Commons.



Figure 36. *Brachythecium velutinum* with capsules, an alternate host for gall aphids in China. Photo by Michael Lüth, with permission.



Figure 39. *Hypnum callichroum*, an alternate host for gall aphids in China. Photo by Michael Lüth, with permission.



Figure 40. *Erythrodontium julaceum*, an alternate host for gall aphids in China. Photo by Michael Lüth, with permission.

Plagiomnium maximoviczii (Figure 41) is also a common species that serves as the winter host for the Chinese gall aphids (Horikawa 1947; Tang 1976; Lao *et al.* 1984; Li *et al.* 1988). The aphids *Schlechtendalia chinensis* (Pemphigidae; Figure 42), *Nurudea shiraii*, and *Nurudea yanoniella* (Pemphigidae) are important commercially in China because of the galls they make on the sumac (*Rhus*) tree (Tang 1976; Min & Longton 1993). These galls are highly prized for medicines (expectorant; treatment of cankers and wounds) and the chemical industry (black dyes for dyers and tanners; ink) (Fagan 1918). The aphids migrate to the mosses for the winter, using them for both shelter and food (Chiu 1976; Tang 1976; Lai *et al.* 1990).

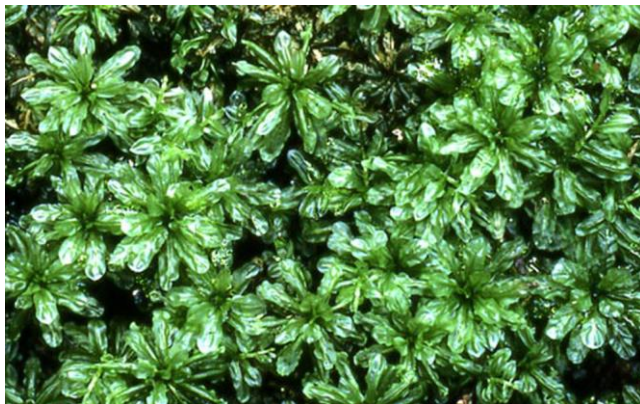


Figure 41. *Plagiomnium maximoviczii*, a winter host for Chinese gall aphids. Photo from Hiroshima University Digital Museum of Natural History, with permission.

Schlechtendalia

Schlechtendalia chinensis (Figure 42) makes its galls on *Rhus chinensis*. It uses *Plagiomnium maximoviczii* (Figure 41), *P. cuspidatum* (Figure 43), and *P. vesicatum* (Figure 44) for its winter shelter (Chiu 1976). When the galls burst open at maturity, the aphids emerge and migrate to their moss hosts. There they produce 20-30 nymphs that will develop into spring migrants. The newly emerged nymphs move to the moss stalks near the ground and cover their bodies with a waxy secretion in preparation for winter. In early spring they develop into the winged females that give live birth. These females are spring

migrants that move to the *Rhus chinensis* (sumac; Figure 45) where they will feed. Their offspring will be wingless. These become wingless adults and will be ready to mate in 4-8 days.



Figure 42. *Schlechtendalia chinensis* gall, a species that uses mosses as overwintering hosts. Photo from SanHerb, with permission.



Figure 43. *Plagiomnium cuspidatum*, one of the winter hosts of the Chinese gall aphid *Schlechtendalia chinensis* (Figure 42). Photo by Michael Lüth, with permission.



Figure 44. *Plagiomnium vesicatum* (formerly included in *Mnium*), a winter host for the Chinese gallnut *Schlechtendalia chinensis* (Figure 42). Photo from the Digital Museum, University of Hiroshima, with permission.



Figure 45. *Rhus chinensis*, host of the Chinese gall aphid *Schlechtendalia chinensis* (Figure 42). Photo from Kinmen National Park Digital Archives, through Creative Commons.

The females lay their eggs on the mosses (Lai *et al.* 1990). Because the host tree, the sumac, grows on dry slopes and the mosses tend to grow on more humid stream banks, there are few places where the mosses are sufficiently close to the trees for the relationship to work for the aphids (Zhang, pers. comm.). Hence, it is desirable to create more suitable habitats, possibly by cultivating mosses, placing them near the sumac at the appropriate season, then culturing the mosses through the winter in a favorable environment.

In addition to the *Plagiomnium* species, *Schlechtendalia* (Figure 42) also uses *Homomallium* (Figure 46), *Palamocladium* (Figure 47) (Liu & Li 1994), and *Herpetineuron toccoe* (Figure 48) (Li *et al.* 1999).



Figure 46. *Homomallium incurvatum*, member of a genus that provides a winter host for *Schlechtendalia chinensis* (Figure 42) in China. Photo by Hermann Schachner, through Creative Commons.

Kaburagia

Another gall-making aphid, *Kaburagia rhusicola* (1.3-1.5 mm), likewise uses mosses for winter hosts in China (Lai & Zhang 1994). These mosses include *Brachythecium* spp. (Figure 35-Figure 37), *Entodon* (Figure 49), and *Oxyrrhynchus* (= *Eurhynchium*?; Figure 94). In northern China, this aphid species moves from galls in late summer, and hibernates in an immature stage on the secondary host, the moss *Eurohypnum leptothallum* (Figure 50) (Chinese Academy of Forestry Science Institute

of Resource Insects 2014; The Aphids 2015). This institution has patented the procedure for growing the aphids on *E. leptothallum*. *Kaburagia ensigallis* (perhaps the same species as *K. rhusicola*) uses *Brachythecium buchananii* (Figure 1) as a host plant (Lou & Chen 2000).



Figure 47. *Palamocladium leskeoides*, member of a genus that provides a winter host for *Schlechtendalia chinensis* (Figure 42) in China. Photo courtesy of Claudio Delgadillo Moya.



Figure 48. *Herpetineuron toccoe*, a species that provides a winter host for *Schlechtendalia chinensis* (Figure 42) in China. Photo by Michael Lüth, with permission.



Figure 49. *Entodon* cf. *myurus* with capsules, member of a genus that provides a winter host for *Kaburagia rhusicola* in China. Photo by Michael Lüth, with permission.



Figure 50. *Eurohypnum leptothallum*, where *Kaburagia rhusicola* migrates in late summer in China and hibernates for the winter. Photo from <prologue.blog.naver.com>, through Creative Commons.

Muscaphis

But China does not have a corner on the gall aphid/moss association. Among the moss inhabitants is *Muscaphis escherichi* (1.7-2.7 mm; Figure 51), a bryophagous species on *Sorbus*, but when it is seasonally unavailable as a suitable habitat, they live primarily on the moss *Rhytidiadelphus loreus* (Figure 52) in the state of Washington, USA (Russell 1979). In Europe *M. escherichi* is common on many species of mosses, but researchers have had poor success in rearing it on any species but *Plagiothecium laetum* (Figure 53) and males have never been found on mosses (Stekolshchikov & Shaposhnikov 1993). *Muscaphis cuspidata* (0.9-1.3 mm) lives on *Calliergonella cuspidata* (Figure 54) and *Drepanocladus aduncus* (Figure 55), either close to the water or just below the water level. *Muscaphis mexicana* (1.7-2.1 mm) migrates to unidentified mosses, where wingless yellow or yellowish green aphids (0.6-0.8 mm) are produced (The Aphids 2015). The species *Muscaphis musci* (1.1-1.5 mm; Figure 56) occurs on many species of mosses, including those in *Amblystegium* (Figure 57), *Atrichum* (Figure 58), *Barbula* (s.l.; Figure 59), *Brachythecium* (Figure 37), *Bryum* (Figure 60), *Calliergonella*, *Eurhynchium* (Figure 94), *Hylocomium* (Figure 61), *Mnium* (probably *Plagiomnium*) (Figure 33-Figure 44), *Polytrichum* (s.l.) (Figure 17), *Pseudoscleropodium* (Figure 62), and *Tortula* (s.l.; Figure 63). In Denmark, Wilkaniec & Borowiak-Sobkowiak (2009) report *Muscaphis musci* from *Calliergonella cuspidata*, *Brachythecium rutabulum* (Figure 37), *Atrichum undulatum* (Figure 58), and *Plagiomnium undulatum* (Figure 64). *Muscaphis utahensis* (0.7-1.1 mm; Figure 65) occurs on mosses in the western USA and is thus far known only from the moss *Cratoneuron filicinum* (Figure 66) (Stekolshchikov & Shaposhnikov 1993). In most of the *Muscaphis* species, the bryophytes serve as alternate hosts and oviposition sites.



Figure 51. *Muscaphis escherichi*, a bryophagous species that lives on *Rhytidiadelphus loreus* in the western USA. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 52. *Rhytidiadelphus loreus*, the primary home for *Muscaphis escherichi* (Figure 51) in Washington, USA. Photo by Michael Lüth, with permission.



Figure 53. *Plagiothecium laetum*, the only species that seems to result in successful rearing of *Muscaphis escherichi*. Photo by Kristian Peters, with permission.



Figure 54. *Calliergonella cuspidata*, home to *Muscaphis cuspidata*. Photo by Michael Becker, through Creative Commons.



Figure 55. *Drepanocladus aduncus*, home to *Muscaphis cuspidata*. Photo by Michael Lüth, with permission.



Figure 56. *Muscaphis musci*, an aphid that occurs on many bryophyte species. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 57. *Amblystegium serpens*, a genus that is home for *Muscaphis musci* (Figure 56). Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.



Figure 58. *Atrichum undulatum*, home to *Muscaphis musci* (Figure 56). Photo by Janice Glime.

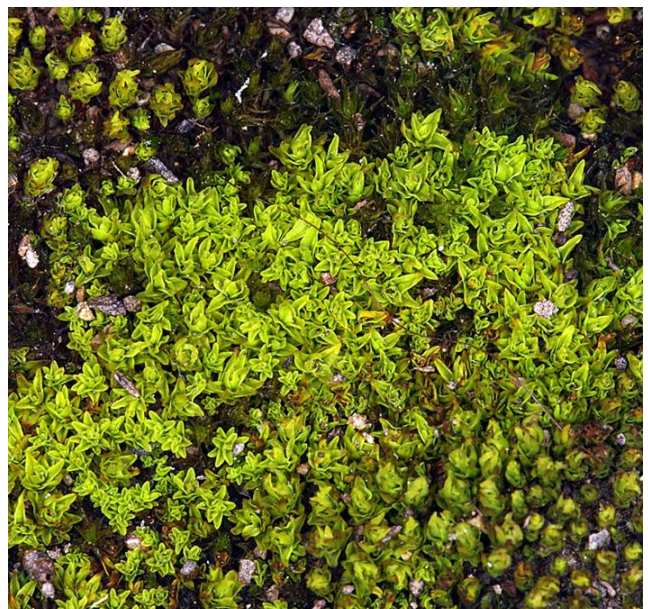


Figure 59. *Barbula convoluta*, home for *Muscaphis musci* (Figure 56). Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 60. *Bryum capillare*, home for *Muscaphis musci* (Figure 56). Photo by James K. Lindsey, with permission.

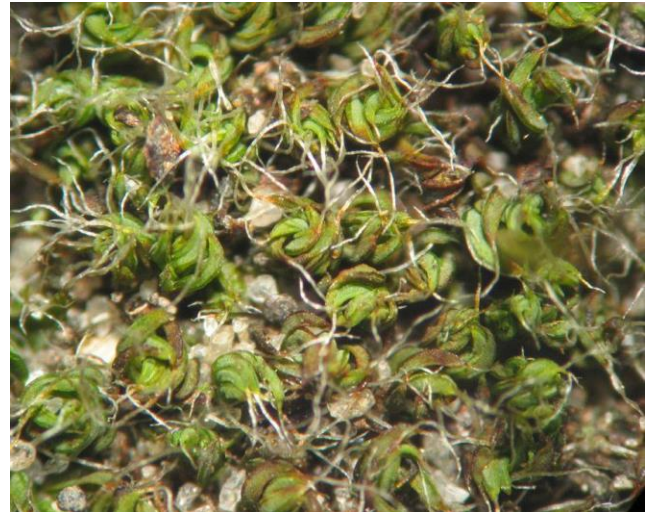


Figure 63. *Tortula muralis* dry. This species is in a genus that provides a home for *Muscaphis musci* (Figure 56). Photo by Kristian Peters, through Creative Commons.



Figure 61. *Hylocomium splendens* where you might find *Muscaphis musci* (Figure 56). Photo by Janice Glime.



Figure 64. *Plagiommium undulatum*, a home for *Muscaphis musci* (Figure 56). Photo by Michael Lüth, with permission.



Figure 62. *Pseudoscleropodium purum*, a species inhabited by *Muscaphis musci* (Figure 56). Photo by Michael Lüth, with permission.

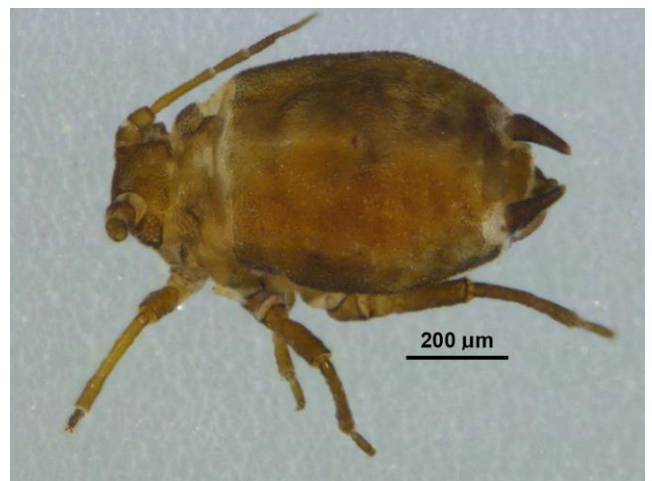


Figure 65. *Muscaphis utahensis*, a species lives on the moss *Cratoneuron filicinum*. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 66. *Cratoneuron filicinum*, home for *Muscaphis utahensis* (Figure 65). Photo by David Holyoak, with permission.

Myzodium

Another moss-dwelling aphid is the genus *Myzodium* (0.9-1.9 mm; Figure 67), one of the few genera of aphids that builds nests among *Sphagnum* (Figure 6) (Gerson 1969), and at least some of them eat mosses.

Aphids tap into the phloem of vascular plants to obtain nutrients. Clever researchers have used this behavior as a means to determine what substances are travelling in the phloem. Thomas and Lombard (1991; Thomas 1993) have used these tiny moss-dwelling aphids on *Polytrichum commune* (Figure 17) to obtain similar information on this moss. Their impact is sufficient to reduce the flow of labelled materials to other individuals that share rhizomes with the infested individuals. *Myzodium* sp. (~1.5-1.9 mm; Figure 67-Figure 68) not only diverts the nutrients from the **leptoids** (moss food-conducting cells) but also alters the normal source-to-sink flow within the moss turf.

Russell (pers. comm.) found many nymphs of *Myzodium modestum* (1.2-1.9 mm; Figure 67-Figure 68), a **bryophagous** species (eats bryophytes) (Müller 1973), overwintering on *Polytrichum* sp. (Figure 17) in early September at Waldo Lake, Oregon, USA. This species lives on other mosses as well, including *Dicranella crispa* (Figure 69), *Dicranum* sp. (Figure 113), *Oligotrichum aligerum* (Figure 70), *Pleurozium schreberi* (Figure 114), *Pogonatum dentatum* (Figure 71), *Polytrichastrum alpinum* (Figure 72), *Polytrichastrum formosum* (Figure 73), *Polytrichastrum longisetum* (Figure 74), *Polytrichum commune* (Figure 17), *Polytrichum juniperinum* (Figure 75), *Racomitrium* sp. (Figure 76), *Roellia roellii* (Figure 77), *Sanionia uncinata* (Figure 78), and *Sphagnum rubellum* (Figure 79) (Pike *et al.* 2010). This list attests to a wide variety of habitats including bogs, alpine, forest, boreal, and others as well as a wide range of bryophyte families from primitive to advanced, and it includes both acrocarpous and pleurocarpous mosses. *Polytrichum juniperinum* seems to have the most collection records. Unlike many species on tracheophytes, *Myzodium modestum* is not attended by ants.



Figure 67. *Myzodium* sp. nymphs, often born among *Sphagnum* (Figure 6). Photo by Andrew Jensen through Creative Commons.

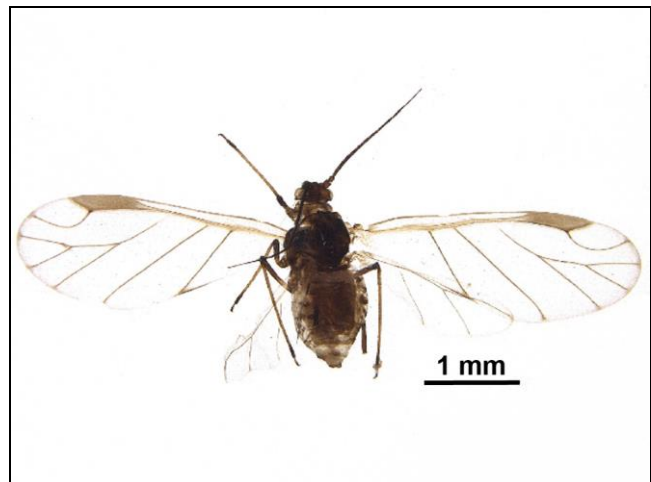


Figure 68. *Myzodium modestum* adult; nymphs spend the winter among mosses and feed on them by injecting a stylet into the leptoids. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 69. *Dicranella crispa*, home for *Myzodium modestum* (Figure 68). Photo by Ivanov, with permission.



Figure 70. *Oligotrichum aligerum*, a species inhabited by *Myzodium modestum* (Figure 68). Photo by Martin Hutten, with permission.



Figure 71. *Pogonatum dentatum*, a northern moss species that hosts *Myzodium modestum* (Figure 68). Photo by Michael Lüth, with permission.



Figure 72. *Polytrichastrum alpinum*, a species inhabited by *Myzodium modestum* (Figure 68). Photo by Andrew Hodgson, with permission.



Figure 73. *Polytrichastrum formosum*, a species inhabited by *Myzodium modestum* (Figure 68). Photo by David T. Holyoak, with permission.



Figure 74. *Polytrichastrum longisetum*, a species inhabited by *Myzodium modestum* (Figure 68). Photo by Hermann Schachner, through Creative Commons.



Figure 75. *Polytrichum juniperinum* male with new growth from antheridial splash cups. This species is home to *Myzodium modestum* (Figure 68). Photo by Janice Glime.

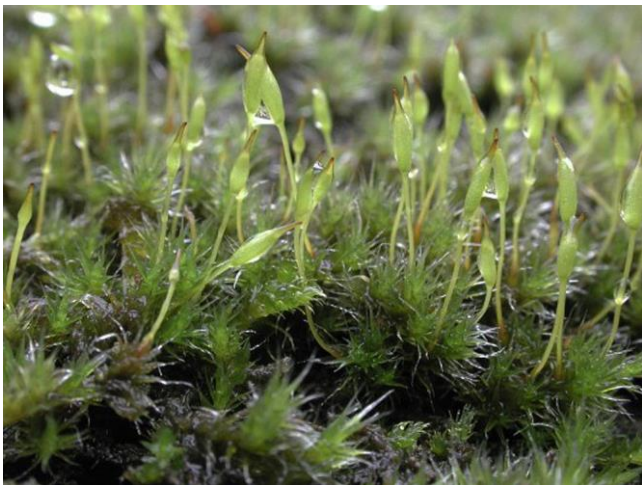


Figure 76. *Racomitrium heterostichum*, home to *Myzodium modestum* (Figure 68). Photo by Jan-Peter Frahm, with permission.



Figure 77. *Roellia roellii*, home to *Myzodium modestum* (Figure 68). Photo by Martin Hutten, with permission.



Figure 78. *Sanionia uncinata*, home to *Myzodium modestum* (Figure 68). Photo by Janice Glime.

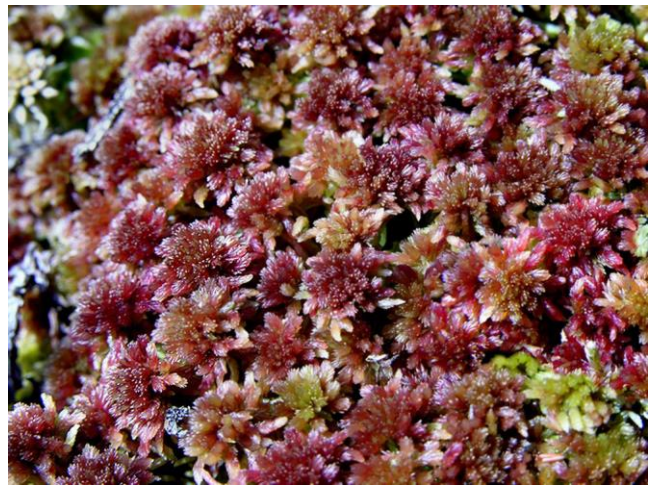


Figure 79. *Sphagnum rubellum*, home to *Myzodium modestum* (Figure 68). Photo by J. C. Schou <<http://www.biopix.com/>>, with permission.

Myzodium mimulicola (0.9-1.9 mm; Figure 80) occurs on *Aulacomnium palustre* (Figure 81), *Brachythecium frigidum* (Figure 82), *Straminergon stramineum* (Figure 83), *Philonotis fontana* (Figure 84), and *Sanionia uncinata* (Figure 78), another mixture of acrocarpous and pleurocarpous mosses, in western North America (Pike *et al.* 2010).



Figure 80. *Myzodium mimulicola* adult, a species that occurs on several moss species in western North America. Photo by Andrew Jensen, through Creative Commons.



Figure 81. *Aulacomnium palustre* with gemmae, a species that is home to *Myzodinium mimulicola* (Figure 80). Photo by Bob Klips, with permission.



Figure 82. *Brachythecium frigidum*, a species that is home to *Myzodinium mimulicola* (Figure 80). Photo by David Wagner, with permission.



Figure 83. *Straminergon stramineum*, a species that is home to *Myzodinium mimulicola* (Figure 80). Photo by David T. Holyoak, with permission.



Figure 84. *Philonotis fontana*, a species that is home to *Myzodinium mimulicola* (Figure 80). Photo by Michael Lüth, with permission.

Melaphis

The sumac gall aphid *Melaphis rhois* (Pemphigidae; Figure 85-Figure 89) is one of these moss aphids in the USA, alternating between mosses and sumac [*Rhus glabra* (Figure 90) and *R. typhina* (Figure 91)] (Moran 1989; Hebert *et al.* 1991; Pike *et al.* 2012).



Figure 85. *Melaphis rhois* galls on sumac (*Rhus*) in the US. This species shifts its habitat to bryophytes when conditions on the leaves are not favorable. Photo from Department Agriculture, Conservation, and Forestry, Augusta, Maine, through Public Domain.



Figure 86. *Melaphis rhois* nymphs in gall, a stage that exists on the sumac host. Photo by Claude Pilon, with permission.



Figure 87. *Melaphis rhois* young nymph, a stage that may be found among mosses. Photo by Claude Pilon, with permission.



Figure 88. *Melaphis rhois* adult, a moss and sumac inhabitant. Photo by Claude Pilon, with permission.



Figure 89. *Melaphis rhois* adult, a species that lives on sumac and uses mosses as alternate hosts for winter and egg laying. Photo by Claude Pilon, with permission.



Figure 90. *Rhus glabra* with flowers, primary host of *Melaphis rhois*. Photo from Superior National Forest, through Creative Commons.



Figure 91. *Rhus typhina*, primary host of *Melaphis rhois*. Photo through Creative Commons.

Moran (1992), an avid aphidologist, was walking in the Santa Catalina Mountains, Arizona, USA, when she discovered 5-cm galls (Figure 85-Figure 86) on a stand of smooth sumac (*Rhus glabra*; Figure 90). Further inspection revealed the sumac gall aphid, *Melaphis rhois* (0.8-1.2 mm; Figure 85-Figure 89). Upon further research, she discovered that this aphid was known from New York and that A. C. Baker had suspected that the tiny aphids he found among mosses in West Virginia, USA, might be the unknown spring migrant stage of *Melaphis rhois*. A return trip to the mountains enabled Moran to gather mosses and find that they indeed were inhabited by tiny aphids. She also transferred aphids from the sumac to the mosses and these produced morphs exactly matching those identified by Baker in West Virginia. After spending the summer inside the gall, where the single female reproduces asexually to make daughters, and they in turn her granddaughters, the granddaughters leave the gall in autumn as the sumac leaves begin dying and winter approaches. The granddaughters must find appropriate mosses where they deposit tiny aphid offspring. There the tiny daughters (great grandchildren of the original gall-maker) feed, develop, and reproduce. Their own waxy secretions protect them from desiccation. In spring of the first – or the second – year these females produce not only females but also males. Within a week they mate, females

deposit their eggs once more on the sumac, and the mating generation dies.

This species depends on the mosses for food (Baker 1919; Heie 1980; Moran 1989; Hebert *et al.* 1991). Pike *et al.* (2012) list a number of mosses that serve as hosts for *M. rhois*: *Rhytidiadelphus loreus* (Figure 52), *Leucolepis acanthoneura* (Figure 92), *Claopodium crispifolium* (Figure 93), *Eurhynchium praelongum* (Figure 94), and *Dicranum scoparium* (Figure 113).



Figure 92. *Leucolepis acanthoneura*, home of *Melaphis rhois*. Photo by Matt Goff <<http://www.sitkanature.org/>>, with permission.



Figure 93. *Claopodium crispifolium*, winter home of *Melaphis rhois*. Photo by Matt Goff <www.sitkanature.org/>, with permission.



Figure 94. *Eurhynchium praelongum*, home for *Melaphis rhois* when sumac leaves are unsuitable. Photo by Blanka Shaw, with permission.

Clydesmithia (Pemphigidae)

Clydesmithia canadensis (1.5-2.7 mm; Figure 95) includes a number of species among its moss hosts and is associated with mosses in Alaska (Pike *et al.* 2012). These moss alternate hosts are summarized in a table in Pike *et al.* (2012) and include such species as *Climacium dendroides* (Figure 96) and *Rhizomnium magnifolium* (Figure 97) that have not been mentioned here for other aphids.



Figure 95. *Clydesmithia canadensis* nymph, a species that is associated with a number of moss species. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 96. *Climacium dendroides*, one of the bryophyte hosts for *Clydesmithia canadensis* (Figure 95). Photo by Michael Lüth, with permission.



Figure 97. *Rhizomnium magnifolium*, an alternate host for *Clydesmithia canadensis* (Figure 95). Photo by Janice Glime.



Figure 100. *Pemphigus spirothecae* gall, member of a genus that uses mosses as alternate hosts. Photo by Georg Slickers, through Creative Commons.

***Pemphigus* (Pemphigidae)**

There seem to be few reports of European gall makers that use mosses as alternate hosts. In the UK, *Pemphigus trehernei* (1.3-2.4; see Figure 98-Figure 100) reproduces only by **parthenogenesis** (reproduction from an unfertilized egg), using roots of grasses and moss mats for oviposition (Alexander 2008). Norzikulov (1964) reported *Pemphigus hydrophilus* (1.9-2.2 mm) from *Cratoneuron filicinum* (Figure 101) and possibly also *Hygrohypnum luridum* (Figure 102) in Russia.

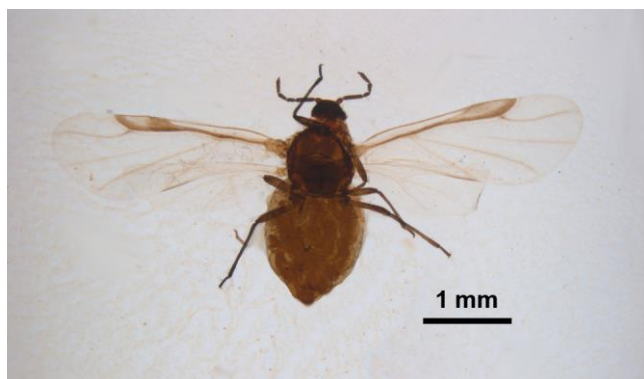


Figure 98. *Pemphigus bursarius*, a gall maker in a genus that uses mosses as alternate hosts. Photo from Pest and Diseases Image Library, through Creative Commons.



Figure 101. *Cratoneuron filicinum*, home for *Pemphigus hydrophilus*. Photo by J. C. Schou, with permission.



Figure 99. *Pemphigus bursarius* showing detail of antenna. Photo from Pest and Diseases Image Library, Bugwood.org, through Creative Commons.



Figure 102. *Hygrohypnum luridum* home for *Pemphigus hydrophilus* in Europe. Photo by Michael Lüth, with permission.

Other Aphididae that Live Among Mosses

Decorosiphon corynothrix (1.4-1.9 mm; Aphididae; Figure 103) lives on basal parts of *Polytrichum* spp. (Figure 17) growing in damp, shady situations and on *Atrichum undulatum* (Figure 104) (The Aphids 2015).



Figure 103. *Decorosiphon corynothrix*, a species that lives on the basal parts of *Polytrichum* spp. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 104. *Atrichum undulatum*, home to *Decorosiphon corynothrix*. Photo by Janice Glime.

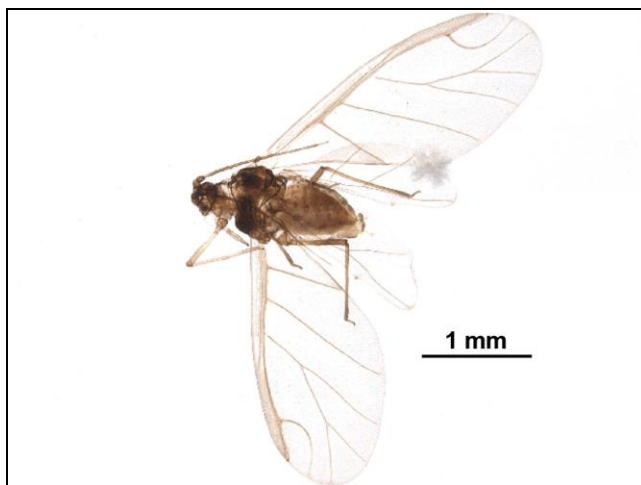


Figure 105. *Jacksonia papillata*, an aphid that often spends time among mosses. Photo through BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Jacksonia papillata (Aphididae; Figure 105) often occurs among mosses (Müller 1973). This is consistent with the mossy habitats of its primary hosts. Müller suspects that it sometimes feeds on mosses. *Pachypappa rosettei* (0.84-1.41 mm; Aphididae or Pemphigidae; Figure 106), *Pachypappa sacculi* (Figure 107), *Prociphilus*

xylostei (~3 mm; Aphididae; Figure 108-Figure 109), and *Thecabius populimonilis* (only once; Aphididae; Figure 110-Figure 111) also occur on mosses (Pike *et al.* 2012). *Prociphilus xylostei* is a strange-looking insect that secretes copious wax to cover and camouflage itself, making it look more like a fungus than an insect.



Figure 106. *Pachypappa rosettei*, a moss inhabitant. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 107. *Pachypappa sacculi*, a moss inhabitant. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

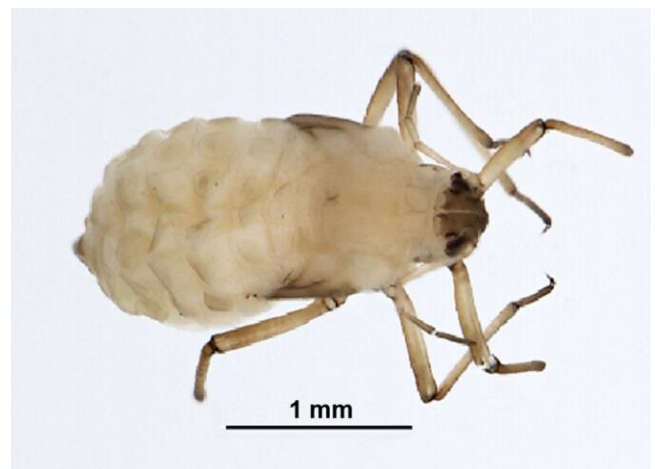


Figure 108. *Prociphilus xylostei* nymph, a moss dweller. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 109. *Prociphilus xylostei* adult, a moss dweller that secretes wax that serves to camouflage it. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 110. *Thecabius populimonilis*, a moss inhabitant. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Pseudacaudella rubida (0.7-1.0 mm; Figure 111- Figure 112) lives on the moss genera *Calliergonella* (Figure 54), *Climacium* (Figure 96), *Dicranum* (Figure 113), *Hylocomium* (Figure 61), *Mnium* (probably *Plagiomnium*; Figure 33-Figure 34, Figure 43-Figure 44), *Pleurozium* (Figure 114), *Polytrichum* (Figure 17), *Pseudoscleropodium* (Figure 62), and *Thuidium* (Figure 31) (The Aphids 2015).

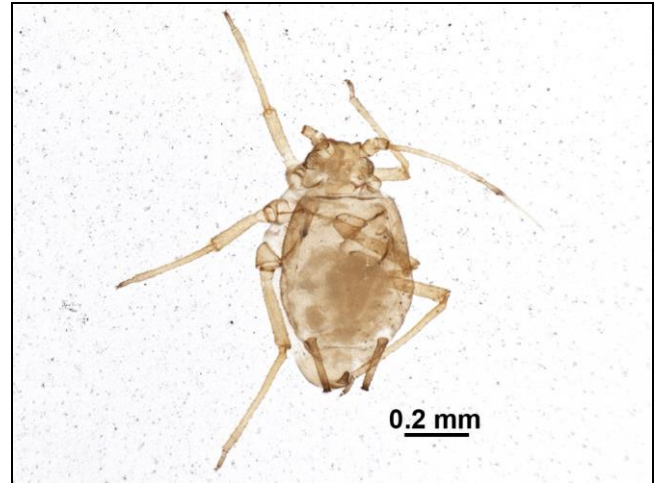


Figure 111. *Pseudacaudella rubida* nymph, a species that lives in a variety of mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

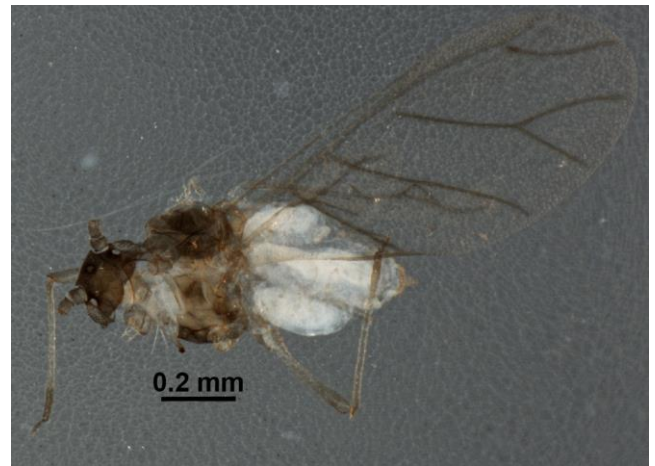


Figure 112. *Pseudacaudella rubida* adult. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 113. *Dicranum scoparium* with developing capsules, a moss that hosts *Pseudacaudella rubida*. Photo by Janice Glime.



Figure 114. *Pleurozium schreberi*, secondary host for *Pseudacaudella rubida*. Photo by Michael Lüth, with permission.

Attractants?

Do aphids help mosses attract more aphids? *Nurudea shiraii* (Aphididae) uses *Hypnum plumaeforme* (Figure 115) as a food plant (Lou & Chen 2000). *Thuidium cymbifolium* (Figure 31) is the host plant of *Schlechtendalia elongallis* (Pemphigidae). Lou and Chen found that these two mosses and the host moss *Brachythecium buchananii* (Figure 1) produce such aliphatic compounds as alcohols, aldehydes, ketones, and esters. They suggested that production of these compounds might be induced by the damage caused by their inhabiting aphids. They further suggested that these compounds might help the aphids locate their host plants. This sounds like an interesting hypothesis in need of testing.



Figure 115. *Hypnum plumaeforme*, food for *Nurudea shiraii*, produces aliphatic compounds that might help aphids to locate these mosses. Photo by Janice Glime.

Why Alternate Hosts?

Moran (1989) speculated on the evolutionary pressures that would cause such a host alternation as mosses and woody plants to evolve. Since this strategy is present in both the Chinese species and the North American ones, she postulated that both had their origins in Alaska and were separated when forced southward before the land bridge across the Bering Strait separated. Moran (1989) had already found fossil evidence of a 48-million-year-old aphid (*Melaphis rhois*; Figure 85-Figure 88) – host plant association with a similar moss/sumac alternation in

Alaska, apparently established prior to the southward retreat of sumac. Unlike the alternation seen in China and North America, in England and Scandinavia the aphid has lost its alternate host behavior and lives entirely on mosses, but has sacrificed all sexual behavior. This type of response is also known in the whitefly parasitoid *Encarsia formosa* (Hymenoptera) (Birkett *et al.* 2003), but both the production of aliphatic compounds by the moss and the insect response to these need to be verified as a consequence of moss herbivory.

Adelgidae – Woolly Conifer Aphids

The Adelgidae made their claim to fame by destroying forests, especially in the Appalachian Mountains, USA. Their connection with bryophytes is indirect, but can be strong. The woolly adelgids (*Adelges tsugae*; 1.5-mm; Figure 116-Figure 118) have had a major impact on the eastern hemlock (*Tsuga canadensis*; Figure 119-Figure 120) in the Appalachian Mountains, as far south as the Smoky Mountains (Jackson & Bellemare 2014). This disturbance has caused a decline in the leafy liverwort *Bazzania trilobata* (Figure 121) because the dying hemlocks open the canopy and the habitat becomes drier. This is accompanied by more deciduous litter (resulting from invasion of black birch – *Betula lenta*), greater light exposure, and higher temperatures.



Figure 116. *Adelges tsugae* on host eastern hemlock (*Tsuga canadensis*). Photo from Connecticut Agricultural Experiment Station Archive, USA, through Creative Commons.



Figure 117. *Adelges tsugae*, a destroyer of eastern hemlock forests. Photo by Shimat Joseph, University of Georgia, through Creative Commons.



Figure 118. *Adelges tsugae* eggs. Photo by Shimat Joseph, University of Georgia, through Creative Commons.



Figure 119. Dead hemlocks (*Tsuga canadensis*) in South Carolina resulting from *Adelges tsugae* infestations. Photo by Steve Norman, U.S. Forest Service, through Public Domain.

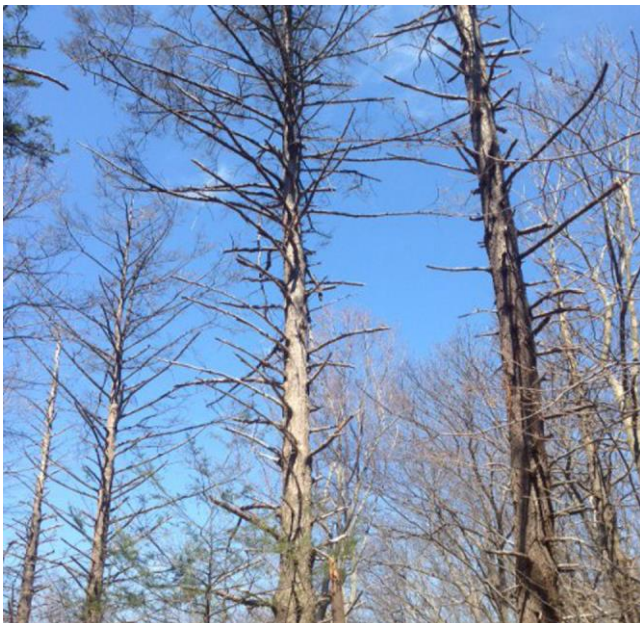


Figure 120. *Tsuga canadensis* showing open canopy after attack by *Adelges tsugae*. Photo by Matthew Willis, through Creative Commons.



Figure 121. *Bazzania trilobata*, a leafy liverwort that is disappearing where hemlocks have been killed by *Adelges tsugae*. Photo by Janice Glime.

Quite the opposite story can be told about one moss in the southern Appalachian Mountains of North Carolina. There, in high elevation locations, the moss *Leptodontium viticulosoides* (Figure 122-Figure 123) had become rather rare (Zander 1980). But prior to 1980 it began spreading. This spread is attributed to *Adelges piceae bouvieri* (Figure 124, Figure 125, Figure 128). In this case, the adelgid aphid causes the bark of the **endemic** (growing in a limited area) Fraser fir (*Abies fraseri*; Figure 126-Figure 128) tree to peel, creating habitat suitable for the moss.



Figure 122. *Leptodontium viticulosoides*, a moss that is spreading in areas where bark of Fraser fir (*Abies fraseri*) is peeling due to infestations of *Adelges piceae*. Photo courtesy of Claudio Delgadillo Moya.



Figure 123. Close view of *Leptodontium viticulosoides*. Photo by Li Zhang, with permission.

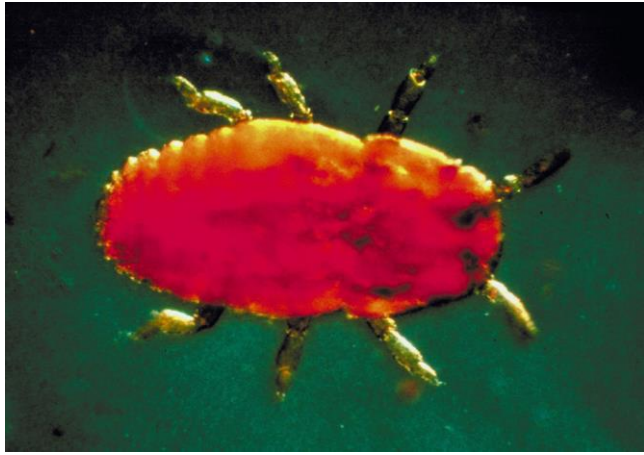


Figure 124. *Adelges piceae*, a species that causes the bark of the Fraser fir to peel, permitting the moss *Leptodontium viticulosoides* to become established. Photo by USDA Forest Service - Ashville Archive, through Creative Commons.

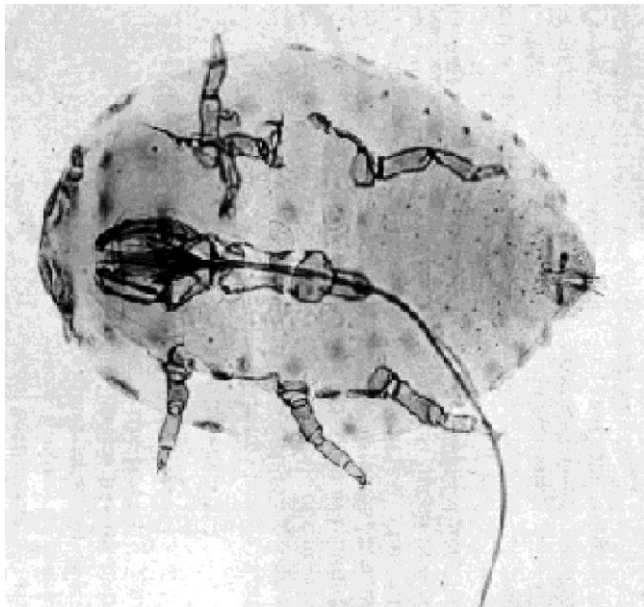


Figure 125. *Adelges piceae*, a species that damages Fraser Fir and opens habitat for the moss *Leptodontium viticulosoides*. Note the long proboscis. Photo from USDA, in Public Domain.



Figure 126. *Abies fraseri* in the Blue Ridge Mountains, USA. Photo by Gene, through Creative Commons.



Figure 127. *Abies fraseri*, home for *Adelges piceae* in the southern Appalachian Mountains, USA. Photo by Steve Baskouf <www.bioimages.vanderbilt.edu>, through Creative Commons.

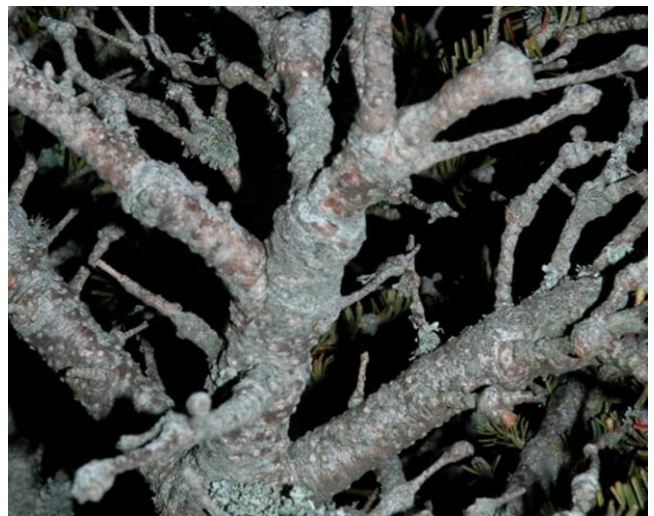


Figure 128. *Adelges piceae* on *Abies fraseri*. Photo by William M. Ciesla, Forest Health Management International, <Bugwood.org>, through Creative Commons.

In the Southern Appalachian Mountains, the hornwort *Megaceros aenigmaticus* suffered a decrease in sexual reproduction. Although this was partly due to its rarity and lack of contact between males and females, Villareal (2009) suggested that its survival is further threatened by habitat degradation due to the adelgid plague on the hemlocks that created its habitat.

SUBORDER COLEORRHYNCHA

(moss bugs or beetle bugs)

The **Coleorrhyncha**, with only one exception, are flightless. They have an extremely reduced **pharyngeal ring** muscle layer (muscles surrounding the pharynx, which is the first part of the foregut) (Spangenberg *et al.* 2013). Spangenberg and coworkers suggest that this reduction prevented any secondary shift in diet (these are bryophyte eaters), preventing them from using a broad range of food sources and consequently preventing radiation of the species into new locations and new species.

Peloriidiidae – Moss Bugs

The **Peloriidiidae** are cryptic species that frequent wet mosses, liverworts, and leaf litter (Spangenberg *et al.* 2013). They are small (2-4 mm), flattened, and cryptically-colored relict **Hemiptera** in the Southern Hemisphere (Evans 1982; Burckhardt 2009), resulting in their remaining undiscovered in Australia until 1932, although they were known elsewhere in the area (Monteith 2015). Cranston (2010) cites this family as one living among *Sphagnum* and liverworts (Austin *et al.* 2004; Cranston 2009). Evans (1941) considered the presence of moss in a habitat that is moist all year round to be a necessity.

One adaptation of bryophyte fauna that is often forgotten is vibration frequency of the "call." Hoch *et al.* (2006) considered the small size of the **Peloriidiidae** to necessitate vibrational signals for mates to locate each other. The low frequency of the signals suggests that they may be adapted to calling from their host of soft mosses. This signal is effective at short range and would therefore be effective to initiate courtship or signal disturbance.

The history of the **Peloriidiidae** is an interesting one. *Peloriidum* (Figure 129) had been collected from Tierra del Fuego in 1892, *Xenophyes* (Figure 131) from New Zealand in 1920, and *Hemiodoecus* (Figure 135) from Tasmania in 1904 (Monteith 2015). But in total, only six specimens had been collected to represent these three genera! All came from dripping wet *Nothofagus* forests (Figure 130). In 1932, Hacker described *Hemiodoecus veitchi* from the Antarctic Beech forest of Lamington National Park, Queensland, Australia. This name was later changed to honor both Hacker and his mentor – *Hackeriella veitchi*. In 1971, a further discovery by Bob Taylor resulted in the description of *Rhacophysa taylori* (Burckhardt 2009) from dripping mosses near Cairns, Queensland, a wet area receiving 8 m of rainfall per year.

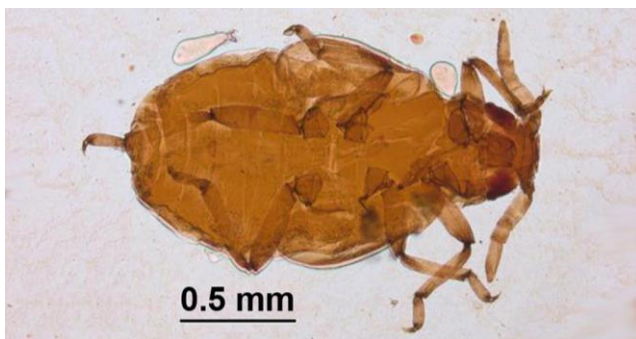


Figure 129. *Pemphigus bursarius*, member of a moss-dwelling genus. Photo from Pest and Diseases Image Library, Bugwood.org, through Creative Commons.

Despite having only 21 species known in 1982 (Evans 1982), the **Peloriidiidae** have been reported from bryophytes many times compared to other **Hemiptera**. These frequent reports, nevertheless, most likely grossly under-represent their presence because of their cryptic habits and small size (Burckhardt *et al.* 2011). Adequate sampling requires sifting of the mosses and forest litter with a sieve. They also tend to occur in remote locations that are hard to reach.

Moss bugs are known from fossils, occurring on mosses in the wet, cool *Nothofagus* (beech) forests (Figure 130) in the Southern Hemisphere (Bechly & Szewo 2007). Today they are most common in the *Nothofagus* forests of southern South America, Australia, Tasmania, New Caledonia, Lord Howe Island, and New Zealand, where they live in damp mosses on decaying mossy trunks and twigs of the *Nothofagus*. In addition to eating the leafy mosses, they may feed on moss rhizoids, wood-decaying fungi, or lichens.



Figure 130. *Nothofagus* beech forest with a dense bryophyte ground cover, Eglinton Valley, NZ. Photo from Department of Conservation of NZ, through Creative Commons.

Drake and Salmon (1948) first reported *Xenophyes cascus* (2.48-3.10 mm; Figure 131) from New Zealand in 1948, identifying it from damp moss. *Xenophyes cascus* is currently distributed in temperate forests and fens in the Southern Hemisphere (Australia, New Zealand, New Caledonia, Chile, Argentina) (Grozeva *et al.* 2014). They also occur on the moss *Notoligotrichum crispulum* (Figure 132) in heavily forested areas where *Weinmannia racemosa* (Figure 133) is dominant (Carter 1950). These are both moss dwellers and moss feeders. Burckhardt *et al.* (2011) reported New Zealand moss dwellers to include *Xenophyes cascus* from moss on an old log, the broadleaf-taraire dominant *Xenophyes adelphus* (2.35-2.63 mm) by sifting mosses from cloud forests and the mosses and liverworts on tree trunks and branches, *Xenophyes goniomus* (2.68-3.10 mm) and *Xenophyes kinlochensis* (2.80-3.23 mm) from mosses, *Xenophyes metoponcus* (2.35-2.55 mm) from mosses in mixed podocarp/broadleaf forest, and *Xenophyes rhachilophus* (2.18-2.95 mm; Figure 134) from mosses under beech trees, sifted mosses, and mosses on a wet bank.

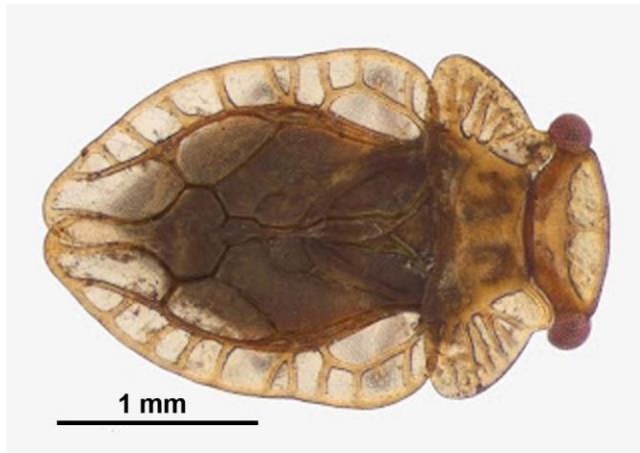


Figure 131. *Xenophyes cascus*, an inhabitant of *Notoligotrichum crispulum* in New Zealand. Photo by Birgit E. Rhodes in Larivière *et al.* 2011, with permission.



Figure 134. *Xenophyes rhachilophus*, a species that occurs among mosses under beech trees in New Zealand. Photo by S. E. Thorpe, through Creative Commons.



Figure 132. *Notoligotrichum crispulum* with capsules, home of *Xenophyes cascus* (Figure 131) in New Zealand and elsewhere. Photo by David Tng <<http://www.davidtng.com/>>, with permission.



Figure 133. *Weinmannia racemosa*, home for the moss *Notoligotrichum crispulum* and inhabiting *Xenophyes cascus*. Phil Bendle, through Creative Commons.

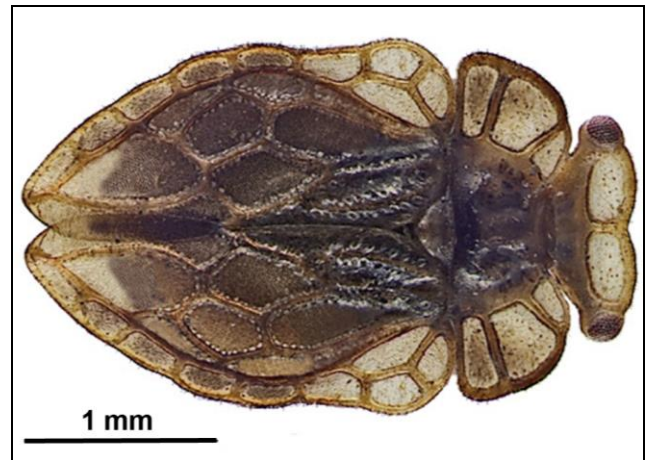


Figure 135. *Hemiodoecus leai*, a species most likely introduced into New Zealand with frozen fish eggs packed in mosses. Photo by Marie-Claude Larivière <www.nzhemiptera.com/>, with permission.



Figure 136. *Ptychomnion aciculare*, home for *Hemiodoecus leai* (Figure 135). Photo by Andy Hodgson, with permission.



Figure 139. *Bartramia* sp., home and food for *Hemiodoecus leai* (Figure 135). Photo by Andy Hodgson, with permission.



Figure 137. *Weymouthia cochlearifolia*, home for *Hemiodoecus leai* (Figure 135). Photo by Juan Larrain, with permission.



Figure 138. *Weymouthia mollis*, home for *Hemiodoecus leai* (Figure 135). Photo by Juan Larrain, with permission.



Figure 140. *Oiophysa ablusa*, a New Zealand bryophyte dweller on a leafy liverwort. Photo by E. Wachmann through M.-C. Larivière, with permission.

The genera *Oiophysa* (2.19-2.98 mm; Figure 140) and *Xenophysella* (2.34-3.00 mm) are among the moss dwellers in New Zealand (Larivière *et al.* 2011). These include *Oiophysa ablusa* (3 mm; Figure 140), *O. cumberi* (2.5 mm; Figure 141), *O. distincta* (2.6 mm), *O. pendergrasti* (2.5 mm), *Xenophysella greensladeae* (2.48-3.0 mm), and *X. stewartensis* (2.34-2.63 mm; Figure 142). *Xenophysella greensladeae* has two 3-lobed **bacteriomes** where bacteria are maintained. Larivière and coworkers presumed that as environmental conditions become drier the **Peloriidiidae** would move deeper into the moss layers where there is greater humidity, remaining there until the surface becomes more suitable.

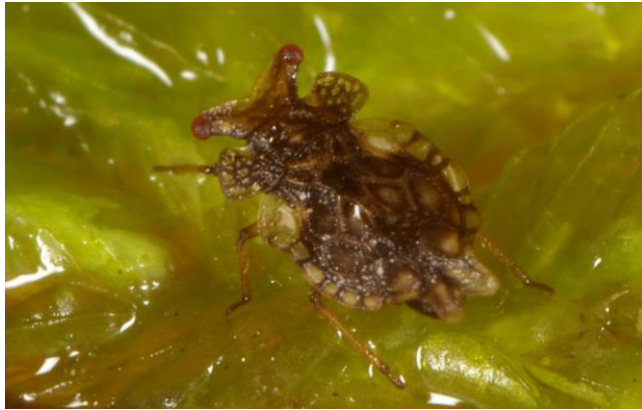


Figure 141. *Oiophysa cumberi*, a New Zealand bryophyte dweller on a moss. Photo by George Gibbs, with permission.

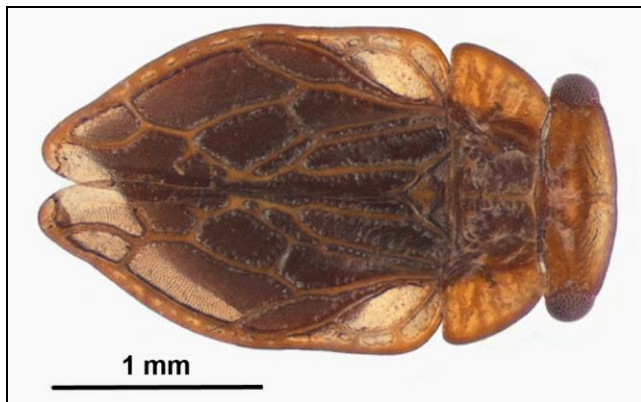


Figure 142. *Xenophysella stewartensis*, a New Zealand moss dweller. Photo by Birgit E. Rhodes in Larivière *et al.* 2011, with permission.

Oiophysa distincta (2.44-2.98 mm) is considered a living fossil relict in native New Zealand forests, where it lives among wet mosses in the temperate and Antarctic rainforests (Figure 143) (Harris 2011; Grozeva *et al.* 2014). Today other *Peloridiidae* likewise occur in damp mosses, frequenting the decaying mossy trunks and branches of *Nothofagus* (Figure 130), where they feed on wood-decaying fungi, lichens, and moss rhizoids (Bechly & Szwedo 2007).



Figure 143. Rainforest, Fiordland National Park, New Zealand, mossy home for *Oiophysa distincta*. Photo by Christiaan Briggs, through Creative Commons.

On Lord Howe Island, *Howeria kingsmilli* (3.0-3.1 mm) occurs on the long pendent moss *Spiridens vieillardii* (Figure 144) and on the leafy liverwort *Porella elegantula* (Figure 145-Figure 146) (Evans 1967).



Figure 144. *Spiridens vieillardii* with capsules, a pendent moss that houses *Howeria kingsmilli*. Photo by Louis Thouvenot, with permission.



Figure 145. *Porella elegantula*, a leafy liverwort that is home to *Howeria kingsmilli*. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.



Figure 146. *Porella elegantula* showing its underside. This pendent leafy liverwort is home to *Howeria kingsmilli*. Photo by Jan-Peter Frahm, with permission.

In Australia, *Hemiodoecellus fidelis*, like *Hemiodoecus leai* (Figure 135) in New Zealand, lives in

damp moss where its movement is limited by its short legs and limited space for movement (Robinson 2003).

In Australia, *Hackeriella veitchi* (3.0-3.3 mm; Figure 147) inhabits the pendent moss *Papillaria crocea* (Figure 148) (Helmsing & China 1937; Carter 1950; Spangenberg *et al.* 2013). On the other hand, a much later visit to the area failed to reveal any individuals of this species on the *P. crocea* (Spangenberg *et al.* 2013). Nevertheless, new locations have been found, making this the most readily available member of the family. *Hackeriella veitchi* is unique among the **Peloridiidae** in being able to jump. This is accomplished without any apparent morphological adaptation, but rather by suddenly rotating the hind **femora** (third segments of legs) on the **coxae** (bases of legs) (Burrows *et al.* 2007).



Figure 147. *Hackeriella veitchi*, an inhabitant of a pendent moss in Australia. Photo by J. Deckert, with permission.



Figure 148. *Papillaria crocea* in cloud forest where it can provide a home for *Hackeriella veitchi*. Photo by Peter Woodard, through Creative Commons.

Burkhardt and Agosti (1991) reported *Peloridora kuscheli* (2.8-3.3 mm; Figure 149), *P. minuta* (~2.6 mm), and *P. holdgatei* (~2.6 mm) from mosses in the *Nothofagus* forests (Figure 130) in Chile. Other Chilean moss dwellers include *Pantinia darwini* (3.2-3.9 mm; Figure 150) and *Pantinia* sp. and several unidentified early instar nymphs.



Figure 149. *Peloridora kuscheli*, an inhabitant of mosses in the *Nothofagus* forests of Chile. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 150. *Pantinia darwini*, a moss dweller in *Nothofagus* forests (Figure 130) in Chile. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Shcherbakov (2014) found that some of the **Peloridiidae** are restricted to one or only a few bryophyte species (**mono-** or **oligophagous**). For example, *Peloridium hammoniorum* (3.8-5.2 mm; Figure 151) in Fuegia in Southern Patagonia was found only on *Pohlia cruda* (Figure 152) (China 1962; Cekalovic 1986), *Polytrichum strictum* (Figure 153) (Estévez & Remes Lenicov 1990), and *Polytrichadelphus magellanicus* (Figure 154) (Shcherbakov 2014), and it is known to eat mosses (Larivière *et al.* 2011; Shcherbakov 2014). [The host *Polytrichum strictum* was not reported previously from that region (Larrain 2007) and may be a misidentification.] The recently described species *Peloridium pomponorum* (3.4-4.1 mm) is only known from *Sphagnum magellanicum* (Figure 156) and *S. cf. recurvum* (Figure 157), both in open areas (Shcherbakov 2014).



Figure 151. *Peloridium hammoniorum* on *Polytrichadelphus magellanicus*. Photo by Roman Rakitov, with permission.



Figure 154. *Polytrichadelphus magellanicus*, home of *Peloridium hammoniorum* in Fuegia in Southern Patagonia. Photo by David Tng <www.davidtng.com>, with permission.



Figure 152. *Pohlia cruda*, a moss where *Peloridium hammoniorum* lives in Southern Patagonia. Photo by Martin Hutten, with permission.



Figure 155. *Peloridium pomponorum* on *Sphagnum magellanicum*. Photo by Roman Rakitov, with permission.



Figure 153. *Polytrichum strictum*, a peatland species where *Peloridium hammoniorum* might live in Southern Patagonia. Photo by Janice Glime.



Figure 156. *Sphagnum magellanicum*, a home for *Peloridium pomponorum*. Photo by Janice Glime.



Figure 157. *Sphagnum recurvum*, a home for *Peloridium pomponorum*. Photo by Jan-Peter Frahm, with permission.

Symbiotic Bacteria

One of the factors that may permit the **Peloriidiidae** to eat mosses is their associated symbiotic bacteria. The **Coleorrhyncha**, including the **Peloriidiidae**, is one of the oldest lineages of **Hemiptera**. Kuechler *et al.* (2013) analyzed **Peloriidiidae** bacterial symbionts from 15 representatives from South America, Australia, Tasmania, and New Zealand. These proved to be an unknown group of **Gammaproteobacteria**, which they named *Candidatus Evansia muelleri*. These bacteria develop at the posterior pole of a developing oocyte and thus are transmitted from parent to offspring before birth. A second bacterium was usually associated with the Malpighian tubules, an endosymbiont in the genus *Rickettsia* (Figure 158).

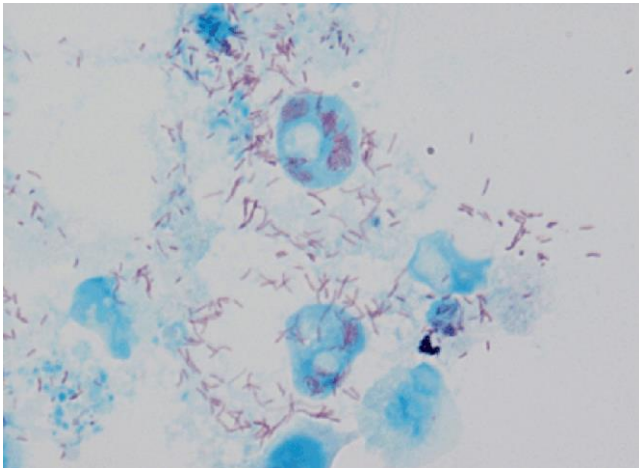


Figure 158. *Rickettsia conorii*, a possible symbiont of **Peloriidiidae** that permits it to digest mosses. Photo by Clarisse Rovey, Philippe Brouqui, & Didier Raoult, through Creative Commons.

ORDER THYSANOPTERA – Thrips

The thrips are tiny, slender insects with fringed wings (Greek *thysanos* = fringe) (Thrips 2015). They feed by sucking cell contents of plants or animals. Their tiny size (<1mm) gives them an ideal fit among bryophytes, but only one sub-tribe among the 6,000 species lives there (Mound

1989). Curiously, the word "thrips" is both singular and plural.

Although an insect most people do not often notice, these insects (**Thysanoptera**) can be associated with mosses (Mound 1989). Bhatti (1979) found two new species in a new genus of thrips (**Thripidae**) living among mosses in West Africa. Mound (1970) reported *Nesothrips lativentris* from this family among mosses on the Solomon Islands.

The Old World genera of *Bournierothrips* and *Muscithrips* are bryophyte dwellers. In fact, *Bournierothrips* seems to be restricted to mosses (Bournier 1979). A recent new genus, *Solanithrips*, was described from Mexico as an inhabitant of *Solanum* (Johansen 1997). This genus is closely related to the two Old World bryophyte-dwelling genera, so it is possible that it too may just use bryophytes when the *Solanum* is seasonally unavailable. Other members of **Thysanoptera** are known from bryophytes (and lichens) in Mexico (Mojica Guzman & Johansen 1990).

In their study of New Zealand **Thysanoptera**, Mound and Walker (1982) found records of a number of species of **Thripidae** in association with mosses: *Anaphothrips obscurus* (1.5 mm), *Anaphothrips woodi*, *Aptinothrips rufus* (1.5mm; Figure 159-Figure 160), *Aptinothrips stylifer* (~1.5 mm; Figure 161), *Ceratohrips frici* (Figure 162), *Lomatohrips paryphis*, *Pseudanaphothrips achaetus*, *Thrips australis*, *T. nigropilosus*, *T. obscuratus*, *T. tabaci* (Figure 163). At least some species, including *Ceratohrips frici*, are attracted to their primary hosts by colors (Teulon & Penman 1992). *Ceratohrips frici* is attracted to white and yellow traps. The associations of all these thrips with a number of flowering plants suggest that the mosses were most likely a refuge and not a food source (Mound & Walker 1982).

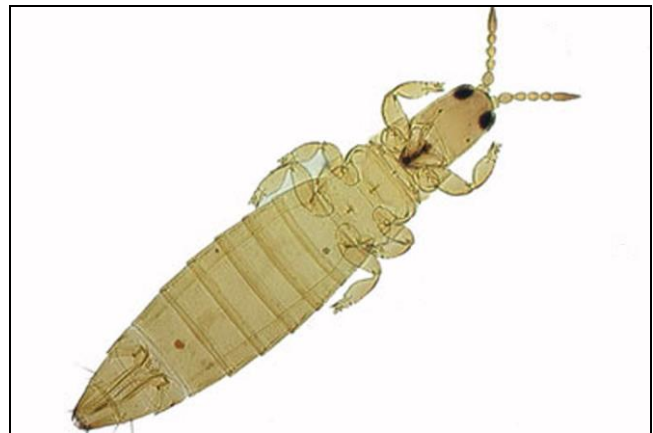


Figure 159. *Aptinothrips rufus*, a moss associate in New Zealand. Photo by John W. Dooley, through Creative Commons.



Figure 160. *Aptinothrips rufus*, a moss associate and flowering plant eater in New Zealand. Photo through Creative Commons.

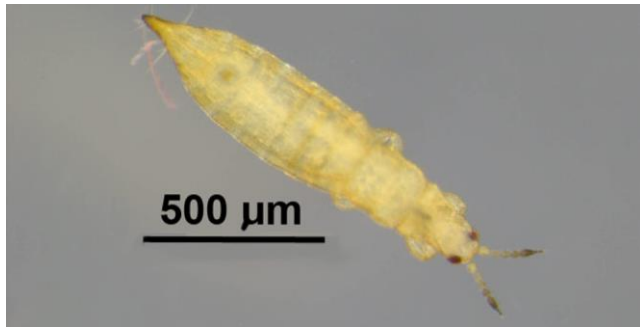


Figure 161. *Aptinothrips stylifer*, a moss associate in New Zealand. Photo through Creative Commons.



Figure 162. *Ceratothrips frici*, a New Zealand moss dweller. Photo by John W. Dooley, USDA APHIS PPQ, through Public Domain.



Figure 163. *Thrips tabaci*, a flowering plant associate that also spends time among mosses. Photo by Alton N. Sparks, through Creative Commons.

Johansen *et al.* (1983) discussed the New World (Eastern Mexico and Costa Rica) *Wegenerithrips* (0.738–1.16 mm; **Thripidae**), a genus with nine species at the time, as a bryophyte feeder. This is a genus thus far known only from females (Taylor 2013). Most likely more of these bryophyte feeders remain unknown.

Mound (1989) reported that only one sub-tribe within **Thysanoptera** feeds on mosses, the **Williamsiella** (family **Phlaeothripidae**). This sub-tribe is comprised of two genera, *Lissothrips* and *Williamsiella*. These are mostly New World species. In addition to their small size, these genera seem further adapted to moss dwelling by

being wingless. And their ability to feed on mosses seems to be a highly derived character. One even bears the name *Lissothrips muscorum* (1.17 mm), a wingless female found among mosses in Illinois, USA, and only known from mosses (Rhode 1955). Chiasson (1986) reported it from *Sphagnum* and moss litter, and it feeds on mosses. An early record of **Phlaeothripidae** among mosses is that of *Liothrips ocellatus* (Figure 164) in Illinois, USA (Hood 1908).



Figure 164. *Liothrips ocellatus*, one of the early known moss dwellers among the thrips. Photo through Creative Commons of Snipeview.

But it may not always be the moss that gives them their nutrition. In Australia and New Zealand species of these two genera have a blue-green gut, suggesting they may eat the associated **Cyanobacteria** (Mound & Tree 2015). The fact that these genera are understudied is indicated by the new finds: two species of *Lissothrips* were recorded from Australia for the first time in 2015, as well as six new species; *Williamsiella* was recorded from Australia for the first time with a new species.

Bryophytes may actually play an important role for leaf-inhabiting thrips. When the weather becomes cool and wet, these leaf dwellers seem to disappear from the landscape (Mound & Walker 1982). But if one uses a Berlese funnel to extract them from leaf litter and ground mosses, many will appear. The mosses serve as a refuge when leaves become inhospitable. Further evidence of bryophytes as a refuge comes from *Iridothrips mariae* (**Thripidae**). In Hungary, this species seeks mosses in the fall as a place to spend the winter (Jenser 2013).

Peck and Moldenke (1999) have been concerned with the invertebrates, especially insects, that are collected with harvestable mosses. Not only does this disturb the communities of origin, in some cases depriving birds, lizards, and other predators of a food source, but also it introduces these creatures to a new ecosystem where they may have no or few natural predators. They could easily become crop pests in some receiving ecosystems. Peck and Moldenke reported that the number of individuals of **Thysanoptera** per gram were greater in those moss samples collected at the bases of shrubs than in those from the tips of branches. They recommended prohibiting the harvesting of mosses from the shrub bases due to their importance in housing insect diversity.

Summary

Several previous orders have been combined into the **Hemiptera**, including leaf hoppers, plant hoppers, aphids, and moss bugs.

Some of the **Cicadellidae** are true **tyrphobionts** (bog dwellers). The **Delphacidae** includes moss eaters, especially on **Polytrichaceae**; few seem to be bog dwellers.

Other important moss-dwelling aphids include members of **Myzodium** and **Muscaphis**, both of which typically use mosses for overwintering and seasonal food. **Derbidae** and **Issidae** have moss dwellers, but little seems to be known about their habits. The latter uses a pair of gears to aid jumping in nymphs. Even less is known about **Eriococcidae** that live among mosses.

This classification includes several kinds of gall makers in the **Aphididae** that depend on bryophytes, especially **Mniaceae**, for part of the life cycle and winter food. For the Chinese gall maker *Schlechtendalia chinensis* and others, and even some North American gall makers, the bryophytes serve as an essential winter host, serving for both food and shelter and often oviposition sites. In the **Aphididae**, a family with a stylet for sucking plant juices, moss specialists have been used to trace the movement of fluids in the leptoids of mosses in the **Polytrichaceae**. Some of these moss inhabitants may respond to aliphatic compounds in the moss, but direct relationships remain to be tested.

Members of the genus *Adelges* (**Adelgidae**) have destroyed habitat for the leafy liverwort *Bazzania trilobata* and in other cases have opened new habitat for the moss *Leptodontium viticulosoides*.

The family **Peloriidiidae** is so common among mosses that the common name of "moss bugs" is applied. They seem to require that constantly moist environment, probably burrowing deeper as the moss dries. At least some members of the family may have bacteria that help in their digestion of the mosses.

Information on thrips (**Thysanoptera**) is limited, but several genera are represented among bryophytes, with the sub-tribe **Williamsiellina** feeding on mosses.

Acknowledgments

Thank you to Chen Peipei for providing a list of references on the gall aphids that use mosses as alternate hosts. John Steel alerted me to the discovery of *Hemiodocus leai* among mosses in New Zealand. Thank you to Marie-Claude Larivière for her encouragement and help in providing images, making suggestions, and reviewing the chapter. Thank you to Robin Stevenson for interesting discussion and followup on the ants that make *Sphagnum* collars to house aphids. Thank you to Andi Cairns for the article on the history of Peloriidiidae by Monteith. Thank you to Timea Deakova for sharing the story and images of the spittlebug on *Polytrichum*. Thank you also to Sean Haughian for sending me the Moran (1989) paper on evolutionary implications of gall aphids.

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CHAPTER 12-8 TERRESTRIAL INSECTS: HOLOMETABOLA – MEGALOPTERA AND NEUROPTERA

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CHAPTER 12-8

TERRESTRIAL INSECTS:

HOLOMETABOLA – MEGALOPTERA

AND NEUROPTERA



Figure 1. *Chauliodes pectinicornis* adult, a species that spends its pupal stage among mosses. Dorothy Pugh <www.dpughphoto.com>, with permission.

MEGALOPTERA – Alderflies, Dobsonflies and Fishflies

This is a small order and most are aquatic as larvae. Nevertheless, some members of the **Corydalidae** (dobsonflies) pupate under mosses, a stage lasting about two weeks (Needham *et al.* 1901). These species include *Chauliodes pectinicornis* (Figure 1-Figure 2), *C. rastricornis* (Figure 3-Figure 4), and *Nigronia serricornis* (Figure 5-Figure 6).



Figure 2. *Chauliodes pectinicornis* pupa, a stage that often develops among mosses. Photo by Patrick Coin, through Creative Commons.



Figure 3. *Chauliodes rastricornis* adult, a species that pupates under mosses. Photo by Seabrooke Leckie, through Creative Commons.



Figure 4. *Chauliodes rastricornis* adult male head showing large eyes and comb-like antennae. Photo by Seabrooke Leckie, through Creative Commons.



Figure 5. *Nigronia serricornis* larva, a species that pupates under mosses. Photo by Donald S. Chandler at <www.Discoverlife.org>, with permission.



Figure 6. *Nigronia serricornis* adult, a species that pupates under mosses. Photo by Richard Orr <www.marylandinsects.com>, with permission.

Barnard (1931) reported pupae of alderflies (**Sialidae**) from *Sphagnum* and other wet or aquatic mosses that grew near or in streams and waterfalls in South Africa. These alderflies required that the mosses be wet.

NEUROPTERA – Lacewings

Not many members of Neuroptera use bryophytes, but Richards and Davies (1977) reported that lacewing larvae search for prey in mosses.

Osmylidae

The larvae of *Osmylus* (Figure 7) live in the mosses on the banks of woodland streams (Elliott 1996). Even the adults are typically found near these small streams that have mossy banks suitable for larval development. In Great Britain, the larvae can be found in these mosses throughout the year. In the winter they migrate deep into the moss rhizoids where they hibernate.

The female *Osmylus fulvicephalus* (Figure 7) lays about 30 eggs 2-3 days after mating (Elliott 1996). These often are laid in small groups. When deposited on mosses they are laid singly or in pairs on the undersides of leaves and near the water (Lestage 1920; David 1936; Ward 1965). The eggs are cylindrical and slightly flattened. These white eggs darken to brown within a few days, making them less obvious than the white version. Eggs hatch in 4-22 days, depending on the temperature (Withycombe 1923; David 1936; Ward 1965).



Figure 7. *Osmylus fulvicephalus* larva, a moss dweller near woodland streams. Photo by Walter Pfliegler, with permission.

When the larvae of the giant lacewing, *Osmylus fulvicephalus* (Figure 7), emerge, they burrow into the mosses (Elliott *et al.* 1996) and live among damp mosses in the splash zones of river banks and streams (Plant 1994; Roper 2001). These larvae are only 5 mm when they hatch, but reach 15 mm by the third (final) instar from which they develop into pupae (Elliott 1996).

In this moss habitat *Osmylus fulvicephalus* (Figure 7) larvae are able to eat small arthropods (Elliott *et al.* 1996). They strike at movement and inject enzymes that paralyze the prey. When they hatch, the first instar larvae eat mites and **Collembola**, but second and third instars switch to

eating larvae of small **Diptera**. The common **Chironomidae** (midges) are paralyzed in 10 seconds by the enzymes. They then suck the contents out of the prey. The larvae may dive into the water to find prey, but if they are forced to remain submersed they die within 8-28 days (Ward 1965).

The third (and final) larval instar overwinters in **diapause** and is able to withstand total immersion during flooding (Elliott *et al.* 1996). When spring arrives, the larvae make a cocoon, incorporating some of the moss in the cocoon, then pupate for 10-14 days before cutting their way out with their mandibles. They then emerge as adults (Figure 8) without further feeding. The adults fly about over the water surfaces in their woodland homes in the evening (**crepuscular**) (Elliott 1996).



Figure 8. *Osmylus fulvicephalus* adult, a species that lays its eggs on moss leaves. Photo from <www.invertebradosdehuesca.com>, through Creative Commons.

Chrysopidae

The modern **Chrysopidae** are not known to live among bryophytes, but they sometimes wear them. The larvae attach various pieces of debris, including bits of mosses and lichens, on their backs (Figure 9) (Skorepa & Sharp 1971; Slocum & Lawrey 1976; Eisner *et al.* 2002; Pérez-de la Fuente *et al.* 2012; Anonymous 2015; Newman *et al.* 2015). This cloak provides camouflage that hides them from both predators and prey.



Figure 9. **Chrysopidae** larva with cloak of debris and lichens. Note the head and large jaws at right. Photo by David Illig, through Creative Commons.

Larvae of the green lacewing *Leucochrysa pavid*a (Figure 10-Figure 13) (Slocum & Lawrey 1976) and the brown lacewing (Anonymous 2015) take their camouflage with them. They make packets of lichen fragments, bark, pollen grains, fungal spores, and moss fragments that they attach to spines on their backs (Slocum & Lawrey 1976). Likewise, immature brown lacewings use lichen and moss coverings to camouflage and protect them from predators and to disguise themselves from their prey (Insects 2014).



Figure 10. *Leucochrysa pavid*a larva with lichen back pack. This species also uses mosses. Photo by Jim McCormac, with permission.



Figure 11. *Leucochrysa pavid*a larva with lichen back pack, ventral view. Photo by Jim McCormac, with permission.



Figure 12. *Leucochrysa pavidula* larva with lichen back pack showing its camouflage against lichen-covered substrate. Photo by Jim McCormac, with permission.



Figure 13. *Leucochrysa pavidula* larva with lichen back pack, mandibles ready. Photo by Jim McCormac, with permission.

Hallucinochrysa diogenesi (Figure 14) is a fossil lacewing that attached plant fibers, bark, leaves, algae, mosses, snail shells, and corpses of its food prey on its back (Pérez-de la Fuente *et al.* 2012). These were held in place by the bristles on the backs of the larvae.



Figure 14. *Hallucinochrysa diogenesi*, representation of the fossil that attached mosses and other substances to its back. Photo by Jose Antonio Penas, through Creative Commons.

Fossil evidence suggests that some larvae of the **Chrysopidae** have been associated with liverworts (Liu *et al.* 2018). *Phyllochrysa huangi* larvae (Figure 15, Figure 16) from Burmese amber (Upper Cretaceous ~100 million years old) exhibit "distinctive foliate lobes" on the thorax and abdomen. This mimicry permits individuals to hide from prey (Figure 16) or to be ambush predators because the larvae are hard to distinguish from their background vegetation.

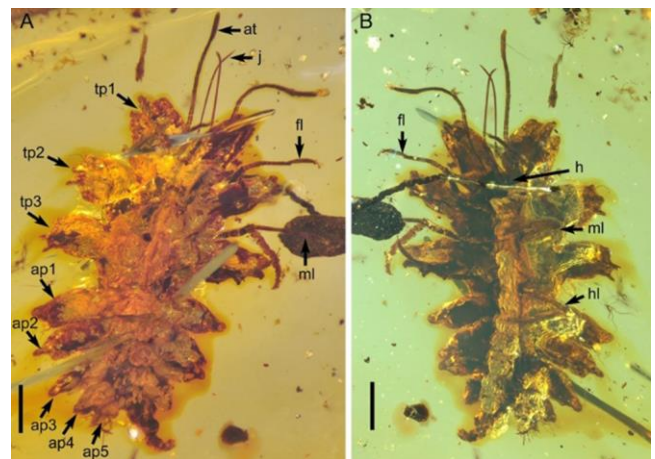


Figure 15. Chrysopid larvae, *Phyllochrysa huangi*, in Burmese amber. Image from Liu *et al.* 2018, with permission.

The shape of this larva is similar to that of bryophytes (Figure 16, Figure 17). Furthermore, its head is small and concealed under the anterior thoracic lobe (Figure 16) (PPI 2018). Antennae are extremely long with enlarged ends. The researchers found several amber fossil bryophyte species with similar morphologies (Figure 17), including size, leaf shape and arrangement, leaf folds, and lines.



Figure 16. Models of *Phyllochrysa huangi* larvae and hypothetical liverworts. Image from Liu *et al.* 2018, with permission.

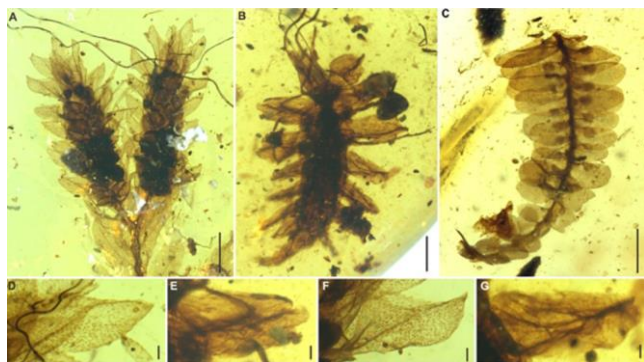


Figure 17. Burmese mosses (B, E, & G) and liverworts in amber – potential hosts for *Phyllochrysa huangi* larvae. Image from Liu *et al.* 2018 and PPI 2018, with permission.

Summary

The **Megaloptera** and **Neuroptera** are small orders. Hence there are few bryophyte dwellers. Some members of **Megaloptera** pupate under mosses. In the **Neuroptera**, the best known bryophyte-dwelling genus is *Osmylus*. *Leucochrysa pavid*a makes packets of camouflage that include moss fragments among other objects.

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Bernard Goffinet alerted me to the story on fossil *Phyllochrysa huangi* larvae that mimicked liverworts. Thank you to all the photographers who placed their images online with Creative Commons permission and to those who gave me permission to use their images.

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CHAPTER 12-9a TERRESTRIAL INSECTS: HOLOMETABOLA – COLEOPTERA BIOLOGY AND ECOLOGY

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CHAPTER 12-9a

TERRESTRIAL INSECTS:

HOLOMETABOLA – COLEOPTERA

BIOLOGY AND ECOLOGY



Figure 1. *Ptychomitrium* in the Neotropics with beetle navigating within the mat. Photo by Michael Lüth, with permission.

COLEOPTERA – BEETLES

I opened my email one morning to see one subject labelled "Catching Beetles." Upon investigation, I found this was an advertisement for a new book, 320 pages, all directed toward the various methods for catching beetles in the myriad of habitats they occupy and the families you might encounter (Julio 2011). This large book attests to the huge number of species, sizes, and wide range of habitats of beetles. The picture of a car with large fine-mesh funnel nets on the top and sides struck me as a symbol of their **ubiquitous** (found everywhere) nature.

It seemed like every time I looked up information on a beetle species, I found three more beetle species that inhabited mosses during part of the life cycle. At some point I had to stop and ignore or this volume would never get past the beetle chapter. Hence, I know there are more records that are out there, but these are adequate to show the wide range of families, uses, habitats, and adaptations.

Among the insects, the **Coleoptera**, those hard-winged insects known as beetles, are the largest group of organisms on the planet, and are likewise abundant within the shelter of bryophytes. A renowned biochemist and friend of the entomologist E. O. Wilson, J. B. S. Haldane, when asked by a theologian what the natural world had taught him about the Creator, replied that he has "an inordinate fondness for beetles." It is unclear whether Haldane is the one who coined the phrase because many variants of it appear in the literature (Farrell 1998).

With such large numbers, it is not surprising that we find some of them among mosses. For example, **Parnidae** and **Elmidae** are common in *Sphagnum* peatlands (Figure 2) (Leng 1913). That means that they can become unwitting passengers on harvested mosses, travelling around the world with them (Reich 1974; Peck & Moldenke 1999).



Figure 2. *Sphagnum* lawn, home for some members of **Parnidae** and **Elmidae**. Photo from Creative Commons.

Moss-dwelling beetles have been known for a long time (for example, Douglas 1871; Waterhouse 1871). Ferguson (1901) enumerated many species of beetles among mosses in the Clyde area of the British Isles, listing the most in the families **Curculionidae** (weevils) and **Staphylinidae** (rove beetles). Day (1907) reported several species from mosses in Cumberland, England. Brown (1972) considered that some seek mosses to maintain their moisture.

Des Callaghan (pers. comm. 3 February 2012) relayed to me his experience with grubs he thought might be beetle larvae. He had saved a sample of *Micromitrium tenerum* (Figure 3) for photography, but when he was ready for the photography all he found was soil covered by capsules! He later observed the grubs eating the leaves of the moss.



Figure 3. *Macromitrium tenerum*, a species for which clumps can be completely devoured by beetle grubs. Photo by Jan-Peter Frahm, with permission.

Bryophagids – Eating and Being Eaten

As seen above, a surprising number of beetles feed on mosses. A variety of small beetles eat mosses and use them as their homes (Drozd *et al.* 2007).

A number of genera in the **Byrrhidae** occur among mosses, use them for egg laying, or eat them. *Exomella pleuralis* (Figure 4) can be found in *Racomitrium heterostichum* (Figure 5), and adults both feed and oviposit on *Eurhynchium oreganum* (Figure 6) (Russell 1979). *Curimopsis albonotata* (Figure 7) and *C. brevicollis* are limited to higher elevations in the Pacific Northwest; *C.*

brevicollis from northern Idaho had moss in its gut. *Lioligus nitidus* (Figure 8) and *L. striolatus* feed on a variety of mosses in the lab: *Eurhynchium oreganum*, *Hylocomium splendens* (Figure 9), *Hypnum circinale* (Figure 10), *Plagiothecium undulatum* (Figure 11), *Racomitrium heterostichum*, *Rhytidiadelphus loreus* (Figure 12), and *R. triquetrus* (Figure 13). One specimen was reared from an egg to an adult on the leafy liverworts *Diplophyllum plicatum* (Figure 14) and *Scapania bolanderi* (Figure 15). On the other hand, adults refused to eat *S. bolanderi* and other liverworts or *Metaneckera menziesii* (Figure 16).



Figure 4. *Exomella pleuralis* adult, a species that feeds on *Eurhynchium heterostichum* and oviposits there. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 5. *Racomitrium heterostichum* with capsules, home for *Exomella pleuralis*. Photo by Kristian Peters, with permission.



Figure 6. *Eurhynchium oreganum*, home, food, and site for oviposition for *Exomella pleuralis*. Photo by Matt Goff <<http://www.sitkanature.org/>>, with permission.

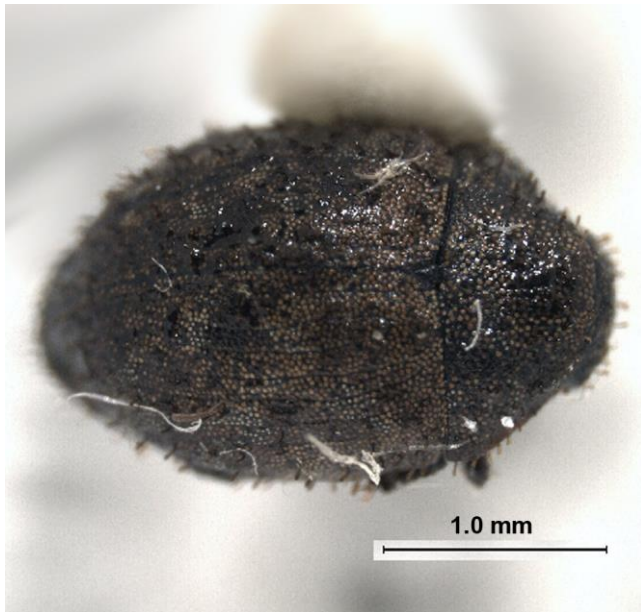


Figure 7. *Curimopsis albonotata* adult, a moss consumer at higher elevations. Photo by CNB-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 8. *Lioligus nitidus*, a species that eats a variety of mosses. Photo by Matt Goff <<http://www.sitkanature.org/>>, with permission.



Figure 9. *Hylocomium splendens*, food for *Lioligus striolatus*. Photo by Chmee2, through Creative Commons.



Figure 10. *Hypnum circinale*, food for *Lioligus striolatus*. Photo by Matt Goff <www.sitkanature.org>, with permission.



Figure 11. *Plagiothecium undulatum*, food for *Lioligus striolatus*. Photo by David T. Holyoak, with permission.



Figure 12. *Rhytidiadelphus loreus*, food for *Lioligus striolatus*. Photo by Hermann Schachner, through Creative Commons.



Figure 13. *Rhytidiadelphus triquetrus*, food for *Lioligus striolatus*. Photo by Eric Schneider, with permission.

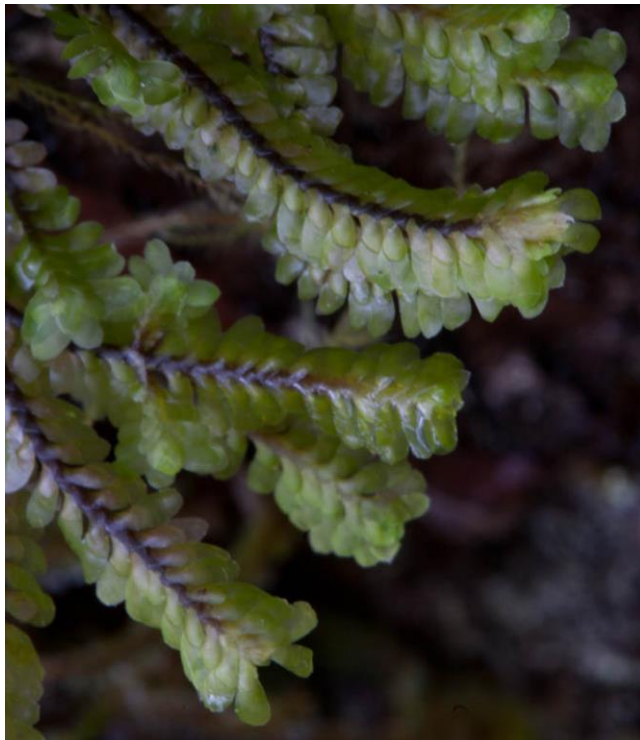


Figure 14. *Diplophyllum plicatum*, food for larvae of *Lioligus striolatus*. Photo by Martin Hutten, with permission.



Figure 15. *Scapania bolanderi*, food for larvae of *Lioligus striolatus*. Photo by Matt Goff <www.sitkanature.org>, with permission.



Figure 16. *Metaneckera menziesii*, a moss the adults of *Lioligus striolatus* refuse to eat. Photo by Dale Vitt, with permission.

Adults of *Lioon puncticeps* and *L. simplicipes* (Figure 17) live among many kinds of mosses (Russell 1979). In the laboratory, *Lioon puncticeps* adults and larvae both feed on *Dicranum fuscescens* (Figure 18), *Rhytidiadelphus loreus* (Figure 12), *Antitrichia curtipendula* (Figure 19), *Eurhynchium oreganum* (Figure 6), and *Plagiothecium undulatum* (Figure 11). On *Polytrichum commune* (Figure 20), they eat only lamellae and leaf tips while avoiding the tougher parts.



Figure 17. *Lioon simplicipes* adult, a species that lives among many kinds of moss. Photo by Joyce Gross, with permission.



Figure 18. *Dicranum fuscescens*, food for *Lioon puncticeps*. Photo by Michael Lüth, with permission.



Figure 19. *Antitrichia curtispindula*, food for *Lioon puncticeps*. Photo by Dale Vitt, with permission.



Figure 20. *Polytrichum commune*, food for *Lioon puncticeps*. Photo by Michael Lüth, with permission.

Listemus acuminatus (Figure 21) and *L. formosus* grow among mosses on soil, rocks, and logs, but not among epiphytes (Russell 1979). In the lab they feed on *Eurhynchium oreganum* (Figure 6), *Hypnum circinale* (Figure 10), and *Plagiothecium undulatum* (Figure 11). Larvae occur in mats of the leafy liverworts *Gyrothya underwoodiana* (Figure 22) and *Nardia scalaris* (Figure 23), but they may only feed on associated mosses.



Figure 21. *Listemus acuminatus*, a species that lives among mosses on soil, rocks, and logs, but does not venture up the boles of trees. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 22. *Gyrothya underwoodiana*, a home that doesn't seem to be eaten by *Listemus acuminatus*. Photo by Li Zhang, with permission.



Figure 23. *Nardia scalaris* with capsules, a home but not food for *Listemus acuminatus*. Photo by J. C. Schou <<http://www.biopix.com/>>, with permission.

Byrrhus americanus (Figure 24), *B. concolor* (Figure 25), and *B. kirbyi* (Figure 26) have been found with mosses in their guts (Russell 1979). Hradílek and Boukal (2003) reported *Polytrichaceae* cells from the gut of *Byrrhus luniger*. These were lamellae with papillae on the terminal cells (Figure 28, Figure 30), suggesting either *Pogonatum urnigerum* (Figure 27-Figure 28) or *Polytrichastrum alpinum* (Figure 29-Figure 30).



Figure 24. *Byrrhus americanus* adult, a moss feeder. Photo by Tom Murray, through Creative Commons.



Figure 25. *Byrrhus concolor*, a moss feeder. Photo by Tom Murray, through Creative Commons.



Figure 26. *Byrrhus kirbyi* adult, a moss consumer. Photo by Tim Loh, with permission.



Figure 27. *Pogonatum urnigerum*, probable food for *Byrrhus luniger*. Photo by David T. Holyoak, with permission.

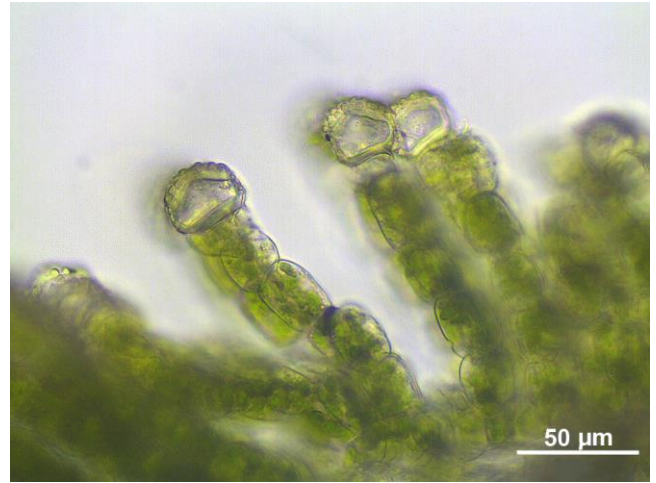


Figure 28. *Pogonatum urnigerum* lamellae showing papillae on the terminal cells like those in the gut of *Byrrhus luniger*. Photo by Kristian Peters, with permission.



Figure 29. *Polytrichastrum alpinum*, probable food for *Byrrhus luniger*. Photo by Andrew Hodgson, with permission.

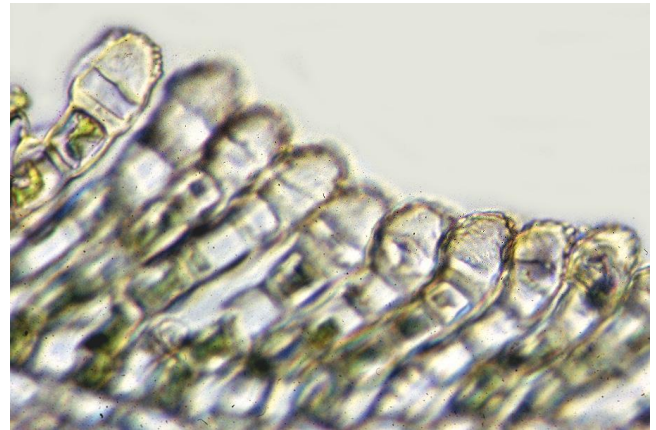


Figure 30. *Polytrichastrum alpinum* lamellae showing papillae on the terminal cells like those in the gut of *Byrrhus luniger*. Photo by Janice Glime.

It appears that all North American species of the *Artematopodidae* might be bryophagids (Russell 1979). Adults of *Macropogon* (Figure 31) and larvae of *Eurypogon* (Figure 32) in western Washington and Oregon usually occur on trees or shrubs near moss-covered rocks, but some larvae have been collected under the moss *Ceratodon purpureus* (Figure 33).



Figure 31. *Macropogon testaceipennis* adult, a North American bryophagid. Photo by Joyce Gross, with permission.



Figure 32. *Eurypogon niger* adult, a North American bryophagid. Photo by Tom Murray, through Creative Commons.



Figure 33. *Ceratodon purpureus*, habitat for larvae of *Eurypogon*. Photo by Jiří Kameníček <BioLib, Obázek>, with permission.

A beetle in the family **Lagriidae** in the Afromontane forest of South Africa feeds on both living and dead parts of the moss *Braunia secunda* (**Hedwigiaceae**; Figure 34–Figure 35), as evidenced by gut analysis (Chown 1993), but whether it is specific to this food is not known. Among the weevils (**Curculionidae**) in the sub-Antarctic Prince Edward Islands, *Antarctonesiotes elongatus*, *Bothrometopus randi*, *Ectomnorrhinus marioni*, *Mesembriorrhinus brevis*, and *Palirhoeus eatoni*

(**Brachyceridae**) all feed on cryptogams, including bryophytes (Chown & Scholtz 1989a). Similar relationships are known from Marion Island in the Antarctic (Smith 1977), where *Mesembriorrhinus brevis* and *Ectomnorrhinus marioni* prefer bryophytes over flowering plants (Chown & Scholtz 1989a). *Ectomnorrhinus similis*, a weevil (**Curculionidae**), consumed 1.67 mg per day of *Brachythecium rutabulum* (Figure 36) on an Antarctic island. On the other hand, mosses and lichens consumed by microfauna in two other Antarctic moss communities were less than 0.2 g m⁻² yr⁻¹.



Figure 34. *Braunia secunda* wet, food and home for a member of the **Lagriidae**. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 35. *Braunia secunda* dry, food and home for a member of the **Lagriidae**. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 36. *Brachythecium rutabulum*, food and home for a member of the **Lagriidae**. Photo by Michael Lüth, with permission.

Lazarenko *et al.* (1960) reported the use of mosses as food for flax flea beetles (**Chrysomelidae**). Wallin *et al.* (1999) examined the food habits of beetles inhabiting *Sphagnum* (Figure 2) mosses as a possible cause of mandibular wear. The species that exhibited the greatest mandibular wear was not the one with the highest consumption of mosses. Rather, they found that mandibular wear in the carabid beetles *Chlaenius costulatus* (Figure 37) and *C. sulcicollis* (Figure 38) appeared to be caused by their activities in biting and burrowing into *Sphagnum*-hummocks.



Figure 37. *Chlaenius costulatus* adult, an inhabitant of a protected bog in Sweden. Photo by Tim Faasen, with permission.



Figure 38. *Chlaenius sulcicollis* adult, a species that suffers mandibular wear from biting and burrowing into *Sphagnum*. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

Chown (1990) found that even in the presence of the abundant grass *Agrostis magellanica* (see Figure 39), some larvae of the weevil *Ectemnorhinus* (see Figure 40) in the sub-Antarctic feed on bryophytes, primarily the leafy liverwort *Blepharidophyllum densifolium*. The smaller of the two species found by Chown and Scholtz (1989b), *E. marioni*, lives among the mosses, feeding on them at all stages and having a generation time of one year or less. By contrast, the larger species, *E. similis*, feeds on detritus as larvae and flowering plants as adults. It has a generation time of more than one year and has more instars. The advantage to *E. marioni* of a bryophyte diet appears to be that the bryophytes are both abundant and available year-round. Furthermore, they contrast with the flowering plants in their seasonal N distribution. The seed plants have the highest concentrations in spring, whereas the mire bryophytes have the highest concentrations in autumn. It is

interesting that the bryophytes have high concentrations of polyphenolic lignin-like compounds that interfere with digestion, whereas the flowering plants lack these.

On Heard Island, Chown and Klok (2001) found that the weevil species complex of *Ectemnorhinus viridis* feed on both tracheophytes and bryophytes. Cryptogams, including both lichens and bryophytes, serve as a primary source of energy and nutrients for 5 of the 6 species of weevils on the sub-Antarctic Marion Island (Crafford & Chown 1991).



Figure 39. *Agrostis curtisii*, a relative of *Agrostis magellanica*, which is ignored as food by *Ectemnorhinus* that eats bryophytes in the same habitat of the sub-Antarctic. Photo by Malcolm Storey through <www.discoverlife.org>, through Creative Commons.



Figure 40. *Ectemnorhinus vanhoeffenianus*; several members of this genus in the sub-Antarctic feed on bryophytes, primarily on the leafy liverwort *Blepharidophyllum densifolium*. Photo by Alex Puzyr, with permission.

Carabid beetles also seem to find bryophytes, particularly in peat bogs, to be suitable habitats. Främbs (1994) found that the Swedish *Agonum ericeti* (Figure 41) and *Pterostichus rhaeticus* (Figure 42) use the damp lawns in the summer and migrate to drier hummocks for overwintering. Therefore, larger populations were restricted to areas with distinct hummock-hollow complexes (Figure 43).



Figure 41. *Agonum ericeti* in its summer habitat among moist *Sphagnum* leaves. Photo by Walter P. Pfliegler, with permission.



Figure 42. *Pterostichus rhaeticus*, a species that requires a hummock-hollow complex in Swedish bogs. Photo by Niels Sloth <www.biopix.com/>, with permission.



Figure 43. Bohemian bog with *Sphagnum cuspidatum*, *S. denticulatum*, and other species creating a hummock-hollow complex. Photo by Jonathan Sleath, with permission.

Beetles in geothermal areas seek refuge from the heat of the soil by inhabiting the cooler bryophytes (Elmarsdottir *et al.* 2003). In turn, bears may eat the beetles, as suggested by their piles of feces (Figure 44) in the area (personal observation).



Figure 44. Bear dung at Ponponyama, Japan. Many beetles are present in this dung. The moss in the foreground is *Campylopus japonicus*. Photo by Janice Glime.

Epichorius longulus and *E. aucklandiae* (Byrrhidae) live in the coastal rata (*Metrosideros*) forest (Figure 45) of Auckland Island, New Zealand (Farrell 1974). *Epichorius longulus* lives in the ground layer, whereas *E. aucklandiae* lives in the canopy. The former species was abundant in the liverwort *Riccardia* spp., but rarely occurred among *Bazzania adnexa* (Figure 46). When larvae were reared on the *Riccardia* (Figure 47), they gained more weight than on *Bazzania adnexa*. The adults of *E. longulus* sought shelter under the leaf litter in the daytime but moved about to feed on bryophytes at night.



Figure 45. Coastal rata forest where *Epichorius* lives among liverworts. Photo by James Russell <islandconservation.auckland.ac.nz>, with permission.



Figure 46. *Bazzania adnexa*, rarely a home for *Epichorius aucklandiae* in the rata canopy in New Zealand. Photo by Andy Hodgson, with permission.

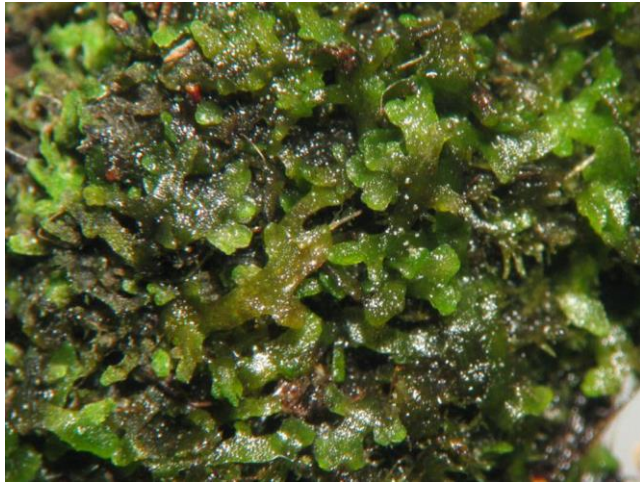


Figure 47. *Riccardia chamedryfolia*, a genus that is home and food for *Epichorius aucklandiae* in the New Zealand. Photo by Kristian Peters, with permission.

Some bryophytes apparently are eaten unintentionally by animals searching for food, including the beetle fauna. The carnivorous salamander *Phaeognathus hubrichti* (Red Hills Salamander; Figure 48) typically has a diet that is nearly 70% arthropods, including beetles (Gunzburger 1999). But also in the gut and feces one can find moss fragments, most likely consumed as the salamanders forage for arthropods among the mosses.



Figure 48. *Phaeognathus hubrichti*, a salamander that eats insects among mosses. Photo by Danté B. Fenolio, with permission.

Sampling

Most researchers have used the same sampling methods for bryophytes as they use for leaf litter. But bryophytes provide small spaces, and some insects never leave those small spaces. This behavior impacts the suitability of trapping methods.

Nelson and Hauser (2012) used both Berlese funnels and water sampling for bryophyte fauna, accounting for many small invertebrates that are usually not found in these associations. Nevertheless, small insects, including tiny beetles, might not have crawled out of the moist moss and into the funnels. The bias of sampling methods is demonstrated by the near absence of overlap between the two sampling methods.

Beetles (Coleoptera) are so common among the *Sphagnum* plants (Figure 2) (Brink 1983; Runtz & Peck

1994) that sifting through squeezed mosses can be the best method of collecting (Leiler 1983). Boháč and Bezděk (2004) once again emphasized the role of sampling method in determining the bryophyte fauna. This may be especially true for beetles, where a number of species are wingless and do little moving around. In the Mrtvy Luh peat bog they found that of 38 species in their traps, only 3 were found in both pitfall and light traps.

Boháč and Bezděk (2004) found that the light traps in the Czech Republic peat bog had more species, but many were accidental species that were not typical bog inhabitants. Among these the dominant species were species that are good fliers. Based on these findings, Boháč and Bezděk (2004) recommended that sifting and **trampling** (pressing the moss down to create a pool of water and causing the beetles to float) be included in the sampling strategies. But be aware that sifting and hand grabs are destructive and should be avoided in fragile systems or where repeated sampling is planned.

Leiler (1983) was particularly successful in finding beetle fauna by sifting squeezed wet *Sphagnum*. Wallin *et al.* (1999) used pitfall traps that were connected with a gutter and embedded into large *Sphagnum* hummocks. Lindroth (1974) considered the ordinary insect sieve to be indispensable for sampling in leaf litter and "not too wet" moss, especially for hibernating insects. He suggested that litter samples could also be put under water to force the insects to the surface. For pitfall traps, he suggested adding a few drops of detergent to the formalin to break the surface tension.

Based on the differences seen among these methods, I once again recommend hand picking using a dissecting microscope if an unbiased, quantitative sampling is desired. Some insects move too slowly to get away from a heat source before they die. Some may burrow deep into the mat without vacating it. In any case, not all insects will enter traps equally.

Habitat Relations

The bryophytes are different in different habitats, and so are the beetles. But the correlations are likely to be secondary, with both of them correlating with moisture and bryophytes also with light and suitable substrate availability.

Forests

Pavel *et al.* (2007) found the **Coleoptera** to be the most abundant of the insect taxa in a forest study in the Czech Republic. Pitfall traps were used in three sites to compare those in *Polytrichum* cushions (Figure 49) with those at least 10 m away with no moss. Of the 56 species found, ~25% were found only among the mosses. These, combined with those also found in other parts of the forest floor, demonstrated a higher species richness among the mosses. Nevertheless, only one of these species (*Symplocaria* sp., **Byrrhidae**) was a **bryophage** (one that eats bryophytes). Monte-Carlo permutation tests suggest that the beetles are correlated with moisture and the mosses just happen to provide the right moisture conditions. Those beetle species in dry habitats tend to be restricted to moss cushions, making them strict **bryobionts** (living only on bryophytes).



Figure 49. *Polytrichum* cushions that form habitat islands for *Cytillus sericeus* and other beetles, providing moisture in exposed areas. Photo by James K. Lindsey, with permission.

Nelson and Hauser (2012) surveyed the epiphytic bryophyte communities at the Tryon Creek State Natural Area in Oregon, USA. Among the five phyla represented, insects were among the top five taxonomic sub-groups (except for the recently ousted *Collembola*). In addition to the five more dominant insect taxa, **Diptera** and **Coleoptera** were present. Hence, beetles were not represented in proportion to their prominence among species numbers on Earth.

Hitch-hikers

Peck and Moldenke (1999) were concerned about the export of potential pest insects in commercial harvests of bryophytes in Oregon, USA. They likewise used the Berlese funnel extraction for arthropods on 200 samples of harvestable mosses. They compared the invertebrate populations at the bases and tips of shrubs of the vine maple (*Acer circinatum*; Figure 50). The base mosses had substantially higher species richness and total abundance overall. For **Coleoptera**, the bases had greater numbers of individuals than did the tips of the shrubs. Mites were the most common arthropods at the base, whereas spiders (*Micryphantidae*) and *Sminthurus* (*Collembola*) were the predominant taxa in mosses at the tips.



Figure 50. *Acer circinatum*, home for **Coleoptera** in mosses at base and on branches. Photo by Ken Gilliland, through Creative Commons.

Forest Disturbance and Recovery

The carabid beetle *Agonum fuliginosum* (Figure 51) in Europe seems to have a generalist approach to canopy closure, but it does depend on the presence of *Sphagnum* (Figure 2) mires in the forest (Koivula 2002a, b; Koivula & Niemela 2002; Koivula *et al.* 2002). Even small islands of *Sphagnum* within a clear-cut forest will permit it to remain, presumably providing needed moisture. *Patrobis assimilis* (*Carabidae*; Figure 52) likewise requires the presence of *Sphagnum* to survive in forests (Koivula 2002b). On the other hand, *Agonum mannerheimii*, despite being a mire specialist, is unable to survive in remaining mires if the forest is clearcut (Niemelä *et al.* 1993a, b). It can take 50-60 years for a spruce mire (Figure 53) to recover its forest cover after clearcutting, but it takes longer if there is serious disturbance of the ground layer (Koivula *et al.* 2002).



Figure 51. *Agonum fuliginosum*, a species that seems to depend on *Sphagnum* for moisture in exposed or disturbed forest sites. Photo by Trevor and Dilys Pendleton <www.eakingbirds.com>, with permission.



Figure 52. *Patrobis assimilis*, a species that requires mosses to survive in forests. Photo by Roy Anderson ©Roy Anderson <www.habitas.org.uk>, with permission.



Figure 53. *Picea mariana* forest in Northern Alberta, Canada, with *Pleurozium schreberi* and *Hylocomium splendens*. Photo by Richard Caners, with permission.

Species of beetles in old-growth forests (Figure 54) are especially affected by logging (Figure 55) (Niemelä 1997). Microhabitats such as coarse woody debris, large deciduous trees, and patches of wet swamp forest and mires may disappear or be greatly reduced. These disturbances tend to cause the old-growth specialists to disappear, including those of beetles. Instead, species richness may increase as generalists remain and numerous open-habitat species invade. This trend is especially true for the ground beetles, which include moss dwellers.



Figure 54. Old Growth in Cathedral Grove, British Columbia, Canada, showing moss-covered logs (dead wood) and low-light plants. Photo by Sang Trinh, through Creative Commons.



Figure 55. Clearcut forest patches at Lewis and Clark River, Oregon, USA. Photo by Walter Siegmund, through Creative Commons.

Niemelä *et al.* (1993b) concluded that retaining habitat diversification on a regional scale was the best management strategy for retaining diversity of ground-dwelling arthropods, including beetles. Hence, retaining moss corridors for those species like the flightless *Agonum mannerheimii* may be necessary to permit these species to disperse and to retain the original species richness in the stand (Hoyle & Gilbert 2004). On the other hand, Jonsson and Jonsell (1999) showed that the occurrences of bryophytes are not good predictors for the species richness of beetles. Djupström *et al.* (2010) found only a weak positive correlation between beetles and bryophytes in Swedish boreal forests, and none between beetles and lichens. Like Jonsson and Jonsell, they found that the tested taxa did not provide reliable surrogates. On the other hand, dead wood diversity (Figure 54) represented both **saproxylic** (those that eat dead wood) beetles and bryophytes better than did random samples.

Effects of Beetles on Forest Bryophytes

Clear cutting (Figure 55) removes shade, changes the temperature, and eliminates many kinds of microhabitats. But bark beetles can also have an impact on the forest, removing cover and permitting the sun to raise the temperature. Nevertheless, a bark beetle outbreak in the Central European mountain spruce forests did not have the devastating effect on bryophytes that was experienced under clear cutting (Jonášová & Prach 2008). The latter causes a loss of forest floor bryophytes and the invasion of open habitat pioneers. The beetle outbreak left standing dead (Figure 56) that permitted the bryophytes to remain. Instead of promoting pioneer invasions, the beetle attack left the forest in a state that was more likely to avoid the pioneer stage and to promote a direct forest recovery, including the bryophytes.



Figure 56. Spruce bark beetle damage to the spruce forest in Rio Grande National Forest, USA. Standing dead spruce trees still provide shade, permitting bryophytes to survive. Photo from US Forest Service, through Public Domain.

Dunes

Following habitat restoration of dry dunes (Figure 57) on the Belgian coast, several dune-living ground beetles increased in population size (Maelfait *et al.* 2007). The researchers concluded that the rapid development of the ground vegetation, including both bare sand and moss patches, contributed to the rapid improvement of the insect fauna.



Figure 57. Sand dune in Belgium, where the invasive *Campylopus introflexus* is becoming a problem. Photo through Creative Commons.

Heathland

Beetles seem to prefer some mosses and to avoid others. In the *Empetrum* heathlands (Figure 58), beetles avoid the moss *Pleurozium schreberi* (Figure 59), but in the *Calluna* heath (Figure 60), with different bryophytes, the beetles were much more common (Barkman 1979, p. 138, in van Tooren 1990).



Figure 58. Dune heath with *Calluna* and *Empetrum*. In *Empetrum* heaths, beetles avoid the *Pleurozium schreberi*. In the *Calluna* heaths, beetles live among the different moss species there. Photo by Pat Doody, National Coastal Consultants, UK, with permission.



Figure 59. *Pleurozium schreberi*, a moss that is avoided by beetles in *Empetrum* heathlands. Photo by J. C. Schou <www.biopix.com/>, with permission.



Figure 60. Heath with *Calluna vulgaris* (pink flowers) and *Ulex europaea* (yellow flowers), where bryophytes seem to be an important part of the habitat for beetles. Photo by Magnus Manske, through Creative Commons.

In a wet heathland in Scotland, the heather beetle *Lochmaea suturalis* (Chrysomelidae; Figure 61) is a herbivore on *Calluna* (Figure 62) (Scandrett & Gimingham 1991). The result of this herbivory is that cover decreases and the mosses *Sphagnum plumulosum* (Figure 63) and *Hypnum jutlandicum* (Figure 64) increase. The increases in these mosses is concurrent with the decline of *Sphagnum compactum* (Figure 65) and *Pleurozium schreberi* (Figure 59), thus improving the habitat for bryophyte-dwelling beetles. The *Calluna* regenerates mostly by layering, with only limited restoration through seedlings that germinate in the moist *Sphagnum*.



Figure 61. *Lochmaea suturalis* adult, a herbivore on *Calluna*, causing an increase in *Sphagnum plumulosum* (Figure 63) and *Hypnum jutlandicum* (Figure 64) as light increases. Photo by James K. Lindsey, with permission.



Figure 62. *Calluna vulgaris* – food source for *Lochmaea suturalis*. Photo by Janice Glime.



Figure 63. *Sphagnum plumulosum* (= *S. subnitens*), a species that increases when cover decreases. Photo by J. C. Schou <www.biopix.com/>, with permission.



Figure 64. *Hypnum jutlandicum*, a species of mosses that increases in dunes following herbivory by *Lochmaea suturalis*. Photo by Andrew Spink, with permission.



Figure 65. *Sphagnum compactum*, a species that declines when *Sphagnum plumulosum* and *Hypnum jutlandicum* increase following loss of cover due to herbivory by *Lochmaea suturalis*. Photo by Andrew Hodgson, with permission.

In the *Racomitrium lanuginosum* heaths (Figure 66), the Dotterel *Charadrius morinellus* (Figure 67) adults eat a large number of beetles (Galbraith *et al.* 1993). Both chicks and adults prefer habitats where both montane bogs and *Racomitrium lanuginosum* heaths are available to

meet the feeding requirements of both adults and chicks. Overgrazing by sheep has endangered these suitable habitats.



Figure 66. *Racomitrium lanuginosum* hummocks in the UK. Photo by Alan Silverside, with permission.



Figure 67. *Charadrius morinellus* male, a forager for beetles in *Racomitrium lanuginosum*. Photo by Helwig Brunner, through Creative Commons.

Bogs and Wetlands

Boháč and Bezděk (2004) found that in the Mrtvy Luh, Czech Republic, peat bog the species of **Staphylinidae** differed significantly between the bog margin and the center. Only 1 **tyrphophilous** (bog affiliate) species occurred in the marginal peat, whereas there were no **tyrphobionts** (species living only in bogs) or **tyrphophiles** (bog affiliates, breeding in bogs and elsewhere) in the center. Rather, the center of the bog was home to *Drusilla canaliculata* (Figure 68), a staphylinid that eats ants.



Figure 68. *Drusilla canaliculata* adult male, a bog dweller that eats ants. Photo by Christoph Benisch <www.kerbtier.de>, with permission.

Likewise, Bordoni (1972) found 179 species of Coleoptera, representing 25 families) in a Tuscan fen. Many were generalists and few were bryophilous. On the other hand, the Staphylinidae were the best represented and are moss feeders (Mani 1962). And *Cretinis punctatostrata* (Hydrophilidae) spends its entire life cycle in *Sphagnum*, making it a true **bryobiont** (Matthey 1977). Its eggs are deposited in the *Sphagnum* and its pupation cell is constructed from bryophytes. On the other hand, many of the **bryophilous** mosses do not feed on the mosses, but rather feed on the epiphytic algae (LeSage & Harper 1976).

Using yellow pan traps and emergence traps, Runtz and Peck (1994) found 5734 beetles, representing 30 families, in a mature spruce-*Sphagnum* bog (fen?) (Figure 69) in Algonquin Park, Ontario, Canada. Among these, members of the **Ptiliidae** were the most abundant and **Staphylinidae** was the most taxonomically diverse family. The **Carabidae** were also important, ranking second in diversity and third in abundance. But, as in many other studies, there are few beetle species specific to the bog. Most of the species in the bog are from adjacent habitats.



Figure 69. Boreal forest fen with spruce (*Picea mariana*) and *Sphagnum fuscum*, home for many **Ptiliidae** and **Staphylinidae**. Photo by Richard Caners, with permission.

Kvamme (1976) found similar relationships to these in mires at Eidskog, Norway. He trapped (pitfall) 18 species of **Carabidae** and 4 of **Curculionidae** in thirteen mire habitats there. Only *Agonum ericeti* (Figure 41) seemed to

be a true **tyrphobiont** (restricted to bog and mire habitats). Six species of **Carabidae** were **tyrphophiles** (typical in bogs and mires but not restricted to them). The greatest number of species occurred in the transition zone between the mire and the forest.

On the other hand, bogs are habitats where rare species occur. Wallin *et al.* (1999) found the rare carabid *Chlaenius costulatus* (Figure 37) in a protected bog in central Sweden. Wallin *et al.* (2000) likewise found the rare *Chlaenius sulcicollis* (Figure 38). *Chlaenius costulatus* overwinters in the bog; larvae (Figure 70) and newly emerged adult beetles appeared in pitfall traps, suggesting that they have surface activity during all developmental stages.



Figure 70. *Chlaenius* sp. larva, a rare bog dweller. Photo by Tom Murray, through Creative Commons.

Carabid beetles have specific requirements within the bog that determine their distribution. The development of that fauna is closely related to the presence of a mosaic of hummocks and hollows (Främbis 1994). On the Swedish Ryggmossen *Agonum ericeti* (Figure 41) and *Pterostichus rhaeticus* (Figure 42) use damp *Sphagnum* lawns (Figure 2) for summer activities but migrate to drier hummocks for overwintering, accounting for the need for the mosaic. The rare carabid *Chlaenius sulcicollis* (Figure 38) was discovered in Sweden in a bog dominated by large *Sphagnum* hummocks (Wallin *et al.* 1999, 2000). Severe mandible wear in this beetle could be caused by intensive biting and burrowing needed to navigate the *Sphagnum* hummocks.

Hydroporus morio (Figure 71) has a similar topography requirement (Jackson 1956). This member of the **Dytiscidae** lives in bog pools, but when the pools dry out in summer it bores small, round holes in the deep *Sphagnum*. There it **aestivates** (spends hot or dry period in prolonged state of torpor or dormancy) until the rain returns.



Figure 71. *Hydroporus morio* adult, a species that bores into *Sphagnum* when the bog pools dry out. Photo by Niels Sloth <www.biopix.dk>, with permission.

The genus *Sphaerius*, a member of the family **Sphaeriidae**, has members that live among mosses in bogs (Wikipedia 2015). The bog dwellers are able to store air under the **elytra** (hardened outer wings). *Sphaerius acaroides* is a minute scavenger beetle that occurs in moss and plant litter at the edge of slumping cliff seepages (Boyce 2002). Other scattered records exist from sites throughout England, including other wetland habitats such as fens.

It appears that some carrion beetles may be specific to peatlands (Beninger & Peck 1992). *Nicrophorus* carrion beetles (Coleoptera: Silphidae; Figure 72-Figure 73) utilize small mammal carcasses; some are able to spend their entire lives in the bog, using the bog carrion for reproduction, whereas others migrate to the nearby forest to reproduce (Beninger & Peck 1992). In the genus *Nicrophorus* (Coleoptera: **Silphidae**), the proportion of dead mice (*Mus musculus* – house mouse; Figure 74) utilized in the peatland as a resource did not differ from that of the nearby forest. *Nicrophorus* buries its carrion under mosses and leaf litter (Eggert & Müller 1997). However, *N. vespilloides* (Figure 72) reproduced exclusively in the *Sphagnum*, whereas *N. defodiens* (Figure 73) reproduced exclusively in the nearby mixed forest. Furthermore, three other species in the genus rarely occurred on bog carrion but were common on forest carrion. In other cases, it is the larvae of the beetles that live among the mosses (LeSage 1983).



Figure 72. *Nicrophorus vespilloides* adult, a species that reproduces in *Sphagnum*. Photo by Holger Gröschl, through Creative Commons.



Figure 73. *Nicrophorus defodiens* adult, a species that leaves the *Sphagnum* to reproduce in the forest. Photo by John and Jane Balaban, through Creative Commons.



Figure 74. *Mus musculus*, a mouse that provides small carrion for reproduction of some species of *Nicrophorus*. Photo by Ozwildlife, through Creative Commons.

Parthenogenesis (reproduction from an egg without fertilization) is common in bogs, and *Ptiliopycna moerens* is one such species in the beetle family **Ptiliidae** (Dybas 1978). These featherwing beetles live mostly in *Sphagnum* bogs and similar habitats in swamp forests in eastern North America. In addition, *Acrotrichis* (Figure 75), *Bythinopsis tychoides*, and *Ptinella mekura* are all small beetles in these bogs and all are parthenogenetic there.



Figure 75. *Acrotrichis discolorides* adult, member of a genus of small, parthenogenetic beetles of *Sphagnum* bogs. Photo through Creative Commons.

Antarctica and Antarctic Islands

Beetles are one of the groups of organisms that are able to survive in the harsh conditions of the Antarctic (Figure 76). On this icy continent, the **Curculionidae** exhibit two feeding groups – those that feed on flowering plants and those that feed on cryptogams (algae, lichens, and bryophytes). These feeding constraints result in habitat constraints. For example, on Heard Island, *Ectemnorhinus viridis* lives from sea level to 600 m, where it feeds on tracheophytes and bryophytes (Chown & Klok 2001). *Candonopsis sericeus* likewise feeds on these two plant groups, but in a narrower altitudinal range. Further details of Antarctic feeding habits in this family are discussed in the sub-chapter on Coleoptera Families.



Figure 76. Mosses in Antarctica, a safe refuge for beetles. Photo by Sharon Robinson, through Creative Commons.

Home for Rare Species

Bryophytes can often hold surprises, species that have been considered rare or were previously unknown. Such was the case when a group of British entomologists were forced to abandon collecting due to very cold, wet weather on the Isle of Wight (Appleton 1986). In a last furtive effort to make the trip worthwhile, the entomologists grabbed handfuls of moss to sample at home. As they sieved through them, they found three individuals of *Baris analis* (Curculionidae; Figure 77), unknown for a century, from mosses that had grown on low cliffs. Shepard and Barr (1991) were able to describe the larva of *Atractelmis* (Elmidae; Figure 78) from a bryophyte habitat. In Sweden, several red-listed *Chlaenius* (Carabidae; Figure 38) species inhabited the mosses (Wallin *et al.* 2000).



Figure 77. *Baris analis* adults mating, a rare species known from mosses. Photo by Roger Key, with permission.

Some moss beetles have been even more elusive. Duckett *et al.* (2006) described *Ivalia korakundah* (Chrysomelidae) as a new species from the Doddabetta Valley, India, where it inhabits mosses. On rocks, adults of this species occur among the branches of the moss *Isopterygium* sp. (Figure 79). Both adults and larvae were found by sifting mosses from large pine tree trunks.



Figure 78. *Atractelmis* larva, a bryophyte inhabitant. Photo by Joseph Fortier, through Creative Commons



Figure 79. *Isopterygium elegans*, home for *Ivalia korakundah* on rocks. Photo by Kristian Peters, with permission.

In addition to rare species, new species are likely to be lurking among the mosses, and until more collecting is done in these habitats, these will seem rare. For example, Konstantinov and Duckett (2005) found a new member of Chrysomelidae – *Clavicornaltica dali* (Figure 80) – in Asia. Its type locality is in Yunnan, China, where it was found under a moss. This is a tiny, rounded beetle (1.13–1.24 mm) and the only known species of *Clavicornaltica* that has wingless males – a possible adaptation for moss-dwelling that can reserve more space and energy for developing the gut or other structure. In the same collection in China they found a new species of *Benedictus* together with *Clavicornaltica dali* (Konstantinov & Lourdes Chamorro-Lacayo 2006). No moss-inhabiting weevils were known from the New World until 2006 when these same researchers found the new genus *Kiskeya* (Chrysomelidae; Figure 81) and named two new species in the Dominican Republic.

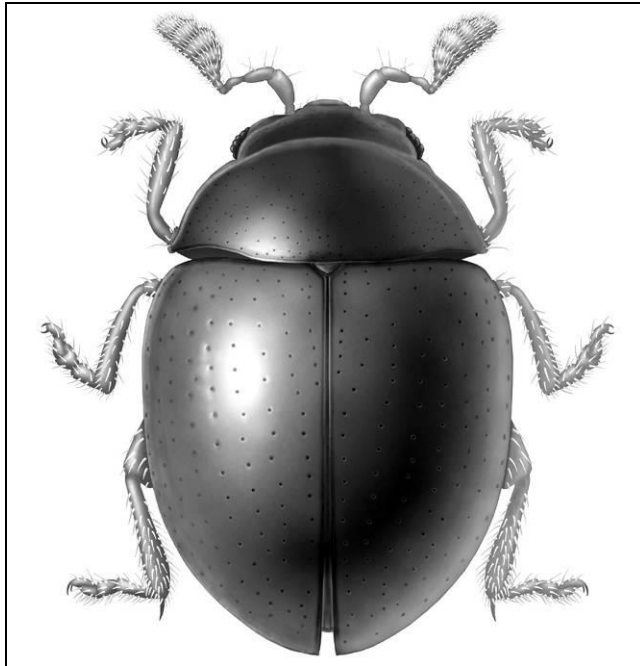


Figure 80. *Clavicornaltica dali*, a moss-inhabiting flea beetle. Photo by Alexander Konstantinov; permission pending.



Figure 81. *Kiskeya baorucae*, a moss-inhabiting flea beetle. Photo by Alexander Konstantinov; permission pending.

Invasive Bryophytes

We know that *Curimopsis* (Byrrhidae; Figure 7) eats the invasive moss *Campylopus introflexus* (Figure 82) (Brian Eversham, pers. comm.). On the other hand, Schirmel *et al.* (2011) found that the invasion of *Campylopus introflexus* into acidic coastal dunes (grey dunes; Figure 83) at the southern Baltic Sea shore coincided with a reduction among plant-eating beetles in **Carabidae** compared to those in native dune habitat. They considered this reduction to be the result of reduced food supply of arthropod food items in areas with dense carpets of this invasive moss. This is concerning because the dunes are home to many endangered species of arthropods.

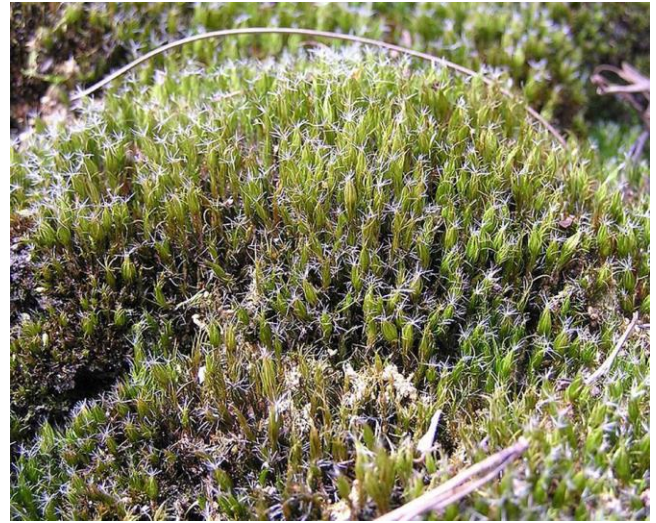


Figure 82. *Campylopus introflexus*, an invasive moss in Europe that is food for *Curimopsis*. Photo by Michael Becker, through Creative Commons.



Figure 83. *Campylopus introflexus* invading sand dunes. Photo from BIOSOS, permission pending.

Campylopus introflexus (Figure 82) forms dense carpets in these acidic coastal dunes, replacing native vegetation. Using pitfall traps, Schirmel and Buchholz (2013) compared trait composition of beetles and spiders. They found that this invasive moss caused body size and feeding preference of the **Carabidae** to shift. The species examined were smaller in the native habitats, perhaps because percentages of web-building spiders decreased in the sites of moss invasion. But the plant-eating beetles were reduced as well. Hence, the functional diversity of the **Carabidae** was likewise reduced. The functional diversity of spiders increased in the invaded dunes, but that of the carabid beetles decreased.

On South Georgia Island, introduced reindeer reduced the native grass vegetation of *Poa flabellata* (Christie 2010). This grass, home of *Hydromedion sparsatum* (Perimylopidae; Figure 84-Figure 87), was replaced by short grass *Poa annua*, moss carpets, bare soil, and other unsuitable substrata for *Hydromedion sparsatum*. As a result, this abundant beetle was reduced from more than 33% of the invertebrate fauna to 7-9%.



Figure 84. *Hydromedion sparsatum* larva, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.



Figure 87. *Hydromedion sparsatum* adult, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.



Figure 85. *Hydromedion sparsatum* pupa, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.



Figure 86. *Hydromedion sparsatum* adult, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.

Summary

Beetles comprise the largest order of insects and live in almost every imaginable habitat. Their membranous wings are protected by the outer hardened **elytra**, but many of the bryophyte dwellers are flightless. The greatest numbers among bryophytes are **Curculionidae** and **Staphylinidae**, both very large families, but some, like the **Byrrhidae**, are moss specialists, living mostly in bryophytes and eating them.

The moss-dwelling beetles are typically tiny and rounded. Some are able to play dead (**Byrrhidae**) and can retract their legs into grooves on the lower surface. This family, and others, lay their eggs among the mosses. Some live in water as larvae and adults, but come to land to pupate among the mosses. Some migrate up and down in *Sphagnum* hummocks to adjust to changing moisture conditions or to overwinter.

Many beetles not only live among mosses, but also eat them. A wide range of mosses seem to be suitable for food, but some are refused. Few beetles, however, seem to eat liverworts. In geothermal areas, the mosses provide a moist and warm refuge in these polar climates.

In forests, bryophytes provide a more moist refuge following a disturbance that opens the canopy. In other cases, the beetles may attack the forest canopy, exposing the bryophytes and causing species changes. Many forest species are likely to be transported around the world as hitch-hikers among horticultural mosses.

In dunes, the invasion of the moss *Campylopus introflexus* is changing the kinds of species of beetles occurring there, reducing the beetle functional diversity. Different kinds of heathlands differ in kinds of bryophytes and their beetle fauna.

Bogs are often home to rare beetle species, and some are tiny, wingless, and parthenogenetic, hence poorly dispersed. Here, and elsewhere, sampling bias can miss these tiny, immobile beetles. Hand sorting is the only reliable, albeit time-consuming, method for finding all the species.

On one hand, bryophytes often harbor rare or unknown species. On the other hand, invasive bryophytes can cause reductions in the number of beetle species or their abundance due to replacing food plants.

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CHAPTER 12-9b

TERRESTRIAL INSECTS:

HOLOMETABOLA – COLEOPTERA

FAMILIES

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CHAPTER 12-9b

TERRESTRIAL INSECTS:

HOLOMETABOLA – COLEOPTERA

FAMILIES



Figure 1. *Elaphrus* sp. on moss, a genus known to live on and among bryophytes. Photo by Bob Armstrong, with permission.

The **Coleoptera** are divided into the **Adephaga** and **Polyphaga**. This chapter has used this division and within the larger group **Polyphaga**, superfamily groupings are used. However, the order if these superfamilies and the families within them is alphabetical.

ADEPHAGA

Whereas five families of **Adephaga** are among the aquatic bryophyte-dwelling beetles, I know of only one family (**Carabidae**) with bryophyte dwellers among the terrestrial beetles. Nevertheless, there are a number of species among the terrestrial members of this family that live among bryophytes.

Carabidae – Ground Beetles

The **Carabidae** have many genera and species represented among bryophytes and were among the early reported bryophyte dwellers. For example, Westwood (1839) reported *Carabus coriaceus* (Figure 2) larvae living under mosses. Several species of *Carabus* have been

photographed on mosses, perhaps only traversing them or getting a bit of remoistening (Figure 3-Figure 5).



Figure 2. *Carabus coriaceus* adult, a species that seeks refuge among mosses. Photo by Rotatebot, through Creative Commons.



Figure 3. *Carabus cancellatus* adult on moss. Photo by Ladislav Tábi, with permission.



Figure 4. *Carabus glabratus* adult on moss. Photo by Ladislav Tábi, with permission.



Figure 5. *Carabus nemoralis* adult on moss. Photo by Ladislav Tábi, with permission.

Waterhouse (1871) reported *Bradycellus collaris* (Figure 6) from mosses. Later, Lindroth (1974) reported that *Bradycellus sharpi* (Figure 7) lives under leaves and mosses in shady places, usually near water. Luff (1998) noted that *Bradycellus csikii* (Figure 8) occurs on mosses and other substrata in Central Europe.



Figure 6. *Bradycellus collaris* adult on *Sphagnum*. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 7. *Bradycellus sharpi* adult with moss where it dwells near water. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 8. *Bradycellus csikii* adult, a moss dweller in Central Europe. Photo through Creative Commons.

In Japan, Bates (1883) reported *Leistus subaeneus* living under forest mosses at high elevations and *Leistus obtusicollis* occurs in mosses on the trunks of *Cryptomeria*. In Europe, *Leistus rufomarginatus* (Figure 9) and *L. ferrugineus* (Figure 10) occur among mosses (Lindroth 1974).



Figure 9. *Leistus rufomarginatus*, a moss dweller in Europe. Photo by Niels Sloth <www.biopix.com>, with permission.



Figure 10. *Leistus ferrugineus*, a moss dweller in Europe. Photo by František Šaržik, through Public Domain.

This family has 40,000 species worldwide and are among the 10 largest families of animals worldwide (Wikipedia 2015a). Common habitats are under the bark of trees, under logs, or among rocks or sand by the edge of ponds and rivers. Most species are active nocturnal carnivores. Some are able to run swiftly to catch prey, up to 9 km h⁻¹ (Friedlander 1998). They are larger than most moss-dwelling beetles and most don't seem to have any camouflage adaptations. Rather, these most likely visit the mosses to find food organisms and to replenish moisture.

Many members of the family overwinter under mosses (Anonymous 1879). This habit of overwintering under mosses serves for *Elaphrus fuliginosus* (Figure 11) and *E. clairvillei* (Figure 12) in low woodlands (Kilman 1889).



Figure 11. *Elaphrus fuliginosus*, a species that overwinters under mosses. Photo by Yves Bousquet, through Creative Commons.



Figure 12. *Elaphrus clairvillei* adult, a species that hibernates under mosses in winter. Photo by Gimenez de Cordoba, Beatriz through Creative Commons.

Unlike the many tiny beetles with limited distribution, many of these species are widespread. *Pterostichus diligens* (5-7 mm; Figure 13) is numerous among mosses, widespread (Eurasian Boreo-temperate), and common in wet heath, mire, and grass tussocks (Stenhouse 2007). *Pterostichus strenuus* (Figure 14) stays in shady places, especially damp deciduous forests on clayish soil, where it lives among mosses and leaf litter (Lindroth 1974). *Ocys harpaloides* (4-6 mm; Figure 15) is widespread among mosses in the UK (Stenhouse 2007) and along the European and African Atlantic coast (Anderson *et al.* 2000).



Figure 13. *Pterostichus diligens* adult, a species that is numerous among mosses in mires in the UK. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 14. *Pterostichus strenuus* adult, a species of shady places, especially damp deciduous forests on clayish soil, where it lives among mosses and leaf litter. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 15. *Ocys harpaloides* adult on moss, a widespread moss-dweller in the UK. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

One of the more comprehensive treatments of the **Carabidae** is that of Lindroth (1974). He cited many species that live among mosses in the British Isles. These include *Notiophilus germinyi* (Figure 16) among mosses in the open; *Blethisa multipunctata* (Figure 17) with mosses and *Carex*; *Elaphrus lapponicus* (Figure 18) on wet mosses near wells and streams and in bogs; *Asaphidion pallipes* (Figure 19) on fine, slightly moist sand with patches of "tiny moss;" *Miscodera arctica* (Figure 20) on fine, dry sand with fine mosses; *Platyderus depressus* (Figure 21) in open country among leaves and mosses; *Amara communis* (Figure 22) under mosses and dry leaves in a wide range of open habitats and forests with light shade; *Amara lunicollis* (Figure 23) in similar shade situations on peaty soil and under moss carpets of rocks; *Harpalus pimalicus* (see Figure 24) among mosses and leaves under bushes and trees on gravel moraines; *Badister unipustulatus* (Figure 25) among leaves and mosses on moist, shaded places, typically near pools; and *Syntomus obscuroguttatus* (Figure 26) in moist habitats on heavy soil among mosses.



Figure 16. *Notiophilus germinyi* adult on *Sphagnum*. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 17. *Blethisa multipunctata* adult, a moss inhabitant. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 18. *Elaphrus lapponicus*, a species of bogs and wet mosses. Photo by Gimenez de Cordoba, Beatriz through Creative Commons.



Figure 19. *Asaphidion pallipes* adult on mosses; this species occurs on sand with patches of tiny mosses, as shown here. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 22. *Amara communis* adult, a species that lives under mosses and dry leaves. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 20. *Miscoderes arctica* adult on leafy liverwort. This species lives on fine, dry sand with fine mosses. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 23. *Amara lunicollis* adult, a species of peaty soil or under moss carpets of rocks. Photo by Tom Murray, through Creative Commons.



Figure 21. *Platyderus depressus*, a litter and moss inhabitant. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 24. *Harpalus rufipes* adult. *Harpalus pimalicus* lives among mosses and leaves under bushes and trees on gravel moraines. Photo by Rasbak, through Creative Commons.



Figure 25. *Badister unipustulatus* adult, a species that lives among leaves and mosses near pools. Photo by Gábor Keresztes (xespok.net), with permission.



Figure 26. *Syntomus obscuroguttatus* adult, a species that lives among mosses in moist habitats. Photo by Brian Eversham, with permission.

Such widespread species as *Notiophilus biguttatus* (Figure 27) will traverse mosses in some of their habitats as they travel across the terrain. They may find cover there from the sun, search for food, gain moisture, or even take a drink, but they do not necessarily live there.



Figure 27. *Notiophilus biguttatus* adult on moss. Photo by Ladislav Tábi, with permission.

Trechus rivularis (Figure 28) occurs among mosses in lowland fens and upland mires of northern and eastern Europe (Luff 1998). *Patrobus septentrionis* (Figure 29) lives near water as well, living among mosses in the UK, but at lower elevations in other parts of its circumpolar distribution. Its widespread distribution is most likely facilitated by its ability to fly.



Figure 28. *Trechus rivularis* adult, an inhabitant of lowland fen mosses and upland mires. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 29. *Patrobus septentrionis*, a species that lives among mosses near water. Photo ©Roy Anderson <habitas.org.uk>, with permission.

The genus *Agonum* has a number of bryophyte-dwelling species (Lindroth 1974), occurring in the Holarctic and Mediterranean regions to a southern limit in Central Asia (Wikipedia 2015b). These beetles are small to mid-sized and often have a metallic sheen. *Agonum obscurum* (Figure 30) lives among leaves and mosses in

damp deciduous forests and densely vegetated marshes (Lindroth 1974). The very **hygrophilous** (water-loving) *A. livens* (Figure 31) lives in marshy deciduous forests among leaves and *Sphagnum*. *Agonum versutum* (Figure 32) lives at the margin of fresh water where it keeps sufficiently moist among mounds of the sedge *Carex* and mosses. *Agonum fuliginosum* (Figure 51) lives among mosses and leaves in moist, shady places under bushes and forest trees. *Agonum gracile* (Figure 33) likewise lives in very damp, shady places such as quagmires with *Sphagnum* (Figure 35-Figure 36) and mossy lake shores. *Agonum sexpunctatum* (Figure 34) lives in wet peatlands in Europe (Wikipedia 2015c). It also occurs on moist, mossy ground near water where low, mossy vegetation occurs, including damp patches in otherwise sandy heathland in Europe (Luff 1998).



Figure 30. *Agonum obscurum* adult, a species typical of leaves and mosses in damp deciduous forests and densely vegetated marshes. Photo by Brian Eversham, with permission.



Figure 31. *Agonum livens* adult, a species of marshy deciduous forests among leaves and *Sphagnum*. Photo by Brian Eversham, with permission.



Figure 32. *Agonum versutum* adult, a species at the margin of fresh water among the sedge *Carex* and mosses. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 33. *Agonum gracile* adult, a species of quagmires with *Sphagnum* and mossy lake shores. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 34. *Agonum sexpunctatum* adult on mosses, a species that seems to be tied to bryophytes in its habitat. Photo by Christoph Benisch <www.kerbtier.de>, with permission.

In comparing *Sphagnum* bog habitats (Figure 35) on several continents, Främbs (1994) considers the open *Sphagnum* mat to be an extreme habitat with only a few carabid species. Furthermore, the behavior of *Agonum ericeti* (Figure 36) and *Pterostichus rhaeticus* (Figure 37) indicates that the carabids may only use the damp *Sphagnum* lawn habitats in the summer, moving to drier hummocks (Figure 38) to overwinter. In fact, these two species of ground beetles are scarce in bog areas in which there is no clear pattern of hummocks and hollows to allow them to escape the water.



Figure 35. *Sphagnum* in Turbal in Valle de Andorra in the east Pyrenees. Photo through Creative Commons.



Figure 36. *Agonum ericeti* adult on *Sphagnum*, its summer habitat. Photo by Niels Sloth <www.biopix.dk>, with permission.



Figure 37. *Pterostichus rhaeticus* on wet mosses. Photo by Christoph Benisch <www.kerbtier.de>, with permission.



Figure 38. *Sphagnum papillosum* and *Sphagnum capillifolium* forming a hummock where Carabidae can spend the winter. Photo by Janice Glime.

The carabid species *Carabus menetriesi* (Carabidae) is associated with *Sphagnum* (Figure 35) in northern Europe and northern Russia (Barbara Knoflach-Thaler, pers. comm. 9 June 2011). It is an **FFH-species** (endangered all over Europe) and needs *Sphagnum* for overwintering; otherwise it would disappear. *Carabus arvensis* (Figure 39) hibernates under mosses as well as tree stumps (Lindroth 1985). *Carabus glabratus* (Figure 40), a widespread species of central and northern Europe, is day active and prefers damp areas such as peat hummocks (Figure 38) and other mosses (Weiss-Roessler 2015).



Figure 39. *Carabus arvensis*, a species that hibernates under mosses. Photo by Christoph Benisch <www.kerbtier.de>, with permission.



Figure 40. *Carabus glabratus* adult on moss, a species that prefers damp areas such as peat hummocks and other mosses. Photo by Stanislav Krejčík, through Creative Commons.

Carabus clathratus (23-24 mm; Figure 41), a widespread Palaearctic species, is day active and lives an amphibious life style, including under mosses (Obydov 2006), diving under water to search for food. Its larvae develop in the summer and it overwinters as an adult to breed in early to late summer (Wallin *et al.* 1999). This overwintering can be far from water where it hibernates on drier land.



Figure 41. *Carabus clathratus* adult on *Sphagnum*. Photo ©Roy Anderson <habitas.org.uk>, with permission.

In Finland, several species of **Carabidae** live in *Sphagnum* habitats (Figure 41) (Ljungberg 1999; Wallin *et al.* 1999). Among these is *Chlaenius costulatus* (striped velvet runner, hairy ground beetle; Figure 42; Figure 43). This species is a 13-14 mm predator. In other European mires, with mosses like *Drepanocladus* (Figure 44), one can find *Chlaenius sulcicollis* (swamp velvet runner; Figure 45). In Sweden, *Chlaenius sulcicollis*, a species of Europe and Asia north to the Arctic Circle, is a critically endangered species that lives among *Sphagnum* in bogs (Wallin *et al.* 2000). *Chlaenius nigricornis* (Figure 46) lives in sheets of mosses in damp places (Bates 1843). *Chlaenius nitidulus* (Figure 47) lives among grasses and mosses in silty and damp places along the coast (Lindroth 1974).



Figure 42. *Chlaenius* sp. larva, frequently a moss dweller. Photo by Tom Murray, through Creative Commons.



Figure 43. *Chlaenius costulatus* adult, a *Sphagnum* inhabitant. Photo by Tim Faasen, with permission.



Figure 44. *Drepanocladus aduncus*, home for several beetle species in the Czech Republic. Photo by Heike Hofmann ©swissbryophytes <swissbryophytes.ch>, with permission.



Figure 45. *Chlaenius sulcicollis* adult, a species found in *Drepanocladus* in mires. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.



Figure 46. *Chlaenius nigricornis* adult on moss like the sheet mosses where it lives. Photo by Niels Sloth <www.biopix.dk>, with permission.



Figure 47. *Chlaenius nitidulus* adult, a coastal species that lives among grasses and mosses in silty and damp places. Photo by Gernot Kunz, with permission.

In other European mires with mosses like *Drepanocladus* (Figure 44), one can find *Panagaeus cruxmajor* (great cross runner; 8-10 mm; Figure 48). The Wikipedia author for this family recounted this from Charles Darwin (1846), regarding his attempted capture of *Panagaeus cruxmajor*:

"I must tell you what happened to me on the banks of the Cam in my early entomological days; under a piece of bark I found two carabi (I forget which) and caught one in each hand, when lo and behold I saw a sacred *Panagaeus crux major*; I could not bear to give up either of my carabi, and to lose *Panagaeus* was out of the question, so that in despair I gently seized one of the carabi between my teeth, when to my unspeakable disgust and pain the little inconsiderate beast squirted his acid down my throat and I lost both carabi and *Panagaeus*!"

In European mires with mosses like *Drepanocladus* (Figure 44), one can find *Agonum hypocrita* (lacquer runner; Figure 49). In Finnish boreal forests, *Sphagnum* (Figure 41) is a refuge for some carabids following cutting of the forests (Figure 50) (Koivula 2001). *Agonum fuliginosum* (Figure 51), *Amara brunnea* (Figure 52), *Carabus glabratus* (Figure 53), *Carabus hortensis* (Figure 54), *Cychrus caraboides* (Figure 55), and *Pterostichus niger* (Figure 56) were almost exclusively in the *Sphagnum* mires after cutting. On the other hand, *Calathus micropterus* (Figure 57) did not inhabit the mires and diminished in numbers after cutting, presumably due to

increased exposure. *Platynus mannerheimii* (Figure 58) likewise disappeared after clearcutting, but distribution of *Agonum fuliginosum* is not affected by canopy cover, permitting it to survive in the more open *Sphagnum* mires. Hence, the *Sphagnum* provides a refugium that can permit at least some of the **Carabidae** to re-inhabit the forest when it regrows.



Figure 48. *Panagaeus cruxmajor* adult, a species found in *Drepanocladus* in mires. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 49. *Agonum hypocrita* adult, a bog dweller. Photo by Marko Mutanen, through Creative Commons.

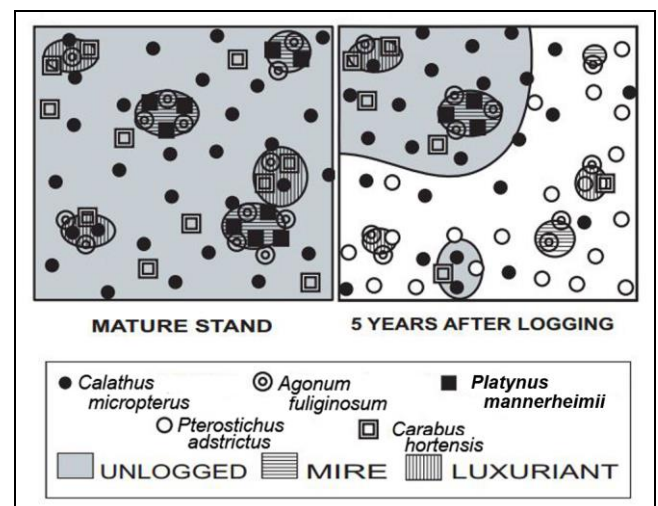


Figure 50. Response in abundance of major **Carabidae** species following clearcut logging in a mature spruce forest with three mires and three "luxuriant" sites. Modified from Koivula 2001.



Figure 51. *Agonum fuliginosum* adult, a species that associates with *Sphagnum* in boreal forests. Photo by Niels Sloth <www.biopix.dk>, with permission.



Figure 52. *Amara brunnea* adult, a species that associates with *Sphagnum* in boreal forests. Photo by Niels Sloth <www.biopix.dk>, with permission.



Figure 53. *Carabus glabratus* adult on moss. Photo by Dodoni, through Creative Commons.



Figure 54. *Carabus hortensis* adult, a moss dweller shown here on moss. Photo from <brouci.fotobarvinek.cz>, for non-commercial use.



Figure 55. *Cychrus caraboides* adult on moss, a species that uses *Sphagnum* as a refuge following forest disturbance. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 56. *Pterostichus niger* adult, a moss dweller shown here on moss. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 57. *Calathus micropterus* adult on moss in forest. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 58. *Platynus mannerheimii* adult, a species that is unable to live in mires and thus disappears after clearcutting. Photo by Derek Sikes, through Public Domain.

It is unusual for any invertebrate to show host specificity among the bryophytes, although some bryophytes are certainly avoided by many bryophagous species. However, the carabid beetle *Acupalpus dubius* (Figure 59) seems to be restricted to the wetland moss *Drepanocladus aduncus* (Figure 44), at least in one study in the Czech Republic (Kopecký 2001). On the other hand, *A. brunnipes* (Figure 60) and *A. flavicollis* (Figure 61) seem to lack such specificity (Luff 1998). *Acupalpus brunnipes* occurs in both mosses and litter on mud near water in northern and western Europe, Greece, and North Africa. *Acupalpus flavicollis* sometimes occurs in bogs, but it is more common on river banks and in gravel pits in fine silt-covered sand where there is sparse vegetation and some mosses.

Cold temperatures seem to preclude most **Carabidae**. In the geothermal areas of Iceland, some of the geothermal areas are covered by the mosses *Archidium alternifolium* (Figure 62) and *Campylopus introflexus* (Figure 94) and the leafy liverwort *Gymnocolea inflata* (Figure 63) (Elmarsdottir *et al.* 2003). In some of these hotter areas, the carabids *Bembidion bipunctatum* (Figure 64) and *Nebria rufescens* (Figure 65) could survive, whereas they were not present in the colder, non-geothermal areas. Lindroth (1974) reported *Nebria brevicollis* (Figure 66)

among mosses in UK forests and Barry (2014) found it under moss in a flower bed.



Figure 59. *Acupalpus dubius* adult on liverwort, a beetle that lives among *Drepanocladus aduncus* in the Czech Republic. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 60. *Acupalpus brunnipes* adult, a species that lives among mosses and litter on mud near water. Photo by Wim Rubers, through Creative Commons.



Figure 61. *Acupalpus flavicollis* adult, a species that sometimes occurs in bogs as well as river banks and in gravel pits where there are some mosses. Photo by Tim Faasen, with permission.



Figure 62. *Archidium alternifolium*, a geothermal moss that supports several species of **Carabidae**. Photo by Michael Lüth, with permission.

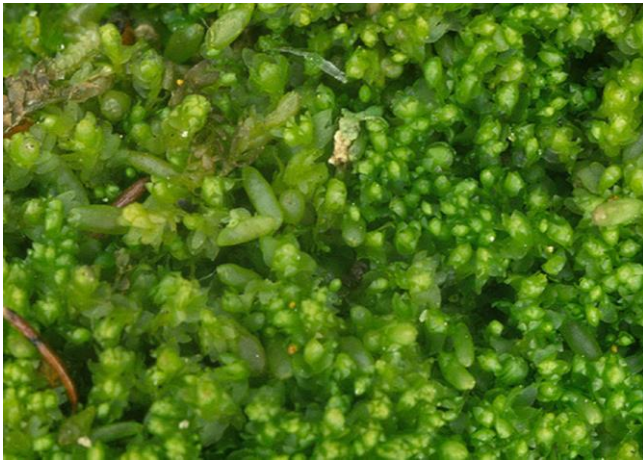


Figure 63. *Gymnocolea inflata* with perianths, a geothermal leafy liverwort that supports several species of **Carabidae**. Photo by Malcolm Storey, through Creative Commons.



Figure 64. *Bembidion bipunctatum*, moss inhabitants in geothermal areas of Iceland. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 65. *Nebria rufescens* adult, a species that takes advantage of geothermal mosses in cold regions. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 66. *Nebria brevicollis* adult with moss, a species known to occur under mosses. Photo by Fritz Geller-Grimm, through Creative Commons.

Elsewhere, in the UK, *Bembidion gilvipes*, *B. biguttatum*, and *B. mannerheimii* live among mosses (Lindroth 1974). The first two of these live in forests. *Bembidion mannerheimii* lives in forests and fens. All three species also live among leaf litter and other substrata as well. Darwin even reported the genus from a nest of mosses (Smith & Freeman 1987).

The **Carabidae** are generalist feeders, suggesting they should be able to find food among any of the bryophytes, including fungi, bacteria, detritus, and various invertebrates (König *et al.* 2011). Thus far there seems to be no evidence that they eat the bryophytes.

POLYPHAGA

Artemotopoidea

Artematopidae – Soft-bodied Plant Beetles

Larvae and adults of beetles often live in different places. And if they are both in the same aquatic habitat, the pupae are typically on land. Even among the terrestrial bryophytes, the physiology and morphology differ sufficiently that many prefer different habitats. On the other hand, many are flightless, restricting their ability to move around.

Such habitat difference seems to be the case for members of *Macropogon*. Adults of *Macropogon testaceipennis* (Figure 67) and *M. piceus* (Figure 68) in western Washington and Oregon, USA, usually live on trees and shrubs near moss-covered boulders or rock outcrops (Loren Russell, pers. comm.). *Macropogon* larvae, on the other hand, can be found under mosses such as *Ceratodon purpureus* (Figure 69) and others growing on sandy loam of a stream bank in Viento State Park, Oregon.



Figure 67. *Macropogon testaceipennis* adult, a species that seems to prefer trees and shrubs with moss-covered rocks nearby. Photo by Joyce Gross, with permission.



Figure 68. *Macropogon piceus*, a species whose adults seem to prefer trees and shrubs with moss-covered rocks nearby. Photo by Jim McClarin, with permission.

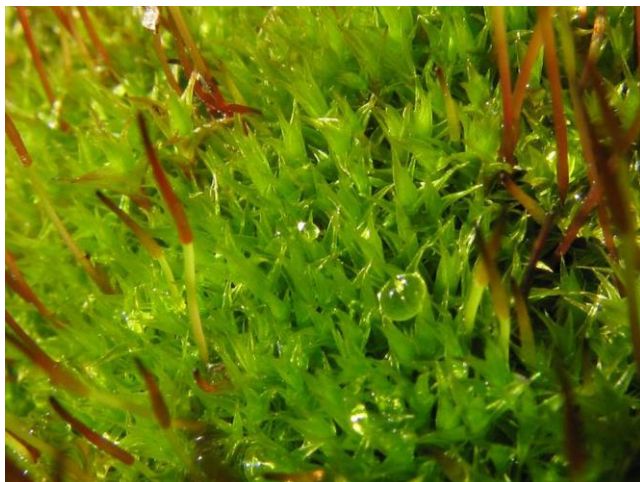


Figure 69. *Ceratodon purpureus*, home for larvae of *Macropogon* species. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Larvae of another member of this family, *Eurypogon* cf. *californicus* (Figure 70), occur under mosses growing on exposed rocks of road cuts at Mary's Peak, Oregon, and near the Alsea River (Loren Russell, pers. comm.).



Figure 70. *Eurypogon californicus*, species that lives under mosses on exposed rocks. Photo from Museum of Comparative Zoology, Harvard, through Creative Commons.

Byrrhoidea

Byrrhidae – Pill Beetles

The **Byrrhidae** are known for their habit of living among mosses. Not only do they live there, but the mosses serve as their food source in most cases (pers. comm. Loren Russell & Paul Johnson, 21 March 2012). A few actually feed on liverworts, and some on **tracheophytes** (lignified vascular plants, including flowering plants). In the Pacific Northwest, USA, the genus *Amphicyrta* (Figure 71) is the only member of the family known to feed on tracheophytes and no bryophytes, becoming a pest in lily fields. But generally, members of this family are adapted to living in transitional **ruderal** (wasteland) microhabitats where mosses dominate (Majka & Langor 2011), including such open habitat mosses as *Ceratodon purpureus* (Figure 69), *Polytrichum juniperinum* (Figure 72), and *P. piliferum* (Figure 73) growing on moist, thin or scarified soil (Johnson 2002).



Figure 71. *Amphicyrta* sp. adult, an unusual member of **Byrrhidae** not known to eat bryophytes. Photo by Joyce Gross, with permission.



Figure 72. *Polytrichum juniperinum* with males, common home for **Byrrhidae**. Photo by Dale Vitt, with permission.



Figure 73. *Polytrichum piliferum*, common home for **Byrrhidae**. Photo by Thomas Brown, through Creative Commons.

Several of the byrrhid characteristics suit them for the moss habitat. Their small size (1-10 mm) (Johnson 2002) and convex, compact shape, and retractile appendages (Johnson 2013) permit ease of movement among the moss maze and make them inconspicuous to most predators. When detected, they have the ability to play dead by retracting their legs and antennae into grooves on the lower surface (Figure 74-Figure 75), remaining motionless (Lindquist & Ingram 1968). This motionless behavior along with their shape has earned them the common name of pill beetles. Their ability to subsist on mosses suggests that they may have special digestive adaptations as well.

The **Byrrhidae** are common farther north and at higher altitudes than most of the insects. Majka and Langor (2011) suggest that this may be possible due to their ability to eat bryophytes. The bryophyte species diversity changes little with latitude (Shaw *et al.* 2005), whereas tracheophyte diversity diminishes. Furthermore, most bryophytes have longer growing seasons than most tracheophytes and are available immediately upon snow melt as a source of food. We know that bryophytes produce **arachidonic acid** (a fatty acid) (Shinmen *et al.* 1991; Kajikawa *et al.* 2008) and it would be interesting to explore whether the arachidonic acid in bryophytes may help to keep membranes of bryophyte consumers more fluid at cold temperatures. Furthermore, it may be helpful in promoting larval growth (Fraenkel & Blewett 1947), permitting these beetles to complete their life cycles in the short growing season of cold ecosystems.



Figure 74. *Byrrhus* sp playing dead in Scotland. Photo by Roger S. Key, with permission.



Figure 75. **Byrrhidae** feigning death. Note how the legs fit into grooves on the underside. Photo by Barbara Thaler-Knoflach, with permission.

Members of the **Byrrhidae** (*Cytilus sericeus*, *Byrrhus fasciatus*, *Byrrhus pilula*, *Byrrhus glabratus*) often travel some distances from the mosses where they sleep, preferring acrocarpous mosses to pleurocarpous ones (Pyszko *et al.* in prep). Their guts contain considerably higher moss species richness than that in their immediate microhabitats.

Although several authors have considered that the direct evidence for associations of Byrrhidae with mosses is still rare (Reichenbach 1844; Watt 1971; LeSage 1983; Johnson 1986; Hradilek & Boukal 2003), that family is better known among terrestrial bryophyte inhabitants than other groups. *Cytilus sericeus* has been reported from *Sphagnum* spp. (Mateleshko, 2009), *Tortula muralis* (Reichenbach 1844) and *Amblystegium varium* (Pristinskaya 2003). *Byrrhus fasciatus* is known from *Aulacomnium* spp. (Böcher 1988), *Andreaea* spp., *Brachythecium velutinum*, *Bryum* spp., *Myurella* spp. (Pristinskaya 2003), *Philonotis tomentella* (Lindroth 1931), and *Racomitrium* spp. (Janetschek 1949); *Byrrhus pilula* occurs with *Sphagnum* spp. and *Polytrichum* spp. (Pristinskaya 2003; Sushko 2007); and *Byrrhus glabratus* with *Plagiomnium cuspidatum* and *Rhizomnium punctatum* (Reichenbach 1844).

The slow or incomplete digestion of bryophytes permits identification from the guts of bryophagous insects (Haines & Renwick 2009; Kočárek *et al.* 2008).

Amphicyrta

This genus (Figure 71), restricted to California and Oregon, USA, is the exception among the **Byrrhidae**. Larvae and adults of this genus are not bryophyte feeders (Johnson 2013). Rather, they feed on succulent leaves and stems of forest and meadow herbs and on deciduous shrubs.

Byrrhus

Byrrhus (Figure 76) ranges from tiny to small (1-10 mm) (Johnson 2013). All the adults in this genus that feed on bryophytes are surface grazers. In addition to bryophytes they may occasionally feed on conifer seedlings, grasses, and clover in the moist areas that have abundant mosses. The larvae, on the other hand, burrow through the bryophyte layers and feed at the tunnel entrance by extending part of the body out to graze on bryophyte leaves and shoots.



Figure 76. *Byrrhus fasciatus* on moss in UK, showing underside with legs tucked into grooves while it plays dead. Photo by Roger S. Key, with permission.

Byrrhus luniger eats its own home. In Štramberk, a small town in the Moravian-Silesian Region of the Czech Republic, these beetles spend at least part of their lives among **Polytrichaceae**. Gut analysis reveals cells of these mosses in the gut (Hradílek & Boukal 2003). Papillae on the terminal lamina cells suggest that the mosses were either ***Pogonatum urnigerum*** (Figure 77) or ***Polytrichastrum alpinum*** (Figure 78).

In northwestern United States, Loren Russell and Paul Johnson (pers. comm. 21 March 2012) found different species of ***Byrrhus*** as moss dwellers: ***Byrrhus americanus*** (Figure 80), ***B. concolor*** (Figure 81), and ***Byrrhus kirbyi*** (~6.5 mm; Figure 82). Gut analysis of museum specimens of all three species revealed that mosses had served as food items. Not surprisingly, these beetles have seldom been collected, perhaps because the tiny creatures seldom venture out of their cozy cushions to fall into pitfall traps.



Figure 77. *Pogonatum urnigerum*, a likely food of *Byrrhus luniger*. Photo by James K. Lindsey, with permission.



Figure 78. *Polytrichastrum alpinum*, likely food for *Byrrhus luniger*. Photo by David T. Holyoak, with permission.

Some records of this genus among mosses are old. Ferguson (1901) reported ***Byrrhus pilula*** (Figure 79) from mosses in the Clyde Area of the British Isles.

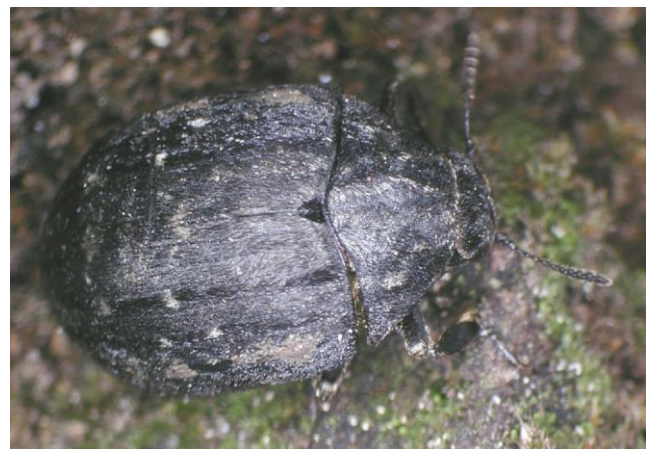


Figure 79. *Byrrhus pilula*, a moss dweller in the British Isles. Photo by Petr Kočárek and Pavel Drozd, with permission.



Figure 80. *Byrrhus americanus* adult, a moss dweller and consumer in northwestern United States. Photo by Tom Murray, through Creative Commons.



Figure 81. *Byrrhus concolor*, moss feeder in northwestern USA. Photo by Tom Murray, through Creative Commons.



Figure 82. *Byrrhus kirbyi* adult, a moss dweller in northwestern USA. Photo by Tim Loh, with permission.

Chaetophora

Yes, *Chaetophora* is also a genus of green algae. Neither group of nomenclatural taxonomists has created a rule to prevent using the same name in another kingdom. The byrrhid *Chaetophora* is a native of Eurasia, but it is adventive in northeastern USA (McLeod 2006). It lives in areas with sparse vegetation, but with mosses.

Chaetophora spinosa (Figure 83) appears to be invasive in North America as a European immigrant (Johnson 1990). On Prince Edward Island, Canada, *Chaetophora spinosa* occurs on the moss *Mnium hornum*

(Figure 84) and the nearby bare mud. In Idaho, USA, adults can be found in large numbers with the mosses *Pohlia atropurpurea*, *Dicranella varia* (Figure 85), and *Aloina brevirostris* (Figure 86), but *A. brevirostris* has not been confirmed as a host for food (Johnson 1990). The beetles also consume the Cyanobacterium *Nostoc* (Figure 87) and it would be interesting to know if the occurrence of *Nostoc* on mosses might serve as an attractant and food source there.



Figure 83. *Chaetophora spinosa* adult, an invasive moss dweller in North America. Photo by Tom Murray, through Creative Commons.



Figure 84. *Mnium hornum*, home for *Chaetophora spinosa*. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

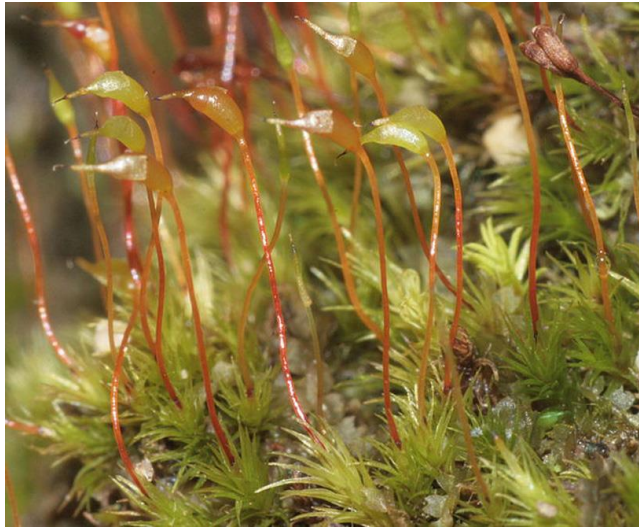


Figure 85. *Dicranella varia* with capsules, home for *Chaetophora spinosa*. Photo by Hermann Schachner, through Creative Commons.



Figure 86. *Aloina brevirostris*, home for *Chaetophora spinosa*. Photo by Michael Lüth, with permission.



Figure 87. *Nostoc* cf. *commune* on bryophytes. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Chalciosphaerium

This moss-dwelling genus (Figure 88-Figure 90) was not known from South Georgia until 2009 when Roger S.

Key (2009) found it with larvae (Figure 88) and pupae (Figure 89) that might be the same species. The species was later determined to be *Chalciosphaerium solox* (Figure 90), a species known from the Falklands (Roger S. Key, pers. comm. 4 December 2015). DNA confirmation is pending. If it is indeed that species, it is likely that it arrived with human traffic. Its apparent absence in other relatively nearby locations (indicated by searches for it) further support this interpretation. The location was a few hundred meters from the dis-embarkation site for many tourists and other visitors. Its small size would make it easy to be a hitchhiker on boots or other clothing or backpacks.

This species occurred with *Polytrichum* that was mixed with grasses (Roger S. Key, pers. comm. 4 December 2015). The researchers were unable to find it among nearby grasses that had no moss associates. More were, however, among other patches of the nearby mosses.



Figure 88. Larva, probably *Chalciosphaerium* sp., among mosses and liverworts at Grytviken, South Georgia. Photo by Roger S. Key, with permission.



Figure 89. Pupa, probably *Chalciosphaerium* sp., among mosses and leafy liverworts at Grytviken, South Georgia. Photo by Roger S. Key, with permission.



Figure 90. *Chalciosphaerium* sp. adult on leafy liverworts from Grytviken, South Georgia. Photo by Roger S. Key, with permission.

Curimopsis

Some of our photographers make great observations! Both my sister and I have been surprised on occasion to find an insect in our pictures when we enlarge them on the computer screen, but we never saw it when we were taking the picture. So I admire and envy these astute photographers who note the interesting behavior of these tiny inhabitants.

One such photographer is Brian Eversham. He shared with me his observations on *Curimopsis* (Figure 95-Figure 98) in Great Britain (Brian Eversham, pers. comm. 21 March 2012). He studied this genus for several years and found that it seems to prefer *Dicranella* [*D. heteromalla* (Figure 91) and *D. cerviculata* (Figure 92)] for shelter and food among the mosses in its habitat. It also eats *Pohlia nutans* (which is common there too; Figure 93) and even the invasive *Campylopus introflexus* (Figure 94).



Figure 91. *Dicranella heteromalla*, home and food for *Curimopsis*. Photo by Janice Glime.



Figure 92. *Dicranella cerviculata* with capsules, home and food for *Curimopsis*. Photo by David T. Holyoak, with permission.



Figure 93. *Pohlia nutans* with capsules, home and food for *Curimopsis*. Photo by J. C. Schou <www.biopix.com>, with permission.



Figure 94. *Campylopus introflexus*, home and food for *Curimopsis*. Photo by Michael Lüth, with permission.

In peat areas, the peat dries out in the summer in Thorne and Hatfield Moors, UK, due to the low rainfall (Brian Eversham, pers. comm. 21 March 2012). When this occurs, the females construct burrows down to 4 cm deep in the peat. These are usually close to the *Dicranella* (Figure 91-Figure 92) species. To build their burrows they collect moss leaves, one at a time, and like ants they carry them in their jaws. These are carried underground to line the burrows in a spiral arrangement around the walls. This "wallpaper" serves to feed the young larvae.

Johnson (1986) found *Curimopsis moosilauke* (Figure 95) to be a characteristic species above the **krummholz ecotone** (transition to stunted windblown trees growing near the tree line on mountains). These beetles often occurred between rocks and boulders where fine, moist, matted mosses grew on the sandy soils.



Figure 95. *Curimopsis moosilauke* adult, a moss associate above the krummholz. Photo by Kirill V. Makarov <www.zin.ru>, through public domain.

Curimopsis nigrita (mire pill beetle, bog-hog; Figure 96-Figure 97) is a tiny beetle only about 1.2 mm long. It burrows in peat and under mosses, lining these burrows with moss leaves (Roger S. Key, pers. comm. 31 October 2014). Perhaps this is the species seen by Brian Eversham, both in the UK.



Figure 96. *Curimopsis nigrita*, on Hatfield Moors, South Yorkshire. Photo by Brian Eversham, with permission.



Figure 97. *Curimopsis nigrita* (mire pill beetle), uncovered from its burrow under mosses. Note how well it blends with its surroundings. Photo by Roger S. Key, with permission.

On Mt. Hood, Oregon, USA, *Curimopsis albonotata* (Figure 98) lives at higher elevations (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). Similarly, *C. brevicollis* lives at high elevations on Mt. Rainier, Washington, USA. The latter, collected in northern Idaho, had mosses in its gut. Both of these species seem to be limited to higher elevations.

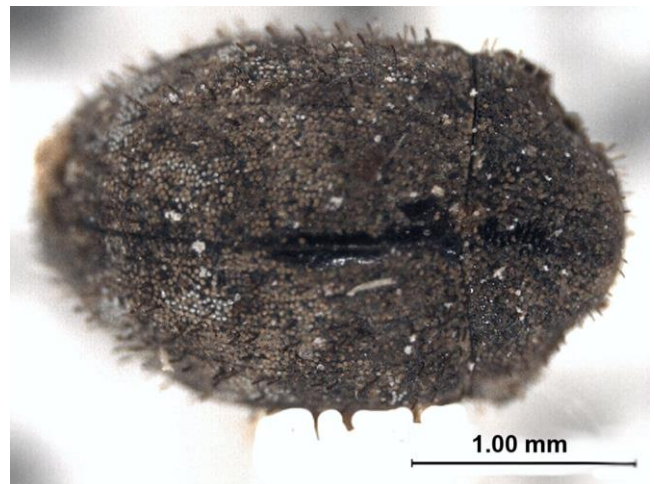


Figure 98. *Curimopsis albonotata* adult, a moss-dwelling, high-elevation species on Mt. Rainier, Washington, USA. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Cytilus

In the Atlantic region of Canada, larvae of the boreal *Cytilus alternatus* (Figure 99-Figure 100) live in thick layers of *Sphagnum* (Figure 35) (LeSage 1983; Majka & Langor 2011). *Cytilus* species, unlike those of most **Byrrhidae**, do not burrow and instead feed at the surface as larvae (Johnson 2013). And unlike most of the **Byrrhidae**, members of *Cytilus* are active in open mossy areas in sunlight (Figure 103) (Johnson 2002). The guts of these larvae contain dead leaves, dead wood of *Ericaceae* (heaths), mosses, liverworts, and other vegetable matter, suggesting that this species is a detritivore. Both adults and larvae include mosses in their diet.



Figure 99. *Cytilus alternatus* larva, a stage that eats mosses, among other things. Photo by Tom Murray, through Creative Commons.



Figure 100. *Cytilus alternatus* eating moss. Note that the tip of the larger *Plagiomnium* at the right has been eaten. Photo by Alex Wild, free for educational use.

In the northwestern United States, *Cytilus alternatus* (Figure 99-Figure 100) is a widely distributed boreal insect of open rocky sites, often near seepages or waterfalls (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). *Cytilus sericeus* (Figure 101-Figure 102) lives among the **Polytrichaceae** (Figure 103), where it feeds on mosses. These are in the typical open habitats known for this genus (Figure 50).



Figure 101. *Cytilus sericeus*, a bryophagid in peatland. Photo by James K. Lindsey, with permission.



Figure 102. *Cytilus* larva, a peatland inhabitant. Photo by Don Loarie, through Creative Commons.



Figure 103. *Cytilus sericeus* habitat with clumps of **Polytrichaceae**. Photo by James K. Lindsey, with permission.

Epichorius

Epichorius hails from the other end of the Earth from Auckland Island, New Zealand (Wahedi *et al.* 1974). Here one can find larvae of *E. longulus* and *E. aucklandiae* among bryophytes in the coastal rata forest (Figure 104-Figure 105). *Epichorius longulus* larvae can be found among bryophytes on the ground, abundantly occupying species of the thallose liverwort *Riccardia* (Figure 106) and rarely in mats of the leafy liverwort *Bazzania adnexa* (Figure 107). This difference may be one of nutrition. Larvae that fed on *Riccardia* thalli gained more weight than those fed on the leafy liverwort *Bazzania adnexa*. The larvae were absent on bare ground and among tree roots. But the larvae were not immobile. They sought shelter under leaf litter during the day and appeared on the liverworts at night to feed.



Figure 104. Rata forest, Auckland Island, where *Epichorius* lives among liverworts. Photo by James Russell <islandconservation.auckland.ac.nz>, with permission.



Figure 107. *Bazzania adnexa*, home for *Epichorius longulus* larvae. Photo by Niels Klazenga, with permission.

Exomella

This genus is restricted to mesic coniferous forests in the Pacific Northwest, USA. *Exomella pleuralis* (Figure 108) inhabits *Racomitrium heterostichum* (Figure 109) (Johnson & Russell 1978). In the lab they both ate and oviposited on *Eurhynchium oreganum* (Figure 110).



Figure 105. Rata forest (*Metrosideros umbellata*), Enderby Island in sub-Antarctic New Zealand. This forest is home for *Epichorius* among the liverworts. Photo courtesy of John Barkla.



Figure 108. *Exomella pleuralis* adult, an inhabitant of *Racomitrium heterostichum* in the Pacific Northwest, USA. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 106. *Riccardia latifrons*, a genus that is home for *Epichorius longulus* larvae. Photo by David T. Holyoak, with permission.



Figure 109. *Racomitrium heterostichum*, home for *Exomella pleuralis*. Photo by Michael Lüth, with permission.



Figure 110. *Eurhynchium oregonum*, suitable food for *Exomella pleuralis*. Photo by Matt Goff <www.sitkanature.org/>, with permission.

Lioligus

Both *Lioligus nitidus* (Figure 111) and *L. striolatus* occur in mossy sites of the coastal mesic coniferous forests in the Pacific Northwest, USA (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). *Lioligus striolatus* is more northern, living in northwest Washington, whereas *L. nitidus* is more common in western Oregon. Russell and Johnson suggest that they may be two forms of the same species. Laboratory experiments indicate that both have broad food choices in both larval and adult stages. In the lab, their foods included the mosses *Eurhynchium oregonum* (Figure 110), *Hylocomium splendens* (Figure 112), *Hypnum circinale* (Figure 113), *Plagiothecium undulatum* (Figure 114), *Racomitrium heterostichum* (Figure 109), *Rhytidiadelphus loreus* (Figure 115), and *R. triquetris* (Figure 116). The moss *Metaneckera menziesii* (Figure 117) was refused. In the lab, Russell and Johnson found that one specimen of *L. striolatus* survived from egg to adult with only leafy liverworts [*Diplophyllum plicatum* (Figure 118) and *Scapania bolanderi* (Figure 119)] to eat. However, this was an isolated success – other adult members of *Lioligus* would not feed on *Scapania* or other liverworts in cultures.



Figure 111. *Lioligus nitidus* adult female, a species that eats both mosses and liverworts. Photo by Louisiana State Arthropod Museum, through Creative Commons.



Figure 112. *Hylocomium splendens*, a suitable food for species of *Lioligus*. Photo by Andrew Spink, with permission.



Figure 113. *Hypnum circinale* with capsules, a suitable food for species of *Lioligus*. Photo by Tab Tannery, through Creative Commons.



Figure 114. *Plagiothecium undulatum*, a suitable food for species of *Lioligus*. Photo by Kristian Peters, with permission.



Figure 115. *Rhytidiadelphus loreus*, a suitable food for species of *Lioligus*. Photo by Andrew Spink, with permission.



Figure 116. *Rhytidiadelphus triquetrus*, a suitable food for species of *Lioligus*. Photo by Janice Glime.



Figure 117. *Metaneckera menziesii*, a potential food that was refused by species of *Lioligus*. Photo by Michael Lüth, with permission.

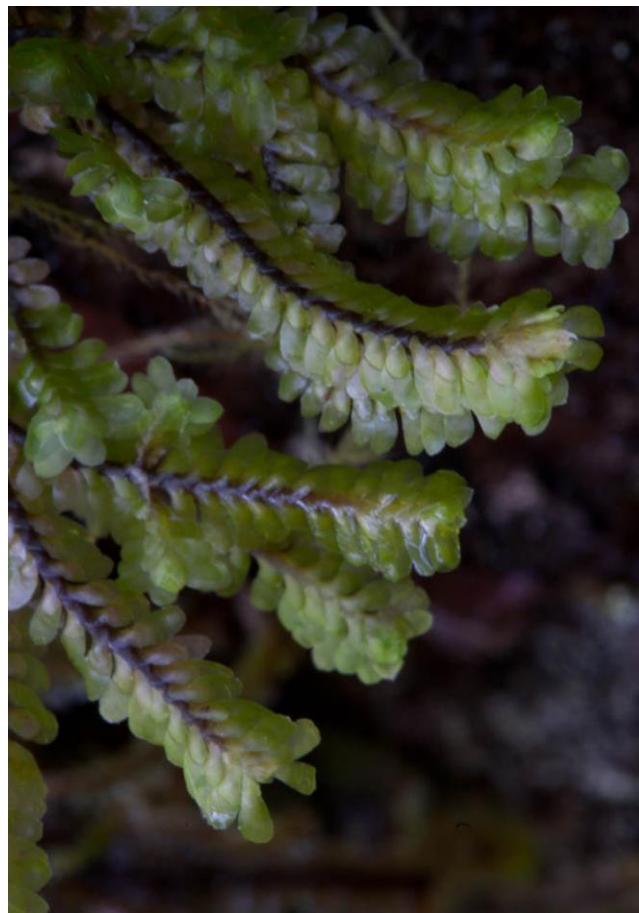


Figure 118. *Diplophyllum plicatum*, a suitable food for *Lioligus striolatus*. Photo by Martin Hutten, with permission.



Figure 119. *Scapania bolanderi*, a suitable food for *Lioligus striolatus* in the lab, but not for other members of the genus. Photo by Matt Goff <www.sitkanature.org>, with permission.

Lioon

Lioon puncticeps and *L. simplicipes* (Figure 120) are closely related species in the coastal coniferous forests of western USA (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). Larvae and adults have a wide range of mossy habitats, ranging from wet, boggy soil to dry epiphytes. Like *Lioligus* (Figure 111), they accept a wide range of host mosses, including *Antitrichia curtipendula* (Figure 121), *Dicranum fuscescens* (Figure 122), *Eurhynchium oreganum* (Figure 110), *Plagiothecium*

undulatum (Figure 114), and *Rhytidiadelphus loreus* (Figure 115) for *L. puncticeps*. They also eat leaf tips and leaf lamellae of *Polytrichum commune* (Figure 123), but they leave the tougher parts such as the stems.



Figure 120. *Lioon simplicipes* adult, a species that lives among mosses in a wide range of habitats in western USA. Photo by Joyce Gross, with permission.



Figure 121. *Antitrichia curtispindula*, a host species for *Lioon puncticeps*. Photo by James K. Lindsey, with permission.



Figure 122. *Dicranum fuscescens*, a host species for *Lioon puncticeps*. Photo by Michael Lüth, with permission.



Figure 123. *Polytrichum commune* habit, common home and food for beetles, including *Lioon puncticeps*. Photo by Sten Porse, through Creative Commons.

Listemus

Listemus is a small genus with three species in northwestern North America. These include *L. acuminatus* (Figure 124) and *L. formosus* (Russell 1979; Loren Russell & Paul Johnson, pers. comm. 21 March 2012). They are restricted to mesic coniferous forests of the Pacific Northwest, USA, but differ from *Lioligus* (Figure 111) and *Lioon* (Figure 120) in being restricted to mosses on soil, rocks, or logs and are not known from epiphytic bryophytes. In the lab both adults and larvae of *Listemus acuminatus* can survive on *Eurhynchium oreganum* (Figure 110), *Hypnum circinale* (Figure 113), and *Plagiothecium undulatum* (Figure 114). In the field one can find larvae of *L. acuminatus* in nearly pure mats of the leafy liverworts *Gyrothya underwoodiana* (Figure 125) and *Nardia scalaris* (Figure 126), but there is no evidence that these beetles feed on them. It is possible that they feed on the occasional mosses that grow with the liverworts.



Figure 124. *Listemus acuminatus* adult, a species among mosses on the ground, rocks, or logs. Photo by Joyce Gross, with permission.



Figure 125. *Gyrothya underwoodiana*, home for larvae of *Listemus acuminatus*, but apparently not suitable food. Photo by Tab Tannery, through Creative Commons.



Figure 126. *Nardia scalaris* with capsules, home for larvae of *L. acuminatus*, but apparently not suitable food. Note the accompanying mosses. Photo by J. C. Schou <www.biopix.com>, with permission.

Nothochaetes

Nothochaetes howensis (see Figure 127), a new genus and species, lives among mosses on trees in Australia (Lawrence *et al.* 2013).

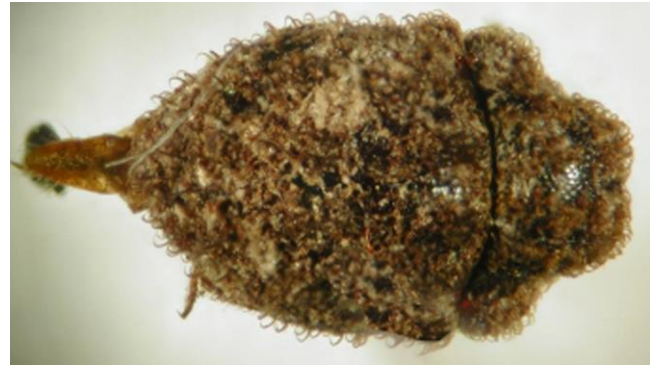


Figure 127. *Nothochaetes fasciculatus* adult. *Nothochaetes howensis* lives among mosses on Australian trees. Photo by Lynne Forster, with permission.

Notolioon

Lawrence *et al.* (2013) described six new genera from the **Byrrhidae** in Australia (Figure 128-Figure 129) and made nomenclatural changes in how some of the existing species are classified. This study suggests that many more **Byrrhidae** might be found around the world if more bryophytes are searched.

Notolioon nodipennis (Figure 128-Figure 129), a member of the most water-loving of the Australian **Byrrhinae**, occurs in the wet forests of southeastern Australia and Tasmania (Lawrence *et al.* (2013). Both adults and larvae appear to be adapted to feeding on mosses and liverworts, based on their lack of digging legs in the adult and the occurrence in the larvae of a well-sclerotized dorsal cuticle that has defensive glands.



Figure 128. *Notolioon nodipennis* among mosses, a species newly described in 2013. Photo by Kristi Ellingsen, Insects of Tasmania, with permission.



Figure 129. *Notolioon nodipennis* among mosses, demonstrating its ability to play dead by pulling its legs against its body. Photo by Kristi Ellingsen, Insects of Tasmania, with permission.

Simplocaria

In western Europe one can find *Simplocaria metallica* (Figure 130) in the lower part of the alpine zone. In this alpine area it lives among mosses in sandy places, often close to water courses or lakes, attesting to the importance of water in its habitat. It also occurs in the sub-alpine region, but it is rarely found in conifer forests (Böcher 1988). In Greenland, it is typically associated with the mosses *Polytrichum commune* (Figure 123) and *Aulacomnium* sp. (Figure 131), but also with the lichen *Peltigera* sp. (Figure 132) and the flowering plant *Cerastium alpinum* (Figure 133). Johnson (1990) found it with different mosses (*Bryum*?; Figure 134) on sandy gravel in boulder fields. These larvae, like those of *Byrrhus* (Figure 74, Figure 76-Figure 81), burrow into the moss mats (Böcher 1988).



Figure 130. *Simplocaria metallica* adult, a moss dweller in alpine and subalpine zones in Europe. Photo from Louisiana State Arthropod Museum, through Creative Commons.



Figure 131. *Aulacomnium palustre*, home for *Simplocaria metallica*. Photo by Janice Glime.



Figure 132. *Peltigera canina*, a lichen genus that is one of the habitat choices for *Simplocaria*. Photo by J. C. Schou <www.biopix.com>, with permission.



Figure 133. *Cerastium alpinum*, alternate host of *Simplocaria metallica*. Photo by Meneerke Bloem, through Creative Commons.



Figure 134. *Bryum algovicum*, in a genus that can serve as host for *Simplocaria metallica*. Photo by David T. Holyoak, with permission.

Simplocaria semistriata (Figure 135) is a native of Europe, but it has become widespread in North America (McClarín 2006). It grazes on the pioneer moss *Dicranella heteromalla* (Figure 85) and in Scotland on *Mnium hornum* (Figure 84) (Johnson 1990). Like *Chaetophora spinosa* (Figure 83), *Simplocaria semistriata* appears to be an invasive species in North America (Johnson 1990). Here it feeds, mates, and oviposits on mats of *Dicranella heteromalla*. At the same time, both larvae and adults avoid feeding on intermixed *Atrichum angustatum* (Figure 136) in both the field and laboratory. Since *Mnium hornum* is abundant in North America, but in more moist sites than those of *D. heteromalla*, it is likely that *Simplocaria semistriata* will be found on that host in North America as well. Nate Schoonover (BugGuide 2015) reports that this species plays dead when disturbed. His 3 mm adults appeared in his terrarium among "cushion mosses" collected in Dover, New Hampshire, USA.



Figure 135. *Simplicaria semistriata* (Coleoptera: Byrrhidae), a North American invasive moss dweller shown here on mosses. Photo by Vítězslav Plásek, with permission.



Figure 136. *Atrichum angustatum*, a moss that is avoided as food by *Symplocaria semistriata*. Photo by Michael Lüth, with permission.

Chelonariidae – Turtle Beetles

This family, mostly tropical (Harpootlian 2006), was presumed to be aquatic, but Spangler (1980) discovered that it included a number of terrestrial larvae in *Chelonarium* (Figure 137). The adults are larger than most moss dwelling beetles (2.5-10 mm) and have the oval shape and somewhat flattened body typical of swimming beetles. But these lack gills and in the tropics they are associated with roots of a number of species of orchids and a few other epiphytes. Although the larvae have been reported from aquatic habitats, Brown (1972) suggested that these larvae might have been living on damp mosses near the streams and occasionally were washed into streams.



Figure 137. *Chelonarium lecontei* adult. Some members of this genus that have terrestrial larvae associated with mosses near water. Photo by Mike Quinn, through Creative Commons.

Limnichidae – Minute Marsh-loving Beetles

This is a relatively small family (~400 spp.), as beetles go, but it nevertheless has worldwide distribution (Harpootlian 2005). It is small (~2 mm) and rounded and, in the word of Harpootlian, otherwise "unremarkable" (Figure 138). This family is primarily riparian, living streamside, on emergent plants, on wood, or in windrows of debris. The larvae live in damp soil near water. Little is known about their food – they are presumed to be herbivorous.



Figure 138. *Eulimnichus* adult showing the nondescript appearance of the **Limnichidae**. Photo by Tom Murray, through Creative Commons.

Although little is known about the biology of the **Limnichidae**, some are known to feed on algae and mosses (Pütz 1998). Jim McClarin (pers. comm. 30 August 2014) finds **Limnichidae** with bryophytes in the cloud forest zone of eastern Ecuador.

Pütz (1998) reported on members of this family in China. There one can find *Cephalobyrrhus sichuanensis* on algae and mosses of sandy river banks. Champion (1925) earlier reported *Cephalobyrrhus gibbicollis* running over wet mosses on river banks in India.

Summary

The **Carabidae** are the only members of **Adephaga** I have found to associate with bryophytes. The **Carabidae** among bryophytes lack any special adaptations for that habitat. Some are there to feed, including fungi, bacteria, detritus, and various invertebrates. Bryophytes themselves do not seem to serve as a food source for them. Nevertheless, the diversity of **Carabidae** among bryophytes is large. Some use the mosses as a summer refuge where they can find moisture or a place to spend the winter. Some, often rare species, inhabit bogs. *Sphagnum* mires in forests serve as a refuge for carabid species following cutting.

Some members of **Artematopidae** live among bryophytes as larvae.

The **Byrrhidae** are well known as moss-dwelling beetles. They are typically tiny and rounded. Some are able to play dead when disturbed and can retract their legs into grooves on the lower surface. Most of them also eat bryophytes, including a wide range of species, and some are known to eat liverworts. Some burrow into *Sphagnum*. The ability of these beetles to survive at high altitudes and latitudes may be due to the **arachidonic acid** from their bryophyte diet. The family is ancient and worldwide. Because of the difficulty of sampling these tiny moss inhabitants, and their inability to disperse far, one is likely to encounter new species if venturing into an unexplored region. Other species are invasive as passengers with their moss habitat when it is used commercially.

Other moss-dwelling members of **Byrrhoidea** include some species in the **Chelonariidae** and **Limnichidae**.

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CHAPTER 12-9c

TERRESTRIAL INSECTS:

HOLOMETABOLA – COLEOPTERA

FAMILIES

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CHAPTER 12-9c

TERRESTRIAL INSECTS:

HOLOMETABOLA – COLEOPTERA

FAMILY



Figure 1. **Curculionidae** on moss and litter in Ecuador. Photo by Andreas Kay, through Creative Commons.

POLYPHAGA cont.

Chrysomeloidea

Chrysomelidae – Flea Beetles, Leaf Beetles

This family of 35,000 species ranges 1-18 mm in length (Wikipedia 2015c). They are distributed everywhere except the high Arctic and the Antarctic (Benisch 2015a). All the species have wings, although some are slightly shortened so that the tip of the abdomen is visible (Wikipedia 2015c). And most are serious agricultural pests. But some are moss dwellers.

Among the earliest records of the **Chrysomelidae** from mosses is *Plateumaris sericea* (**Donaciinae**; Figure 2). Beare (1899) found several of these in his collecting in Surrey, UK.



Figure 2. *Plateumaris sericea* mating, a species that lives among mosses in the UK. Photo by Hedwig Storch, through Creative Commons.

One of the most frequently reported bryobionts is *Mniophila muscorum* (Figure 3), the moss flea beetle (Champion 1871; Kühnelt 1976; Cox 1997; Konstantinov & Lourdes Chamorro-Lacayo 2006). Its name says it all – a moss-loving moss dweller. It is a true **bryobiont**, living among the "litter" and feeding on mosses (Kühnelt 1976). And it has the typical small size of a moss dweller (1.1-1.6 mm for the genus), is globose, and has reduced hind wings (Nadein 2009). A shiny black elytra is common among small moss-dwelling beetles and is likewise characteristic of these. These characters are shared by *Mniophilosoma*, *Apteropeda* (Figure 4), *Minota* (Figure 5), *Clavicornaltica* (Figure 6), and *Kiskeya* (Figure 40).

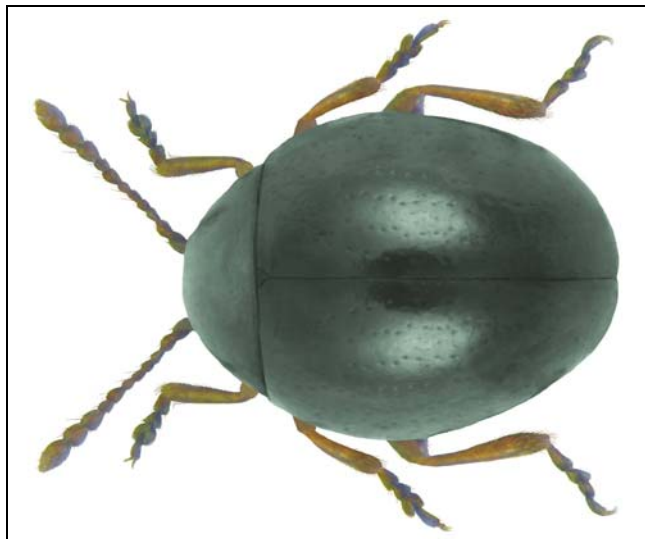


Figure 3. *Mniophila muscorum*, the common moss dweller known as the moss flea beetle. Photo by Udo Schmidt, with permission.



Figure 4. *Apteropeda globosa* adult with moss. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 5. *Minota obesa*, a shiny black and minute moss dweller. Photo by Udo Schmidt, with permission.

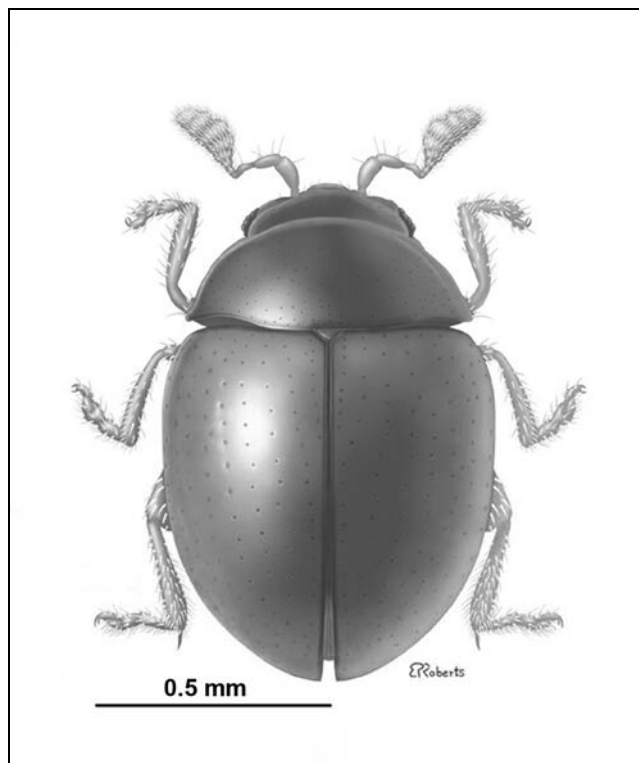


Figure 6. *Clavicornaltica dali*, a common moss dweller. Image by Sasha Konstantinov, with permission.

Unlike many members of the family, *Mniophila muscorum* (Figure 3) is not a leaf miner (Cox 1997). Instead, both larvae and adults occur on mosses, the latter including *Rhytidadelphus loreus* (Figure 7), *R. triquetrus* (Figure 8), and *Eurhynchium striatum* (Figure 9), all of which grow in a variety of habitats and on a variety of substrates (log stumps, fallen trees, tree branches, rocks, walls, and chalky slopes). They are also known from a number of other bryophyte species of both ground, boulders, and tree boles, including liverworts (Nadein 2009). Their substrate preference seems to depend on elevation. Those on vertical surfaces are usually restricted to thicker mats and cushions. And at least the first instar larvae are surface feeders on mosses. Nadein (2009) described the new species *Mniophila taurica*, *M. transcaucasica*, and *M. caucasica* from mosses in the Crimean Mountains. *Mniophila taurica* is known from the

mooses *Brachythecium glareosum* (Figure 10), *Homalothecium philippeanum* (Figure 11), and *Plagiomnium rostratum* (Figure 12). The genus *Mniophila* seems to prefer fresh mosses – not dry or sopping wet. The beetles may be on the surface or within the moss colony.



Figure 7. *Rhytidiadelphus loreus*, home for larvae and adults of *Mniophila muscorum*. Photo by Hermann Schachner, through Creative Commons.



Figure 8. *Rhytidiadelphus triquetrus* Canyon Falls, MI, home for larvae and adults of *Mniophila muscorum*. Photo by Janice Glime.



Figure 9. *Eurhynchium striatum* with capsules, a species of a wide variety of habitats, serving as a home for *Mniophila muscorum*. Photo by J. C. Schou <www.biopix.com/>, with permission.



Figure 10. *Brachythecium glareosum*, home to some *Mniophila taurica*. Photo by Michael Lüth, with permission.



Figure 11. *Homalothecium philippeanum*, home to some *Mniophila taurica*. Photo by Michael Lüth, with permission.



Figure 12. *Plagiomnium rostratum*, home to some *Mniophila taurica*. Photo by Michael Lüth, with permission.

Let's return to those look-alikes for *Mniophila* (Figure 3). Gillerfors (1986) described *Mniophilosoma obscurum* from *Sphagnum* (Figure 13) and other substrata in the Azores. *Mniophilosoma laeve* occurs among mosses and other substrata in Europe (Wollaston 1857). Despite the generic name, which translates to moss-loving body, this

genus often lives under bark. *Apteropeda orbiculata* (Figure 14-Figure 15) and *A. globosa* (Figure 4) both occur on mosses (Tomlin 1913). Tomlin also described *Phaedon tumidulus* (Figure 16-Figure 17), which occurs among mosses in Great Britain (Tomlin 1913). *Cassida viridis* (Figure 18-Figure 19) occasionally overwinters among mosses.



Figure 13. *Sphagnum russowii*, a potential home for many species of beetles. Photo by Andrew Hodgson, with permission.



Figure 14. *Apteropeda orbiculata* larva, a moss dweller. Photo by Willem Ellis, with permission.



Figure 15. *Apteropeda orbiculata* adult, a moss dweller. Photo through Creative Commons.



Figure 16. *Phaedon tumidulus* larva, a resident among mosses at times. Photo by Keith Edkins, through Creative Commons.



Figure 17. *Phaedon tumidulus* adult, a sometimes moss resident. Photo by Keith Edkins, through Creative Commons.



Figure 18. *Cassida viridis* larva, a species that occasionally overwinters among mosses. Note the shed exuvia that the larva is carrying on its back. This is an unusual habit that may have a role in avoiding predation. Photo by James K. Lindsey, with permission.



Figure 19. *Cassida viridis* adult, a species that occasionally overwinters among mosses. Photo by Roger S. Key, with permission.

The adult of *Minota* (Figure 5) occurs among mosses or litter in northern Eurasia (Medvedev 1997). But *Minota nigropicea* feeds on the ferns *Dryopteris erythrosora* (Figure 20), *Pteridium aquilinum* (Figure 21), and *Cyrtomium fortunei* (Figure 22) (Kimoto 1984; Kato 1991). Thus, being tiny, globose, shiny black, and having reduced hind wings adapts these flea beetles for not only mosses, but also for life on ferns and under bark.



Figure 20. *Dryopteris erythrosora*, food for *Minota nigropicea*. Photo by Megan Hansen, through Creative Commons.



Figure 21. *Pteridium aquilinum* habitat at edge of forest, food for *Minota nigropicea*. Photo by Rasback, through Creative Commons.



Figure 22. *Cyrtomium fortunei*, food for *Minota nigropicea*. Photo by Harum.Koh, through Creative Commons.

In a Cornish *Calluna* heath (Figure 23), Brown (1991) noted that the young larval stages of the heather beetle, *Lochmaea suturalis* (Figure 24), are dependent on the moisture of the moss layer. They are only found in older *Calluna* heaths, where *Pleurozium schreberi* (Figure 25) has had time to develop. When there is no moss layer present, these larvae have a density of about 0.4 per sample compared to 25 per sample when a moss layer is present. The mosses are essential to the larvae (Garvey 2011). Adults are destructive of the *Calluna*. This destruction initiates a complex series of events (Scandrett & Gimmingham 1991). The *Sphagnum plumulosum* (Figure 26) and *Hypnum jutlandicum* (Figure 27) increase, while *Sphagnum compactum* (Figure 28) and *Pleurozium schreberi* decrease. The *Calluna* is able to regenerate through layering, no doubt facilitated by the moisture-holding mosses, and by seedling development, especially in the *Sphagnum*.



Figure 23. Heathland, home of the heather beetle, *Lochmaea suturalis*, where the beetle larva lives among the moss *Pleurozium schreberi*. Photo by Willow, through Creative Commons.



Figure 24. *Lochmaea suturalis* adult, a species whose larvae require the moisture of moss mats. Photo by Niels Sloth <www.biopix.dk>, through Creative Commons.



Figure 25. *Pleurozium schreberi*, home for *Lochmaea suturalis* in heathlands. Photo by J. C. Schou <www.biopix.com/>, with permission.



Figure 26. *Sphagnum subnitens*, a species that increases when *Lochmaea suturalis* damages the *Calluna* and increases light penetration. Photo by Michael Lüth, with permission.



Figure 27. *Hypnum jutlandicum*, a species that increases when *Lochmaea suturalis* damages the *Calluna* and increases light penetration. Photo by Janice Glime.



Figure 28. *Sphagnum compactum*, a species that decreases when *Lochmaea suturalis* damages the *Calluna* and increases light penetration. Photo by Michael Lüth, with permission.

In the heathland, *Lochmaea suturalis* (Figure 24) oviposits at the base of the *Calluna* (Figure 23), usually among *Sphagnum* (Beagan 2015). The larvae crawl up the *Calluna* to eat the leaves, developing to as much as 2 cm in length. The mature larvae return to the mosses, where they spend 4 weeks to pupate. Then adults return to eat the *Calluna* leaves again, but once more return to ground level to spend the winter.

Recently, Sasha Konstantinov and associates have entered the picture, specializing in the tiny tribe of **Alticini**, among which are many previously ignored moss dwellers. The tiny size and time-consuming process of separating these beetles from their moss cushions seems to have discouraged most coleopterists. After all, this is the largest order of insects, and there were many much easier beetles to study.

The elusive *Phaelota* beetles living among mosses are typically small, with lengths about 2-3 mm, and are flightless (Prathapan & Konstantinov 2009). Among collections of six new species in the genus *Phaelota* from India, three were from mosses and a fourth moss dweller (*P. semifasciata*) was not new but was longer (up to 5 mm). The new moss-dwelling species include *Phaelota saluki* (Figure 29) from the moss *Forsstroemia thomsonii*, *P. maculipennis* (Figure 30), and *P. viridipennis* (Figure 31) from moss on tree trunks and rocks. The two groups of species are separated by their ability to fly – those living on ferns are capable of flight, but the moss-dwelling species are flightless. This flight restriction may be an adaptation to protect them from the windy mountain habitat (> 1470 m) where they reside in Southern India. In India they occur in the humid tropical evergreen forests of the Western Gats at 1000-2600 m asl (Konstantinov *et al.* 2013). *Phaelota kerzhneri* (Figure 32) from Borneo, like other flightless members of *Phaelota*, is probably also an inhabitant of moss (Prathapan & Konstantinov 2008).

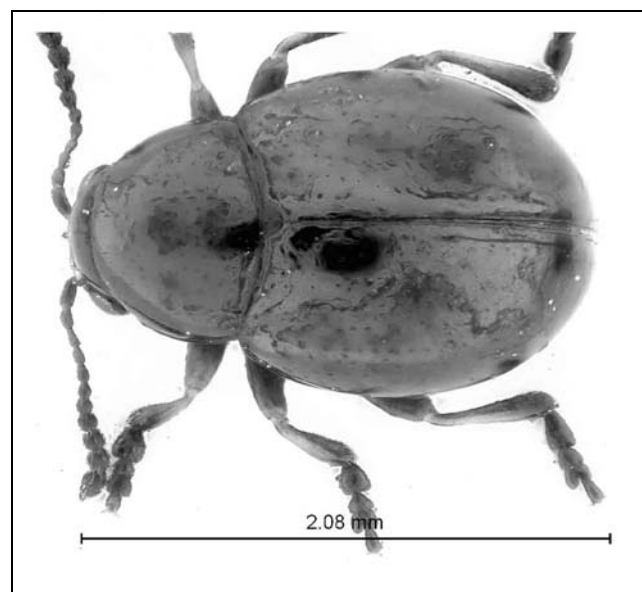


Figure 29. *Phaelota sakuli* adult, a moss dweller in India. Photo courtesy of Sasha Konstantinov.



Figure 30. *Phaelota maculipennis* adult, a moss dweller in India. Photo courtesy of Sasha Konstantinov.

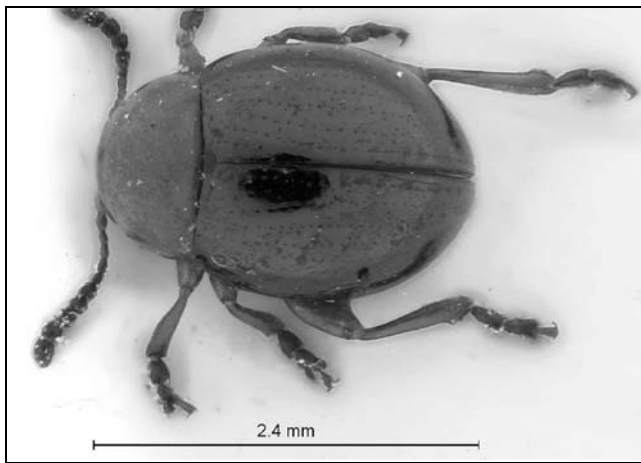


Figure 31. *Phaelota viridipennis* adult, a moss dweller in India. Photo courtesy of Sasha Konstantinov.



Figure 32. *Phaelota kerzhneri* adult, a probable moss dweller from Borneo. Image by Sasha Konstantinov, with permission.

Both Indian species in the genus *Ivalia* are moss dwelling, but their selection of host plants is not related to a loss of flight – their flightlessness apparently evolved before their choice of mosses for food (Prathapan & Konstantinov 2009). Recently, Duckett *et al.* (2006) found both adults and larvae of the new species *Ivalia korakundah* (Figure 33) on mosses in southern India by sifting mosses from the trunks of large pine trees. *Ivalia korakundah* also feeds on mosses. In one case, adults were found on the moss *Isopterygium* sp. (Figure 34). This genus seems to prefer more humid environments of the tropical evergreen forests, especially at altitudes of 1000 to 2600 m asl in the Western Ghats (Konstantinov *et al.* (2013).

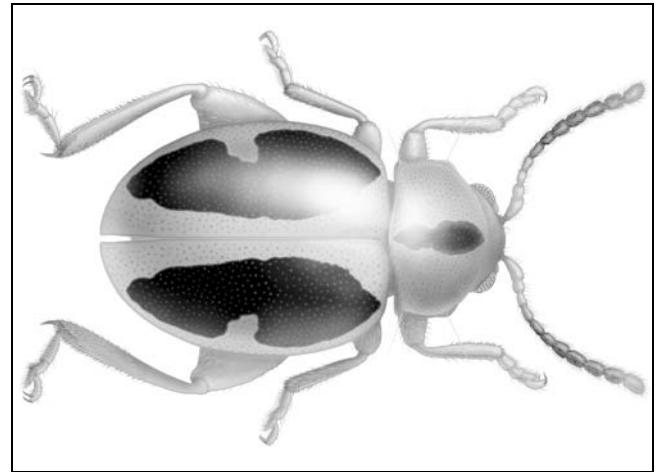


Figure 33. *Ivalia korakundah*, a moss dweller from pine trees in India. Image by Sasha Konstantinov, with permission.



Figure 34. *Isopterygium elegans*, potential home, and probably food, for *Ivalia korakundah*. Photo by Robin Bovey, with permission from Dale Vitt.

In China, Konstantinov *et al.* (2013) described the new genus and species *Cangshanaltica nigra* (Figure 35-Figure 36) from the moss cushions of *Hypnum* (Figure 27). Unlike findings in most of the studies on such tiny beetles, Konstantinov and coworkers were able to find *Hypnum* in the guts of these beetles. These likewise are among the smallest leaf beetles; they have round bodies with robust appendages, reduced hind wings, highly simplified and shortened meso- and metathorax, and their antennae have "more or less" enlarged apical antennomeres.

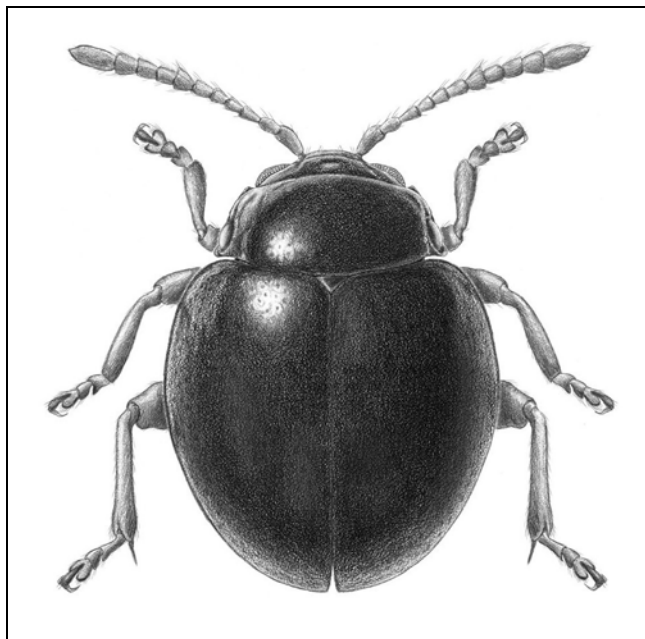


Figure 35. *Cangshanaltica nigra* adult, a species that lives among *Hypnum* in China. Image courtesy of Sasha Konstantinov.



Figure 36. *Cangshanaltica nigra* habitat. Photo courtesy of Sasha Konstantinov.



Figure 37. *Hypnum cupressiforme*, a genus that provides homes for *Cangshanaltica nigra* in China. Photo by Michael Becker, through Creative Commons.

The members of *Cangshanaltica* (Figure 35) are small (0.8.-2 mm) and rounded (Konstantinov & Duckett 2005). The elytra covers the abdomen, but the bodies are fragile and easily broken. The genus is distinctive in having **clavate** antennae (thicker at apex, like a club).

The additions of moss-dwelling species continue. Damaška and Konstantinov (2016) added another species of *Cangshanaltica* *siamensis* (Figure 38) from Thailand. In this case, the beetles are able to survive the dry season in the moss cushions.



Figure 38. *Cangshanaltica siamensis*, a moss dweller from Thailand. Photo by Sasha Konstantinov, with permission

Konstantinov and Duckett (2005) found *Clavicornaltica dali* (Figure 39) at 3300 m in China under mosses. The tiny *Clavicornaltica* are distributed in Sri Lanka, Vietnam, and Thailand, despite their wingless males and mostly wingless females. This new species is among the first known for the genus in China and raises the question of dispersal mechanisms. Could they be distributed with the mosses they inhabit?

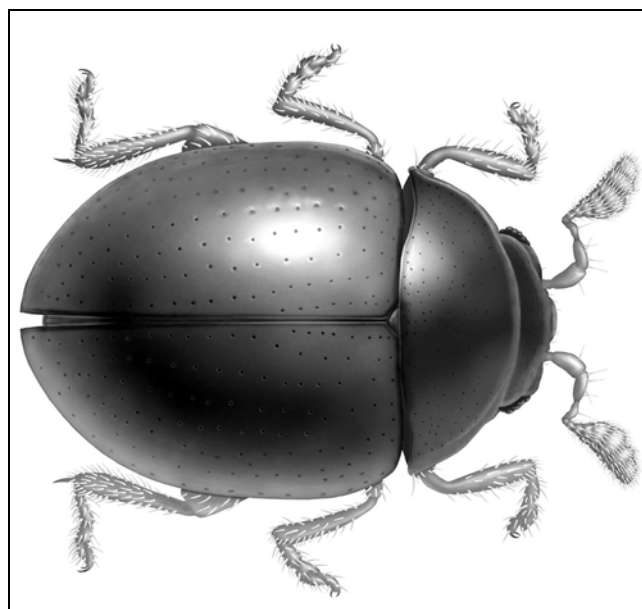


Figure 39. *Clavicornaltica dali*, an Asian species that lives under mosses. Image by Alexander Konstantinov, with permission.

Benedictus (Figure 53), a moss inhabitant in Asia, is not present (or hasn't been discovered) in the New World (Sprecher-Uebersax *et al.* 2009). In fact, it seems that the Eastern and Western Hemispheres have distinct genera.

As is common for the **Alticini** bryophyte dwellers, new species and even genera are lurking in these neglected habitats, and this seems especially true for the Western Hemisphere. Konstantinov and Lourdes Chamorro-Lacayo (2006) sieved moss samples in forests of the Dominican Republic and were able to describe the new genus ***Kiskeya*** (Figure 40), small, rounded beetles at 1.06-1.10 mm long, with two species, ***K. baorucae*** (Figure 40) and ***K. neibae***. ***Kiskeya baorucae*** was collected from mosses in forests where they were growing on rocks, dangling as pendent mosses, and growing on the boles of trees. ***Kiskeya neibae*** was collected in forests from mosses growing on rocks, tree stumps, boles, and branches (Figure 41). Using a Berlese funnel, the researchers also extracted ***Aedmon*** sp. (**Alticini**; Figure 42) from the mosses.



Figure 40. ***Kiskeya baorucae***, a species that lives on mosses in forests – on rocks, tree boles, and pendent mosses. Photo by Alexander Konstantinov, with permission.



Figure 41. ***Kiskeya neibae*** habitat. Photo courtesy of Sasha Konstantinov.



Figure 42. ***Aedmon ferruginea*** adult, a moss dweller in the Dominican Republic. Photo by Celeigher Piñango, through Creative Commons.

Again in 2011, Konstantinov and Konstantinova found a new genus (***Borinken***) and three new species of moss dwellers in Puerto Rico by sifting mosses. ***Borinken elyunque*** (Figure 43) is a tiny (1.08-1.18 mm) beetle from the forest, living in mosses on rocks, tree stumps, tree boles, and branches. ***Kiskeya elyunque*** (Figure 44), an even smaller species (0.81-0.92 mm), lives in similar habitats. By comparison, ***Ulrica eltoro*** (Figure 45) is much larger (1.94-2.16 mm) and likewise lives among mosses in similar locations, whereas ***Ulrica iviei*** (Figure 46), also a new species, is thus far known only from leaf litter.



Figure 43. ***Borinken elyunque***, a moss dweller in Puerto Rico. Photo courtesy of Sasha Konstantinov.



Figure 44. ***Kiskeya elyunque*** adult, a moss dweller in Puerto Rico. Photo courtesy of Sasha Konstantinov.



Figure 45. *Ulrica eltoro* adult, a moss dweller in Puerto Rico. Photo courtesy of Sasha Konstantinov.



Figure 46. *Ulrica iviei* adult, a litter species in the Dominican Republic. Photo by Sasha Konstantinov, with permission.

The moss-inhabiting *Kiskeya* (Figure 40, Figure 44) is known elsewhere in the Neotropics. There are three species in the West Indies, two in the Dominican Republic, and one in Puerto Rico (Konstantinov & Konstantinova 2011).

Konstantinov *et al.* (2013) described *Cangshanaltica nigra* from Yunnan Province in China.

Konstantinov *et al.* (2015) have recently added five new species of *Monotalla* in the West Indies. Of these, *Monotalla maierae* is a new species that occurs in mosses and litter and *M. viridis* is a new species from epiphytic mosses.



Figure 47. *Monotalla maierae* adult, a moss dweller in the West Indies. Photo by Sasha Konstantinov, with permission.



Figure 48. *Monotalla viridis* adult, a species from epiphytic mosses in the West Indies. Photo by Sasha Konstantinov, with permission.

As is clear by these examples, the Western Hemisphere moss inhabitants have remained almost unexplored. Konstantinov *et al.* (2009) found another new genus in Nicaragua. *Nicaltica selvanegra* (Figure 49), a species similar to *Kiskeya*, likewise lives among mosses there. In Bolivia, Konstantinov *et al.* (2014) discovered another new genus of moss and litter dwellers; *Stevenaltica normi* (Figure 50) and *S. erroris* (Figure 51) both include mosses as well as leaf litter as their habitats.

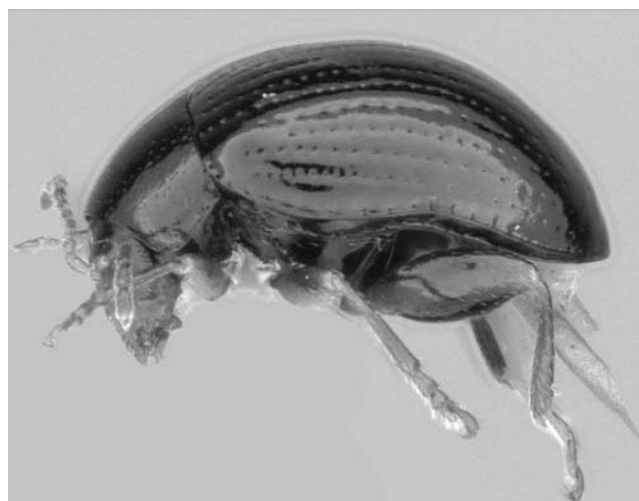


Figure 49. *Nicaltica selvanegra* male, a moss dweller in Nicaragua. Photo courtesy of Sasha Konstantinov.



Figure 50. *Stevenaltica normi* adult, a moss and leaf litter dweller in Bolivia. Photo courtesy of Sasha Konstantinov.



Figure 51. *Stevenaltica erronis*. a moss and leaf litter dweller in Bolivia. Photo courtesy of Sasha Konstantinova.

Distigmoptera borealis (Figure 52) eats mosses in North America (Konstantinov, pers. comm. 26 June 2016). And that's it! Other records for North America are lacking. This species is known from North Dakota (Fauske 2014) and Oklahoma (Palmer 2016).



Figure 52. *Distigmoptera borealis*, the only moss-dwelling genus known in North America. Photo from BIO Photography group, Biodiversity Institute of Ontario, through Creative Commons.

As of 2013, of the 14 known genera of moss-dwelling **Alticini**, only six were true **bryobionts** [*Kiskeya* (Figure 40), *Borinken* (Figure 43), *Cangshanaltica* (Figure 35), *Mniophila* (Figure 3), *Nicaltica* (Figure 49), and *Ulrica* (Figure 45)] (Konstantinov *et al.* 2013). The remaining eight are **bryophiles** [*Benedictus* (Figure 53), *Clavicornaltica* (Figure 39), *Ivalia* (Figure 33), *Monotalla* (Figure 47-Figure 48), *Minota* (Figure 5), *Paraminota* (Figure 54), *Paraminotella* (Figure 55), and *Phaelota* (Figure 29-Figure 32)]. By 2016, the number of known moss-inhabiting **Alticini** genera in the world grew to 15 and the number of species to 30 (Damaška & Konstantinov 2016).

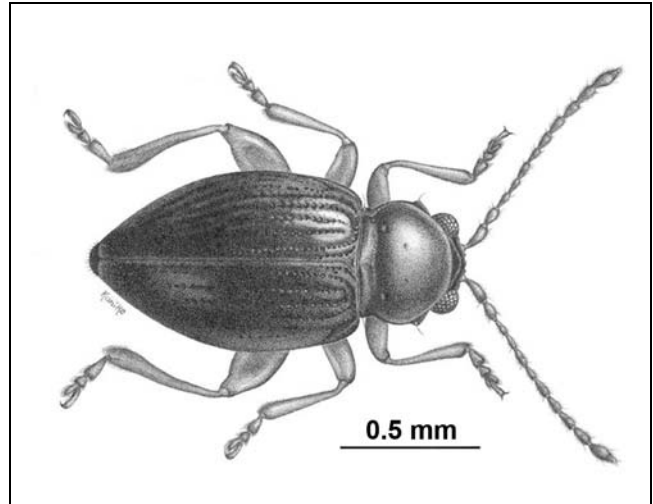


Figure 53. *Benedictus shivalayanicus* adult, Sasha Konstantinov.

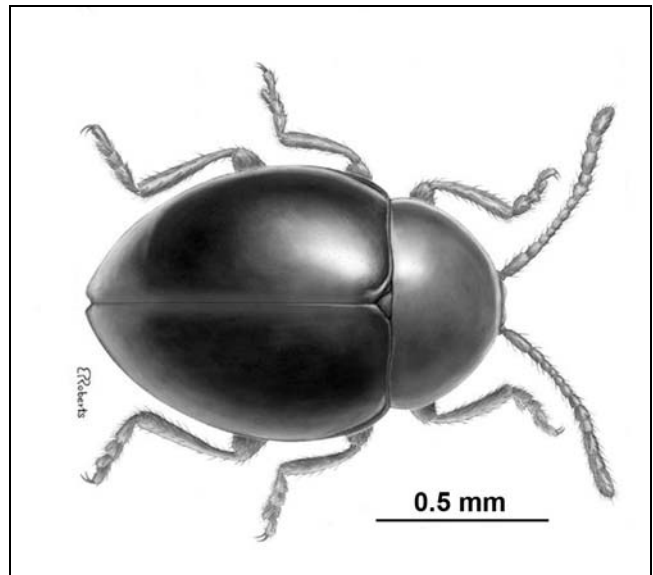


Figure 54. *Paraminota lauribina*, member of a moss-dwelling genus. Image permission from Sasha Konstantinov.

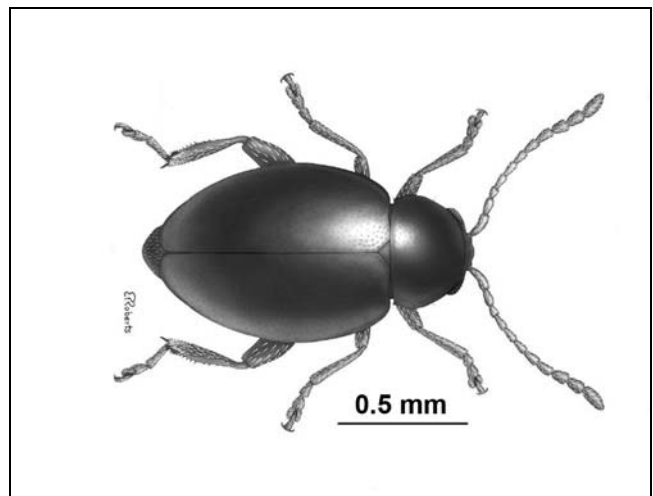


Figure 55. *Paraminotella nigrita* adult, member of a moss-dwelling genus. Image permission from Sasha Konstantinov.

There is good reason why so many new beetle species remain to be found among bryophytes. Many of these bryophyte dwellers are flightless. Furthermore, their moisture requirements are somewhat specific. Many are mountain-dwellers, living only above certain elevations. This combination makes it difficult for the beetles on one mountain to mix with those on another. When one or a few do disperse to a new mountain, both the **founder principle** (small population arrives in a new area and does not represent the genetic frequencies of its parent population) and **genetic drift** (random changes in gene frequencies that are common in small populations) are likely to play a role. As time passes, original and new populations diverge genetically, and over geologic time – or less – they can become separate species. When a single individual arrives in a new location, perhaps carrying fertilized eggs or for some beetles being **parthenogenetic** (reproducing from an unfertilized egg), this individual does not represent the middle of the curve of variation and produces offspring that are recognizably different from most of the individuals at the source. Do they pass the test of reproductive isolation? As long as they are separated by a valley, yes. Could they interbreed if they were joined? That remains to be tested.

Cucujoidea

Latridiidae – Minute Brown Scavenger Beetles

These small (0.8-3 mm) beetles number 1000 species (McClarin 2005). Most are associated with leaf litter, but around habitation they associate with other rotting vegetable matter. They are elongate with sculptured thorax and outer wings. Aside from their small size, they are not well adapted for bryophytes, although their coloration is usually dull and may be mottled. The sculpturing may also help to disguise them.

Some **Latridiidae** (Figure 58) take advantage of moss inhabitants for food. This family of beetles feeds on **Myxomycetes** (slime molds; Figure 56-Figure 57) (Dudka & Romanenko 2006), and these are often found among bryophytes. Decaying logs provide good habitats for slime molds and for mosses. And the slime molds often invade the space of the bryophytes. The mosses may also improve the habitat for the slime molds by increasing the moisture retention. Hence, the bryophytes on these logs provide protected sites where the **Latridiidae** can feed on the slime molds.

Dudka and Romanenko (2006) found 13 species of slime molds on 9 species of mosses and 3 of liverworts at the Crimean Nature Reserve. Most of these slime molds occur on non-bryophyte substrates as well, but some, like **Physarum cinereum** (Figure 56-Figure 57), occur predominantly on bryophyte substrates. Dudka and Romanenko (2006) found that **Enicmus** (Figure 58) and **Dienerella** (Figure 59) were the most common **Latridiidae** on moss-dwelling slime molds. The beetles not only use the slime molds for food, but also for oviposition and cover.



Figure 56. *Physarum cinereum* plasmodium, a bryophyte-inhabiting slime mold that feeds slime-mold-eating **Latridiidae**. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.



Figure 57. *Physarum cinereum* with fruiting bodies, a bryophyte-inhabiting slime mold that feeds slime-mold-eating **Latridiidae**. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.



Figure 58. *Enicmus maculatus* adult, one of the most common **Latridiidae** genera that lives on moss-dwelling slime molds. Photo from Museum of Comparative Zoology Harvard, through Creative Commons.



Figure 59. *Dienerella ruficollis* adult, one of the most common **Latridiidae** genera on moss-dwelling slime molds. Photo by Tom Murray, through Creative Commons.

Curculionoidea

Atelabidae – Leaf-rolling Weevils

This family got its name because the female lays her eggs in leaves, then rolls the leaf around them. It is unlikely that these are regular moss dwellers. It is more likely that these are one of many of the beetles that traverse mosses simply because they are there. Although the mosses can provide moisture and a home for prey items, many species of beetles may arrive there without actually choosing to be in a mossy habitat. Such may be the case for the atelabid *Eugnamptus angustatus* (Figure 60), a 4.8 mm beetle Stephen Cresswell found walking on a moss in West Virginia, USA. Or it may have been searching there for food or replenishing body moisture. Behavioral studies on beetles associated with bryophytes are greatly needed.



Figure 60. *Eugnamptus angustatus* on moss – does it live there, or is it just visiting? Photo by Stephen Cresswell, with permission.

Curculionidae – Weevils

These are the cute little beetles with long "snouts" (Figure 61), somewhat resembling a miniature aardvark. A number of species have been discovered on bryophytes, eat them [Chown (1993) reported records of 35 species eating bryophytes], and some weevils even carry mosses around as camouflage.



Figure 61. *Cionus hortulanus* adult showing long snout with antennae on it. Photo by Lukas Jonaitis, through Creative Commons.

It seems that most beetles treat mosses as if they were litter, much like many soil biologists do. *Ceutorhynchus erysimi* (Figure 62), a species of Europe and invasive in the US, lives among mosses and forest litter around rhododendrons (in The Netherlands) (USDA 1950). *Cryptorhynchus lapathi* (Figure 63) lays its 1 mm long eggs mostly at stem bases, but also high in the crowns of large trees, under soil, or in the moss layer (Broberg 1997).



Figure 62. *Ceutorhynchus erysimi* adult among mosses, a species that lives among mosses and forest litter. Photo by Mick E. Talbot, through Creative Commons.



Figure 63. *Cryptorhynchus lapathi* adult, a species that sometimes lays eggs on mosses. Photo by Gyorgy Csoka, through Creative Commons.

I have been finding the best records of bryophyte-dwelling insects among those of the UK, especially the old records. For example, Moncreaff (1871) reported *Baridius lepidii*, *Phytobius waltoni* (= *Pelonomus waltoni*; Figure 64), and *Litodactylus leucogaster* (= *Phytobius leucogaster*) from mosses in Portsea, British Isles. *Bagous laticollis* was abundant in mosses. Tomlin (1913) was able to find *Liosoma ovatum* among mosses in Glamorgan, Wales, year round.



Figure 64. *Phytobius waltoni* adult, a moss dweller in the British Isles. Photo by Stefan Schmidt, through Creative Commons.

Dyer and Nijholt (2016) reported finding adults of *Pseudohylesinus sericeus* (Figure 65) and *P. grandis* (Figure 66), both pests on conifers in the western part of North America (USDA 2016), hibernating in thick mosses that grew on the trunks of oak trees in Oregon, USA. But in British Columbia, *P. granulatus* (Figure 67) instead penetrated the mosses on the amabilis fir and once there bored into the bark.



Figure 65. *Pseudohylesinus sericeus* adult, a conifer pest that hibernates among mosses. Photo by Javier Marcado, USDA APHIS ITP, Bugwood.org, through Creative Commons.



Figure 66. *Pseudohylesinus grandis* adult, a conifer pest that hibernates among mosses. Photo by Tim Loh, with permission.



Figure 67. *Pseudohylesinus granulatus* adult, a species that enters mosses to bore into the amabilis fir bark. Photo by Steven Valley, USDA APHIS ITP, Bugwood.org, through Creative Commons.

Some beetles only use bryophytes in part of their life cycle. Larvae of the weevil *Palirhoeus eatoni* (syn. = *Mesembriorrhinus eatoni*) develop in tufts of algae (Doyen 1976). But when it is time for pupation, the larvae in Antarctic waters move above the high water line to pupate in clumps of the moss *Grimmia amblyophylla*. Mosses are often a safe haven for Antarctic arthropods in winter.

On the Austral Islands of the South Pacific, a number of new, hence **endemic**, species of *Miocalles* (Figure 68) were located by fogging mosses in the rata forest (Englund 2003). These included *M. albolineatus*, *M. akao*, *M. carinatus*, *M. hemata*, *M. cf irregularis*, *M. perau/maii*, *M. pusillus*, *M. setifer*, *M. cf silvestris*, *M. nr varians*, *M. nr sanctijohni*.

The weevils are among the unique fauna of the Antarctic region. The genus *Bothrometopus* has several members that live among rocks on Marion Island, including *B. randi*, *B. parvulus*, and *B. elongatus* (Van der Merwe *et al.* 1997). All three of these species occur on rock surfaces, in crevices, and within the rock-dwelling bryophytes. On Heard Island, *Bothrometopus brevis* and *B. gracilipes* both feed on cryptogams (Chown & Klok 2001).



Figure 68. *Miocalles* adult, a genus with a number of new endemic bryophyte-dwelling species on the Austral Islands. Photo by April Yang, through Creative Commons.

Bryophagy and Evolution

Bryophagy is known in at least 35 species of **Curculionidae** from the sub-Antarctic (Kuschel 1964, 1971; Chown & Scholtz 1989a). Chown and Scholtz (1989a) suggest that a specialized moss herbivory, rare among **Curculionidae**, may have evolved in response to the adverse conditions during Pleistocene glaciations when bryophyte species were more likely to survive than their tracheophyte counterparts. Let's examine a few examples and then return to the evolution of this bryophyte-curculionid herbivory relationship.

Dichotrachelus stierlini (Figure 69) is a moss-eating weevil, known from 3350 m in the Alps (Thaler 1999). It is easily collected in alpine regions by sieving mosses (Barbara Thaler-Knoflach, pers. comm. 9 June 2011). As seen in Figure 69, this weevil has numerous protuberances that give it texture similar to that of a moss. A shiny weevil would be much more obvious among the mosses.



Figure 69. *Dichotrachelus stierlini*, a curculionid beetle (weevil). Note how this highly textured beetle would blend with the similarly highly textured bryophytes. Photo by Barbara Thaler-Knoflach, with permission.

Smith (1977) examined the consumption of *Ectemnorhinus similis* (formerly *Dusmoecetes similis*) adults on sub-Antarctic Marion Island. These weevils reached densities up to 220 m⁻², representing a biomass of about 1 g m⁻². Their diet included 14% of their body weight per day of *Acaena magellanica* (flowering plant in Rosaceae; Figure 70) and 37% per day of the moss

Brachythecium rutabulum (Figure 71). In fact, it appears that nearly all members of the tribe **Ectemnorhinini** are cryptogam feeders, especially on bryophytes (Chown & Scholtz 1989a). This is unusual in the **Curculionidae**, a family that predominantly feeds on tracheophytes.



Figure 70. *Acaena magellanica*, part of the diet of *Ectemnorhinus similis*. Photo by El Grafo, through Creative Commons.



Figure 71. *Brachythecium rutabulum*, home and food for *Ectemnorhinus similis*. Photo by J. C. Schou <www.biopix.com>, with permission.

Chown (1989) suggests that the near absence of flowering-plant feeders in the **Ectemnorhinini** is due to the previous climatic conditions, claiming that they would preclude flowering plant herbivory. What we know about the habitat use, diet, and species morphology supports this view (Table 1; see also Chown & Klok 2001). Using *Ectemnorhinus* (see Figure 72) in the sub-Antarctic as an example (Chown & Scholtz 1989b; Chown 1990), Chown and Scholtz showed feeding and morphological differences between the larger species, *E. similis*, that feeds on angiosperms [but also on bryophytes (Grobler *et al.* 2006)], as adults and detritus as larvae, and the smaller species, *E. marioni*, that feeds on bryophytes in all its life cycle stages. Both of these species are found on *Azorella selago* (see Figure 74), but *E. marioni* feeds exclusively on the epiphytic bryophytes, whereas *E. similis* only eats bryophytes when the quality of the tracheophytes deteriorates (Chown & Scholtz 1989b).

Table 1. Feeding strategies of the tribe **Ectemnorhinini** of **Curculionidae** from sub-Antarctic Marion and Prince Edward Islands. % of cryptogams (**crypt**) and bryophytes (**bryo**) represent the percentage of individuals examined that fed on each of these groups. Note that bryophytes are included in cryptogams. Data were gathered from field observations and gut analyses. The bryophyte associations are defined by Gerson (1982) with **bryobionts** occurring exclusively in association with bryophytes, **bryophiles** usually living on bryophytes but also occurring elsewhere, **bryoxenes** regularly spending part of their life cycle on bryophytes, and **occasionals** spending part of their time on bryophytes but not dependent on them. n = number in sample. Modified from Chown and Scholtz 1989a.

Species	Stage	n	food		bryo assn
			% crypt	% bryo	
<i>Palirhoeus eatoni</i>	larvae	17	100	6	bryoxene
	adults	40	100	0	occasional
<i>Bothrometopus randi</i>	larvae	38	100	16	bryoxene
	adults	46	100	2	occasional
<i>Antarctonesiotes elongatus</i>	larvae	28	100	18	bryoxene
	adults	62	100	7	occasional
<i>Mesembriorrhinus brevis</i>	larvae	50	100	61	bryophile
	adults	116	98	21	bryoxene
<i>Ectemnorhinus marioni</i>	larvae	67	97	97	bryobiont
	adults	1314	88	88	bryobiont
<i>Ectemnorhinus similis</i>	larvae	82	9	9	occasional
	adults	1037	38	38	bryoxene

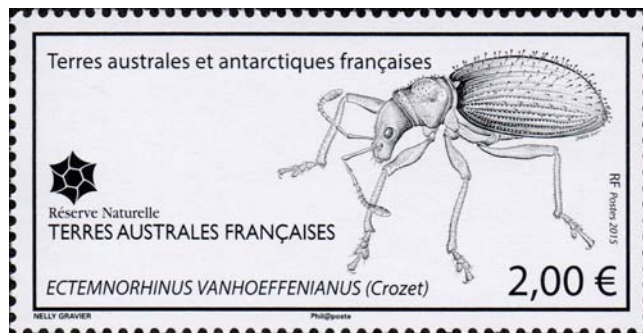


Figure 72. *Ectemnorhinus vanhoeffianus* on French stamp. Photo by Alex Pozyr, with permission.



Figure 73. *Ectemnorhinus vanhoeffianus*. Photo by Alex Pozyr, with permission.

In a later publication, Crafford and Chown (1991) cast doubt on the thesis that a colder climate would preclude these weevils from feeding on flowering plants due to energy constraints. Although five of the six species of weevils in the **Ectemnorhinini** on the sub-Antarctic Marion Island feed on cryptogams, temperature does not seem to be involved. They tested the consumption rate and approximate digestibility for the two native species of *Ectemnorhinus* (Figure 72) and found that the digestibility of the leafy liverwort *Blepharidophyllum densifolium* and dry mass differed little between 5°C and 10°C. Similar results were present for *E. similis* adults fed *Azorella selago* (see Figure 74). On the other hand, the performance ratios for *E. similis* feeding on *Azorella selago* was greater at 5°C than that for *E. marioni* feeding on bryophytes at either temperature. Crafford and Chown (1991) modified their interpretation to suggest that moss feeding more likely evolved in response to an absence of angiosperms during glacial periods, rather than because of a nutritional advantage associated with bryophagy at low temperatures. This is supported by studies on these beetles on islands. These feeding habits constrain species in their habitat distributions in the South Indian Ocean Province Islands where they seem to have been a result of climatic forcing (Chown 1994).



Figure 74. *Azorella compacta* from Tierra del Fuego, a flowering plant that resembles a moss. *Azorella selago* serves as food for *Ectemnorhinus similis* and *E. marioni*. Photo by Heretiq, through Creative Commons.

In *Agrostis* (Figure 75) mires the genus *Ectemnorhinus* (Figure 72) feeds exclusively on bryophytes, mostly the leafy liverwort *Blepharidophyllum densifolium*, even in the presence of the grass *Agrostis magellanica*. Chown (1990) considers the bryophytes to be a relatively poor food source, but they have the advantage of being available year-round. Another factor is that flowering plants have their highest nitrogen concentrations in the spring, whereas the bryophytes have their highest in autumn. Only the bryophytes have secondary compounds that serve as dietary inhibitors, resulting in the bryophyte feeders being smaller than the flowering-plant feeders. In fact, Chown suggests that the differences in feeding strategies lead to both size differences in the beetles and spatial separations between the two feeding groups. These differences keep the species groups from interbreeding.



Figure 75. *Agrostis*, a common genus in mires, but *Ectemnorhinus* species there feed mostly on leafy liverworts. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Bryophytes are well known for their insecticidal properties. Abay *et al.* (2012) demonstrated that extractions of the cosmopolitan moss *Hypnum cupressiforme* (Figure 76) had high levels of contact activity against the granary weevil *Sitophilus granarius*. This research was expanded to include the mosses *Dicranum scoparium* (Figure 77), *Polytrichastrum formosum* (Figure 78), *Homalothecium lutescens* (Figure 79), and the thallose liverwort *Conocephalum conicum* (Figure 80) (Abay *et al.* 2013). Using *Sitophilus granarius* in their bioassays, Abay and coworkers determined that hexane extracts of *Polytrichastrum formosum* exhibited the highest insecticidal activity (70.3%). Mortality was highest (53.34%) from the fatty acid **myristic acid**. **Palmitic acid** resulted in 17.75% mortality and **lauric acid** 4.32%. Abay and coworkers consider liverworts to be preferred foods nutritionally because of the presence of oil bodies (Kang *et al.* 2007; Abay *et al.* 2013). Yet there seem to be few reports of insects feeding on liverworts.



Figure 76. *Hypnum cupressiforme*, a species known to have contact insecticidal properties against some beetles. Photo by J. C. Schou <www.discoverlife.org>, with permission.



Figure 77. *Dicranum scoparium*, a species known to have contact insecticidal properties against some beetles. Photo by Janice Glimme.



Figure 78. *Polytrichastrum formosum*, a species known to have contact insecticidal properties against some beetles. Photo by Alexander Klink, through Creative Commons.

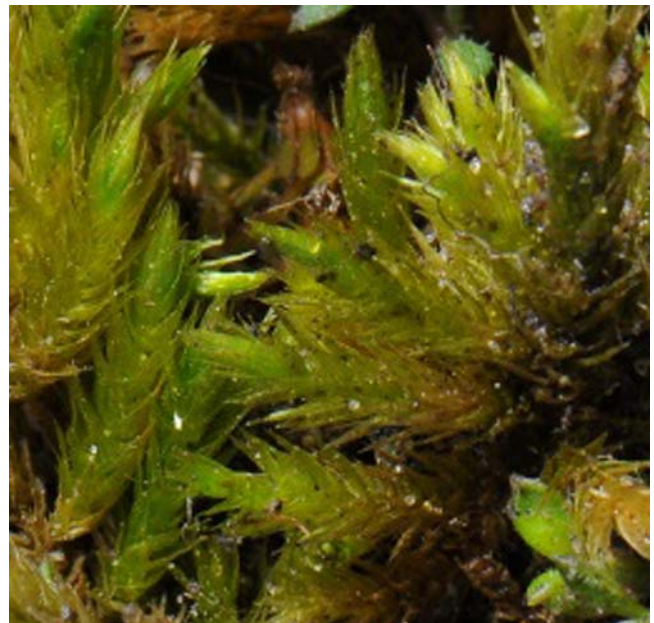


Figure 79. *Homalothecium lutescens*, a species known to have contact insecticidal properties against some beetles. Photo by J. C. Schou <www.biopix.com>, with permission.



Figure 80. *Conocephalum conicum*, a species known to have contact insecticidal properties against some beetles. Photo by Li Zhang, with permission.

Wahedi *et al.* (2013) expanded on the research on the effects of bryophyte compounds with *Sitophilus zeamais*. They tested powders from *Calymperes afzelli* (Figure 81), *Thuidium gratum*, *Bryum coronatum* (Figure 82), and *Semibarbula lambarenensis*. All four species were effective in reducing oviposition and F_1 progeny emergence rate, prolongation of pre-adult duration, and having toxicity. The order of efficacy in toxic effects was *B. coronatum* > *T. gratum* > *C. afzelli* > *S. lambarenensis*, although the symptomatic effects were different among these. The bryophyte powders were so effective that the authors suggested using them as insecticides against the weevils in maize.

New compounds are constantly being discovered in the bryophytes (You *et al.* 2007; Jockovic *et al.* 2008). Many of these are phenolic acids, often unique with the bryophytes. Others are flavonoids or unique or scarce fatty acids. The research on the effects of these compounds on herbivory are limited, especially for mosses. And we don't know if any of these are inducible or if they are always present at similar levels. Likewise, we don't know how they are affected by seasons. Understanding these phenomena could help to explain some of the seasonal food choices of part-time bryophages.



Figure 81. *Calymperes afzelli*, a species that can reduce oviposition and cause other toxic reactions in powder from on at least some beetles. Photo by Scott Zona, with permission.



Figure 82. *Bryum coronatum*, a species with antibiotic properties against at least some beetles. Photo by Michael Lüth, with permission.

Impacts on Ecosystems

The weevils can play important roles in *Sphagnum* (Figure 13, Figure 83, Figure 128) habitats. For example, warming trends have an interesting way of increasing spruce bark beetles in *Sphagnum* fens (Figure 84), ultimately resulting in more frequent fires. Beetles in the Kenai Peninsula of Alaska typically take two years to develop in their *Sphagnum* habitat, but during recent warming the fen increased in temperature (Berg 2008). These longer, warmer summers reduced the life cycle to one year and caused exponential growth in the spruce bark beetle. The beetles declined ultimately as a result of destruction of their food source. At the same time, the warmer summers dried the fens and reduced their role as firebreaks, causing invasion of woody shrubs and white spruce. Instead of being fire breaks, the spruce and woody shrubs became fuel bridges. A 400-600-year fire interval was reduced by the beetles to one of 50 years. The warming and beetle invasion makes the lowland areas more vulnerable to fire, whereas the upland areas are likely to change toward grasslands and hardwoods with lower fire potential.



Figure 83. Spruce, Denali National Park, showing an advancing front of bark beetle damage (right and distance). Photo from National Park Service, through public domain.



Figure 84. Spruce beetle damage, Denali National Forest, Alaska. Photo by Davyd Betchkal, NPS, through public domain.

Another example of the role of these beetles, albeit indirect, is the role of bark beetles following logging (Jonášová & Prach 2008). In the Central European mountain spruce forests (*Picea abies*; Figure 85), logging had a greater impact on the bryophyte cover than did forest damage by bark beetles. Rather, the mountain spruce forests will recover from a bark beetle outbreak without intervention.



Figure 85. *Picea abies* forest, trees that provide cover for bryophytes even when damaged by bark beetles, but not when logging occurs. Photo by Crusier, through Creative Commons.

Camouflage

What better way to look like a bryophyte than to grow them on your back! Weevils of the moss forests of New Guinea "cultivate" the mosses (Gressitt *et al.* 1965, 1968; Gerson & Seaward 1977) and one liverwort species (Gerson 1969) as camouflage. The large moss forest weevils may even have special secretions that encourage the growth of the mosses on their backs (Gressitt *et al.* 1965).

Gressitt *et al.* (1968) reported mosses growing on a *Gymnopholus* weevil (Figure 86). These moss garden weevils seem to be restricted to high moss forest ridges and moist summits of New Guinea. Two of the involved genera are endemic there. These garden transporters include not only *Gymnopholus*, but *Pantorhytes* (Figure 87) and some of the cryptorhynchine weevils. The weevils provide a favorable environment for the mosses and the mosses provide a protective cover and possibly a chemical predator deterrent for the weevils.



Figure 86. The moss *Daltonia angustifolia* living epizootically on the weevil *Gymnopholus reticulatus*. Photo courtesy of Rob Gradstein.



Figure 87. *Pantorhytes* adult with epizootic lichens. Photo by Alex Riedel, with permission.

The leaf-eating weevils *Gymnopholus* (Figure 86) and *Pantorhytes* (Figure 87) have pits in their carapaces and these pits are colonized by algae, lichens, liverworts, and mosses (Gressitt *et al.* 1965, 1968; Gressitt & Sedlacek 1967). Some weevil species (e.g. *Gymnopholus reticulatus*, Figure 86) seem to be moss specialists, especially the moss *Daltonia angustifolia* (Figure 86) (Gradstein *et al.* 1984), and others are lichen specialists. Tiny mites live among these epizootic mosses and may serve as moss dispersal agents to new hosts. The epizootic mosses take advantage of the soft substrate of the beetle. The small branches of montane rainforest trees seem to provide the sources for the mosses and the humidity keeps the garden growing. *Daltonia angustifolia* (see Figure 88) matures quickly, further supporting its suitability for its mobile, short-lived habitat.



Figure 88. *Daltonia* cf. *longifolia* from the Neotropics. Photo by Michael Lüth, with permission.

It appears that the weevils have gained sufficient benefit from their gardens that their evolution has preserved characters that encourage the camouflage growth. In addition to secretions mentioned earlier (Gressitt *et al.* 1965), the genus *Gymnopholus* (Figure 86) provides depressions and grooves on its outer wings, along with specialized scales and hairs (Gressitt 1966). The bryophytes grow on the fused **elytra**, but often also grow on the pronotum. *Symbiopholus* likewise is modified to encourage cryptogamic growth. It has depressions, pits, and grooves. The dorsal surface is rough and may have specially modified hairs or scales. It likewise has secretions that seem to encourage growth of its garden. It appears that the hairs and scales are modified in ways that encourage growth of the flora, and these are the locations where the bryophytes and lichens begin their growth (Gressitt & Sedlacek 1970). The species of *Gymnopholus* that do not have plant associations have normal, flat scales or have a smooth, hairless body surface.

The latest member of this family to be described with attached bryophytes is *Lithinus rufopenicillatus* (Figure 89) from Madagascar. Paul Bertner and his associates are studying this unusual weevil, so look for more information in the future.



Figure 89. *Lithinus rufopenicillatus* with liverworts and mosses in its "backpack." Photo by Paul Bertner, with permission.

But do these gardens help the beetles? Using a reduviid bug, Jackson and Pollard (2007) demonstrated that carrying natural objects such as moss bits or dead ants does indeed reduce predation on the camouflaged bugs. However, such experiments remain to be performed on the camouflaged weevils.

Travelling Ecosystems

Some of these elytral moss gardens are moving microecosystems. Aoki (1966) found an epizootic symbiosis in which the oribatid mite *Symbioribates papuensis* lived on lichens on the backs of weevils in Papua, New Guinea. Gressitt (1970) likewise found epizootic mites in the plant growth on three members of the weevil genus *Gymnopholus* (Figure 86), a genus that lives on leaves of woody plants in moss forests and on alpine shrubs (Gressitt 1966).

Not only were mites part of this travelling ecosystem, but also lichens, fungi, rotifers, nematodes, diatoms, and other microorganisms (Gressitt 1966; Gressitt & Sedlacek 1967). Psocopterans even feed on the plants growing on the weevils. One individual of *Gymnopholus acarifer* had 60 oribatid mites among the resident fungi. The absence of flight in *Gymnopholus* (Figure 86) has resulted in different species evolving on different ridges in New Guinea. This mountain-valley system of geographic separation has resulted in 47 such specialists recognized in *Gymnopholus* in New Guinea (Gressitt & Sedlacek 1967).

Of the 850 *Symbiopholus* specimens examined, 675 had plant growth on their backs (Gressitt 1966). These included the liverworts *Metzgeria* (Figure 90) and members of the epiphytic/epiphyllous family *Lejeuneaceae* (Figure 91). Mites, only 0.2 mm long, were abundant among the fungal growth on the *Symbiopholus*. The mites are able to spread to other weevils when the weevils mate, and the spores of the fungi may likewise spread that way as well as being carried on the bodies of the mites. The mites are absent from three of the weevil species that have hairy-sided, flat-bottomed pits.

Elateroidea

Lampyridae – Fireflies

This family was one of those nice surprises one can find while browsing the internet. I was searching for images on insects on mosses when I found one of eggs of the Japanese firefly on mosses. The eggs of *Luciola cruciata* (Figure 92) were nestled among the apical portions of mosses, and one video image shows a tiny larva crawling about. Another short video shows the emerging larva getting its first view of its larval moss home <<http://www.gettyimages.com/detail/video/closeup-shot-moment-of-firefly-hatch-stock-video-footage/505766040>>. But does the larva stay there and eat the mosses?



Figure 90. *Metzgeria conjugata*, in a genus that is eaten by *Symbiopholus*. Photo by David T. Holyoak, with permission.



Figure 91. *Colura vitiensis* growing on a leaf in the Fiji Islands. Species in this family can colonize members of **Curculionidae**. Photo courtesy of Tamás Pócs.



Figure 92. *Luciola cruciata* larva, a species that can lay eggs on mosses in Japan. Photo by Keisotyo, through Creative Commons.

This species flashes, using luciferase to activate the light (Tatsumi *et al.* 1989). The frequency of the light is dependent on temperature, with more frequent flashes at lower temperatures (Iguchi 2010).

Lycidae – Net-winged Beetles

The **Lycidae** are larger beetles, 10-15 mm long (Wikipedia 2015d). They are protected from predators by their toxicity. The larvae live under bark or in leaf litter and are predaceous.

This family is unusual in that the females are **neotenuous**, whereas the males go through full metamorphosis of larvae, pupae, and adults (Masek & Bocak 2014). **Neotenuous** refers to reaching sexual maturity at an immature morphological stage. In this case, the females are sexually mature as mature larvae and never change into pupae and adults.

Platerodrilus paradoxus (syn. = *Duliticola paradoxa*) (trilobite beetle; Figure 93) seems to be an exception to the carnivorous habit, but perhaps it is just hunting for prey. Nevertheless, the prey must be small.



Figure 93. *Platerodrilus paradoxus* (larval trilobite beetle) foraging on moss from Borneo. Note the tiny head protruding from the triangular prothorax at the bottom of the picture. Photo by Nick Garbutt, with permission.

Platerodrilus paradoxus (Figure 93) has only been observed in copulation twice, but that proves that mating does occur. Crew (2014) described the mating process of *Platerodrilus ruficollis* (syn. = *Platerodrilus hoiseni*), based on research by Wong (1998). One can only guess if it is similar in *P. paradoxus*. The female of *Platerodrilus ruficollis* arches her abdomen upward to expose her gonopore. The male, which is much smaller (about 10% the size of the female) climbs onto the female and attaches to the gonopore. About three hours after copulation is completed, the male drops dead. The female incubates the eggs for about three days, then places them among leaf litter. Then she too dies a few weeks later.

Bupestroidea

Bupestriidae – Jewel Beetles

Trachys troglodytes (Figure 94-Figure 95) is a species that likes high humidity. It is widespread and lives in damp, grassy places and *Sphagnum* bogs (Smith & Freeman 1987). As an adult, it hibernates among *Sphagnum*.



Figure 94. *Trachys troglodytes* larva, a species that occurs in *Sphagnum* bogs. Photo by Steve Wullaert, through Creative Commons.



Figure 95. *Trachys troglodytes* adult, a hibernator in *Sphagnum* bogs. Photo by Boris Loboda, through Creative Commons.

Hydrophiloidea

Helophoridae – Water Scavenger Beetles

This is a family of small insects (2-9 mm) with only one genus. They are mostly **Holarctic** (zoogeographical region comprising Nearctic and Palearctic regions combined), but a few occur in the tropics. *Helophorus brevipalpis* (2-3.5 mm; Figure 96) is ubiquitous and common, often occurring far from water in mosses (Stenhouse 2007).



Figure 96. *Helophorus brevipalpis* adult, a member of an aquatic family, but it can live far from water among mosses. Photo by James K. Lindsey, with permission.

Some members of the genus are flightless, but *Helophorus brevipalpis* (Figure 96) always has functioning flight "apparatus" (Landin 1980). This flight ability permits this mostly aquatic species to travel great distances. It is interesting that it rarely has food in its gut when it is flying, suggesting that mosses may provide it with moisture but probably do not provide food.

Hydrophilidae – Water Scavenger Beetles

This family, widespread in Europe, is generally considered to be aquatic. Some of these beetles are amphibious, but require a very moist environment. For

example, *Chaetarthria simillima* (Figure 97) is a tiny water beetle, but it has been found among mosses growing beside a lake in the Outer Hebrides (Bratton 2012).



Figure 97. *Chaetarthria seminulum* adult, an aquatic beetle that can live among mosses near water on land. Photo from Naturalis, Biodiversity Centre, through Creative Commons.

Crenitis punctatostratus (Figure 98) is a true bryobiont. It spends its entire life among *Sphagnum* (Matthey 1977).



Figure 98. *Crenitis punctatostratus* adult, a *Sphagnum* dweller. Photo from SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

Scaraboidea

Scarabaeidae

Darwin reported *Pinotus torulosa* from mosses (Smith & Freeman 1987). This name has apparently been superseded and I can't find its current name or any further information.

Staphylinoidea

Leiodidae – Round Fungus Beetles

This worldwide family (1.2-7 mm long) seems to have dropped off the radar in recent studies. However, Sharp (1865) found *Agathidium varians* (Figure 99) to be abundant among mosses in Great Britain. Most are fungal

feeders (Wikipedia 2015b), a food frequently available among mosses. Most of the members of this genus are known as slime mold beetles (Miller & Wheeler 2005) and their association with slime molds may explain the association of this species with mosses, often the substrate for slime molds.



Figure 99. *Agathidium varians* adult on moss, a once-abundant moss dweller in Great Britain. Photo by Tim Faasen, with permission.

Darwin reported several members of this family from mosses, including *Nargus anisotomoides* (Figure 100), *N. wilkini* (Figure 101), *Ptomaphagus medius* (Figure 102), and *Choleva angustata* (Figure 103), but none of these were bryobionts, having not only mosses but also dead leaves and other substrata among their choices (Smith & Freeman 1987).



Figure 100. *Nargus anisotomoides* adult, a species that includes mosses among its substrata. Photo by NSB, Zoologische Staatssammlung Muenchen, through Creative Commons.



Figure 101. *Nargus wilkini* adult, a species that includes mosses among its substrata. Photo by SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

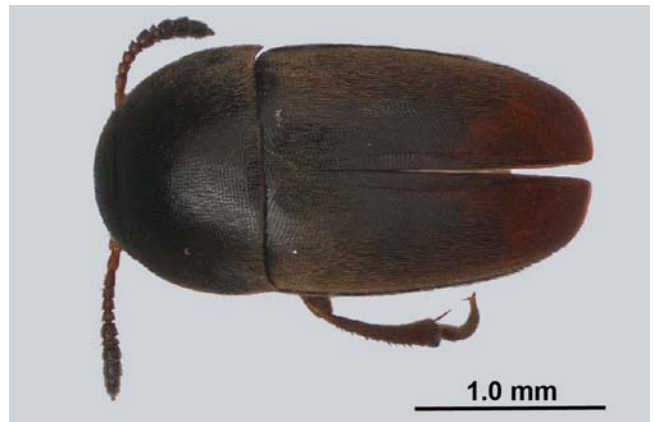


Figure 102. *Ptomaphagus medius* adult, a species that includes mosses among its substrata. Photo from Naturalis, Biodiversity Centre, through Creative Commons.



Figure 103. *Choleva angustata* adult, a species that includes mosses among its substrata. Photo by Stefan Schmidt, SNSB, through Creative Commons.

Pselaphidae – Short-winged Mold Beetles

This is a worldwide family, but it reaches its greatest diversity in the tropics (Benisch 2015b). More than 9000 species are known. Most prefer moist habitats such as the edges of bogs and marshes, under bark of dead trees, and especially in leaf litter and rotten wood. Like the **Staphylinidae**, they have a short elytra, leaving most of the abdomen exposed (Figure 104-Figure 105).

Ferguson (1901) reported three genera in this family living among mosses in the Clyde area of the British Isles: *Bythinus* (Figure 104), *Bryaxis* (Figure 105), and *Pselaphus* (Figure 106).



Figure 104. *Bythinus macropalpus* adult, member of a genus with moss dwellers. Photo by Christoph Benisch <kerbtier.de>, with permission.



Figure 105. *Bryaxis collaris* adult, member of a genus with moss dwellers. Photo by Christoph Benisch <kerbtier.de>, with permission.



Figure 106. *Pselaphus heisei* adult, a British moss dweller. Photo by Rudolf Macek, with permission.

Ptiliidae – Featherwing Beetles

Bogs provide another set of isolated habitats, and they seem to have more than their share of parthenogenetic females. For example, *Ptiliopycna moerens* is a minute (<1.0 mm) featherwing beetle in the northeastern USA and adjacent Canada (Dybas 1978). This moss dweller lives primarily in *Sphagnum* (Figure 84) bogs/poor fens and swamp forests. In most of its range, only females are known, thus making these populations parthenogenetic. Males are known only from the northern part of the range. Other parthenogenetic small beetles in bogs include species of *Pteryx* (Figure 107), *Acrotrichis* (Figure 108), and *Ptinella* (Figure 109) – all in Ptiliidae. Dybas surmised that the incidence of parthenogenesis in small beetles in relict bogs is unusually high. This is advantageous because it means they can remain in the safety of the mosses without having to venture farther and expend a lot of energy to find a mate, often unsuccessfully.



Figure 107. *Pteryx suturalis* adult, a moss dweller in bogs. Photo by Udo Schmidt, through Creative Commons.



Figure 108. *Acrotrichis sitkaensis* adult among mosses. Photo by Tim Faasen, with permission.



Figure 109. *Ptinella pustulata* adult, a parthenogenetic beetle in bogs. Photo by S.E. Thorpe, through Creative Commons.

Staphylinidae – Rove Beetles

This is a family of 58,000 species and thousands of genera, a family even larger than the **Carabidae**. They don't look like most of the other beetles because their hard, outer wings do not cover the abdomen, leaving more than half the abdomen exposed (Figure 110-Figure 111). Their size range is large (<1-35 mm). Even on mosses, the range is large. Like the **Carabidae**, these beetles are elongate and seem to lack morphological adaptations to a bryophyte habitat. They live in every imaginable habitat, including submersion at high tide (Frank & Ahn 2011), and eat almost anything, depending on the species.

The earliest records of occurrences of the **Staphylinidae** among mosses seem to be those of Champion (1871) and Waterhouse (1871). Waterhouse reported *Anthophagus alpinus* (Figure 110) from mosses in Scotland. Champion reported *Syntomium aeneum* (Figure 111) and *Atheta tibialis* (Figure 113) from mosses and *Corticaria fuscula* (see Figure 112) in peat mosses. Klimaszewski *et al.* (2015) found *Atheta graminicola* (Figure 114) in Saskatchewan and Newfoundland, Canada, where mosses near water provided a home for some adults.



Figure 110. *Anthophagus alpinus* adult, one of the early-reported moss dwellers from Scotland. Photo by Udo Schmidt, with permission.



Figure 111. *Syntomium aeneum* adult, one of the earliest species to be reported among bryophytes. Photo by Tim Faasen, with permission.



Figure 112. *Corticaria foveola* adult; *C. fuscula* lives among peat mosses. Photo by Marko Mutanen, University of Oulu, through Creative Commons.



Figure 113. *Atheta tibialis* adult, one of the earliest species to be reported among bryophytes. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.



Figure 114. *Atheta graminicola* adult with mosses. Photo by Tim Faasen, with permission.

Early records from the UK show that *Gymnusa brevicollis* (Figure 115) was a moss inhabitant (Beare 1899). Widespread and common species *Atrecus affinis* (Figure 116), *Phloeocharis subtilissima* (Figure 117), and *Tachyporus obtusus* (Figure 118) occur in mosses in the UK (Stenhouse 2007). *Bythinus burrelli* (Figure 119) occurs in mosses on the ground and on tree stumps (Stenhouse 2007). Others that have been found in mosses at least once include *Aleochara funebris* (female), *Aleochara verna* (female; Figure 120), *Geostiba circellaris* (female; Figure 121), *Gyrophypnus fracticornis* (Figure 122), *Othius subuliformis* (Figure 123), *Oxypoda elongatula* (female; Figure 124), *Quedius nitipennis* (female; Figure 125), and *Stenus impressus* (Figure 126).



Figure 115. *Gymnusa brevicollis* adult on moss. Photo by Tim Faasen, with permission.



Figure 116. *Atrecus affinis*, a widespread species that lives among mosses in the UK. Photo by Udo Schmidt, with permission.



Figure 117. *Phloeocharis subtilissima*, a widespread species that lives among mosses in the UK. Photo by Stefan Schmidt, through Creative Commons.



Figure 118. *Tachyporus obtusus*, a widespread species that lives among mosses in the UK. Photo by Entomart, through Creative Commons.



Figure 119. *Bythinus burrelli*, a widespread species that lives among mosses in the UK. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.



Figure 120. *Aleochara verna*, a species that at least occasionally visits mosses. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 124. *Oxypoda elongatula*, a species that is at least an occasional visitor to mosses. Photo by Tim Faasen, with permission.



Figure 121. *Geostiba circellaris*, a species that is at least an occasional visitor to mosses. Photo by Tim Faasen, with permission.



Figure 125. *Quedius nitipennis*, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.



Figure 122. *Gyrohypnus fracticornis*, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.



Figure 126. *Stenus impressus*, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.



Figure 123. *Othius subuliformis*, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.

Stenus (Figure 126-Figure 127), a moss visitor, has an unusual adult behavior. These species are predators on small invertebrates, including *Collembola* (Piper 2007). To catch their prey, they shoot out the **labium** using blood pressure. This narrow structure ends in a pad of bristles and hooks. Between the bristles are small pores that exude an adhesive that sticks to the prey.

Like some **Carabidae**, some of the **Staphylinidae** obtain their moisture from wet mosses. For example, *Stenus kiesenwetteri* (Figure 127) is a rare species living among very wet *Sphagnum* (Figure 128); *Dianous coerulescens* (Figure 129) lives where water trickles over mosses and liverworts (Butler 1886). And some are aquatic, as discussed in the **Coleoptera** subchapter on Aquatic Insect interactions.



Figure 127. *Stenus kiesenwetteri*, a species that uses terrestrial mosses to create an aquatic habitat (limnoterrestrial). Photo by Udo Schmidt, with permission.



Figure 128. *Sphagnum* in flush, a potential home for the rare *Stenus kiesenwetteri* that prefers very wet *Sphagnum*. Photo by Andrew Hodgson, with permission.



Figure 129. *Dianous coeruleus* adult on leafy liverworts. This is a species that uses terrestrial bryophytes to create an aquatic habitat. Photo by Malcolm Storey, through Creative Commons.

In Great Britain, *Achenium humile* (Figure 130) is widespread. This species is predatory and lives in broad-leaved woodlands, fields, sand dunes, coastal marshes, and alluvial flats (Hyman & Parsons 1994). It takes advantage of habitats under bark on dead wood, under stones, among mosses, at roots of grasses, muddy dykes, and clay banks. *Bryophacis crassicornis* (Figure 131) is more restricted, living in dry mixed woodlands among leaves, moss, and rotting fungi, but also in heathlands among the *Calluna* litter (Lindgren & Palm 2011).



Figure 130. *Achenium humile* adult on mosses, a widespread species with a wide range of habitats, including mosses. Photo by Tim Faasen, with permission.



Figure 131. *Bryophacis crassicornis* adult male, a species that includes mosses among its homes. Photo by Christoph Benisch <kerbtier.de>, with permission.

Philonthus nigrita (Figure 132) lives in high and transitional moors. It is most common in the ecotone between water bodies and peat "bogs," living in the partly submerged *Sphagnum* layer (Figure 133) (Burakowski *et al.* 1980; Koch 1989; Staniec & Pietrykowska-Tudruj 2008).



Figure 132. *Philonthus nigrita* adult on *Sphagnum*. Photo by Christoph Benisch <kerbtier.de>, with permission.



Figure 133. Peatland in Alaska showing the wet *Sphagnum* that borders peatland pools, a potential habitat for *Philonthus nigrita*. Photo by Vita Plasek, with permission.

There is little information regarding the specific eating habits of the moss dwellers among the *Staphylinidae*, but Mani (1962) reported that some staphylinids are moss feeders in high alpine areas.

In Canada, *Trichiusa* (Figure 134) species live in forest leaf litter and mosses, especially at the edges of streams and pools (Klimaszewski *et al.* 2015).



Figure 134. *Trichiusa immigrata* adult, member of a genus that sometimes lives among mosses. Photo by Veli-Matti Mukkala, in Public Domain.

Scydmaenidae – Ant-like Stone Beetles

This worldwide family (Figure 135) lives in moist forests where they often take advantage of the moisture they can find among mosses (O'keefe 2001, 2005). They feed primarily on mites (Wikipedia 2015a), perhaps contributing to their presence on bryophytes, where mites are common. They are closely related to the *Staphylinidae* and Grebennikov and Newton (2009) have proposed their inclusion in that family.



Figure 135. *Microscydus nanus* (Scydmaenidae) adult among mosses. Photo by Tim Faasen, with permission.

The *Scydmaenidae* are frequently associated with ants. And they even resemble ants by having constrictions between the head and thorax and between the thorax and abdomen. O'Keefe (2000) reviewed all the published relationships between ants and these beetles. He suggested that they may occur in the same locations because of a common preferred food. If so, then we should expect some of these associations to be among mosses. Ants are common among a number of kinds of mossy locations, as will be seen in the chapter on *Hymenoptera*. It would be interesting to know just why there are so many members of this family associated with ants and what they gain from the relationship.

Tenebrionoidea

Perimylopidae (=Promecheilidae)

The Antarctic has beetle species that take advantage of the insulation and moisture available when living within the moss clumps. The *Perimylopidae* contribute some of these species. *Perimylops antarcticus* (Figure 136-Figure 137) seems to be well adapted by eating bryophytes (Worland *et al.* 1993) and has cold-adapted low-temperature respiration activation rates (Sømme *et al.* 1989). It lives among the moss *Polytrichastrum alpinum* (Figure 138) and lichens. Worland and coworkers tested **ice nucleation** in these insects – a process that causes ice crystals to form, expand, and ultimately damage cell membranes. They found that the gut freezes at 1°C lower than does the adult insect. The fecal material experiences ice nucleation at temperatures as high as -2°C and the insects themselves nucleate -3°C. The mosses nucleate at -4 to -5°C. They suggest that bacteria may be responsible for the nucleation proteins, since this food has a lower nucleation temperature than does the beetle.



Figure 136. *Perimylops antarcticus* larva on *Polytrichaceae*, South Georgia. Photo by Roger S. Key, with permission.



Figure 137. *Perimylops antarcticus* adult on South Georgia, a species that eats mosses. Photo by Roger S. Key, with permission.



Figure 138. *Polytrichum alpinum*, home for *Perimylops antarcticus*. Photo by Michael Lüth, with permission.

Lagriidae – Long-jointed Beetles

The **Lagriidae** (Figure 139) are medium-sized (Benisch 2015c). They are worldwide, but are concentrated in the tropics. Typical habitats are trees, shrubs, and herbaceous plants, with larvae in decaying wood or leaf litter. Chown (1993) found that **Lagriidae** from the Afromontane forest in South Africa fed on both live and dead parts of the moss *Braunia secunda* (Figure 140), based on both field observations and gut analysis. This unknown species is the only record of bryophagy in the family.



Figure 139. *Lagria* from a West Java mountain rainforest; at least one member of this family eats mosses. Photo by gbohne, through Creative Commons.



Figure 140. *Braunia secunda*, food for an unidentified member of the **Lagriidae**. Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Nevertheless, *Adelium alpicola* (see Figure 141) larvae are known from damp forest moss in Australia (Watt 1974). But there is no evidence that they eat the mosses – or that they don't.



Figure 141. *Adelium pustulosum* adult; *Adelium alpicola* larvae occur among damp forest mosses in Australia. Photo by Tamara Leitch, through Creative Commons.

Tetatomidae – Polypore Fungus Beetles

The **Tetatomidae** is a small Palearctic and Nearctic family (~30 species) that is typically associated with fungi, especially wood-decay fungi and those on tree boles (Lawrence 1991; Pollock 2008, 2012). They are poorly known, both taxonomically and biologically.

Tetratoma fungorum (Figure 142) is not generally a moss dweller, as implied by its name. Nevertheless, it finds mosses to be suitable hiding places to survive the winter (Curtis 1823-1840).



Figure 142. *Tetratoma fungorum* adult with mosses, a species that overwinters under mosses. Photo by Tim Faasen, with permission.

Summary

There are probably more families of beetles among bryophytes than the ones represented here. Some of these are full-time bryophyte dwellers, some go to the bryophytes at specific times in the life cycle or for specific purposes, and others may simply traverse them while going from one point to another.

One of the largest families, **Staphylinidae**, has bryophyte dwellers among them. They range in size from tiny to large, even on mosses, and seem to have little specialization among the bryophyte dwellers. These include both casual visitors and those that spend part of their lives among mosses. Their lack of well-developed wings suggests they don't travel far. Some of these are bog dwellers. For many of them, mosses appear to be just more litter on the forest floor. The best and most common adaptations to living among bryophytes seems to be those of being small, roundish, smooth, and perhaps shiny and black, as seen in many of the **Chrysomelidae**.

There is some suggestion that bryophytes as food may provide a means to survive the cold, providing gut contents that have lower nucleation temperatures than the surrounding beetle.

Families like **Latridiidae** find suitable food among mosses, particularly slime molds.

The weevils (**Curculionidae**) are among the most abundant species among bryophytes. Their sizes vary; some seem to have camouflage. A few unique taxa have depressions in the elytra and bryophytes and lichens grow there, anchoring among hairs or spikes and being facilitated by a type of glue secreted by the beetle. A number of weevil species also eat bryophytes, sometimes on a seasonal basis when tracheophyte food becomes unavailable or unpalatable.

For those that eat bryophytes, suitable food includes a wide range of bryophyte species. Nevertheless, some bryophytes seem to be avoided. Liverworts may be eaten because of the rich food source in their oil bodies. Some beetles may take advantage of the fatty acids that remain fluid at low temperatures.

Sphagnum habitats often have rare species. They also provide places to survive forest disturbance or to survive the dry season (for those that can fly). Beetles can change the form of the habitat in ways that affect the mosses. In bogs, they can destroy the cover, causing the mosses to dry and more tolerant species to replace them. Bark beetles damage the spruce forests, but recovery of the forest, mosses, and moss-dwelling beetles is faster than it is from clear cutting.

Some terrestrial beetles in aquatic families use mosses as a limnoterrestrial habitat, maintaining their moisture because the moss remains damp.

Sunita Kapila suggested several internet images and provided examples of moss-carrying weevils. Rob Gradstein and Tamás Pócs provided me with needed images. Google and Wikipedia have been invaluable in helping me fill in information on families. Thank you to Scott Zona for alerting me to the publication of a picture of *Lithinus rufopenicillatus* as a species that carries bryophytes on its body. Paul Berner has provided me with the image of this species. Thank you to Richard Caner for pointing out my labelling error for the previous Figure 83.

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CHAPTER 12-10

TERRESTRIAL INSECTS:

HOLOMETABOLA – HYMENOPTERA

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CHAPTER 12-10

TERRESTRIAL INSECTS:

HOLOMETABOLA – HYMENOPTERA



Figure 1. Ant hill in Finland with leafy liverworts (*Barbilophozia hatcheri*, *B. floerkei*, *Tritomaria quinquedentata*, *Lophozia ventricosa*) and the moss *Pohlia nutans*. Photo by Des Callaghan, with permission.

HYMENOPTERA – Sawflies, Wasps, Bees, and Ants

Andrew *et al.* (2003) examined the variation in bryophyte fauna in Tasmania and New Zealand using different spatial scales along altitudinal gradients. Among these collections, they found six families of **Hymenoptera**. Although 77% of the faunal families were represented by 44 families, these 44 contributed only 10% of the total abundance.

This order is absent among bryophytes in the aquatic habitat, but in the terrestrial habitat, bees and ants find them useful in a variety of ways. As stated by Gerson (1969), some **Hymenoptera** feed on mosses. But others use them for nest materials, to house eggs, to provide water, and to provide cover. And of course some, including the sawflies, use them for pupation (Nägeli 1936).

Ants

Bryophytes, along with ants and grass, had a unique role for one Marine (Anonymous 1983). Trapped in a ravine in California for weeks, this marine subsisted on ants, moss, and grass! No wonder he lost 75 pounds before he found a way out!

The Phenomenal Ants

Ants are perhaps the most ordered insects on the planet. They work together to hunt and to build their trails and nests. In fact, they have been described as superorganisms because of their ability to work together as a unit (Oster & Wilson 1978). Ants are well endowed with defense, and depending on the species, they can bite, sting, or spray chemicals (Figure 2) such as formic acid (Wikipedia 2016). Their well-developed mandibles (Figure

3) serve for protection and prey capture. When an ant is killed, it emits a chemical that attracts ants from some distance, bringing an army to attack the intruder. Ants can also use chemical senses to identify dead colony members and remove them, and the workers are diligent in keeping the nest clean and free of bacteria. Their chemical signals, along with sounds and contact, permit them to communicate with each other. They also recognize their nest mates through the scent of hydrocarbon-laced secretions from their exoskeletons.



Figure 2. *Formica aquilonia*, preparing to spray and adjusting the position of the abdomen with its legs. Photo by Brian Eversham, with permission.



Figure 3. *Myrmica* sp. mandibles, a genus with a number of bryophyte dwellers. Photo from <fir0002/flagstaffotos.com.au>, through Creative Commons.

Ants are common among bryophytes, especially in bogs. Those that frequent the bryophytes don't seem to have any special adaptations, but this has not really been explored systematically. Their body constrictions give them considerable flexibility compared to most other insects, permitting even large species to maneuver among the bryophytes. The bryophytes provide a temperature-buffered environment where many food organisms can be found. They also provide a suitable underground habitat for growing fungi, cultivated by the ants, and kept moist by the bryophytes that reduce moisture loss at the soil surface.

Where Ants Are Absent

Acacia ants, on the other hand, may actually avoid mosses. In Costa Rica, Angela Newton (Bryonet, 20 November 2006) found that ants under ant-acacias left the bryophytes mostly undisturbed, except for some obvious nibbling around the edges. The green patches of moss in the otherwise clear ant-acacia circles were quite healthy and more numerous than in the surrounding forest. The mosses seemed to benefit from the ants' gardening activities, whereby the ants removed the larger plants that could pose a competition threat.

Food Source?

We generally think of the ants with their large jaws and sharp bite as carnivores. But Plitt (1907) found moss capsules that were gnawed and spores removed. A patch of "*Webera sessilis*" (probably *Diphyscium foliosum*, Figure 4) occurred immediately over an ant's nest. Both *Myrmica ruginodis* (Figure 39) and *Formica picea* (Figure 5) fed on the mosses and managed to gnaw a hole in nearly every capsule to obtain the spores. And beware – they were on the mosses in the collector's vasculum.



Figure 4. *Diphyscium foliosum* with capsules. Spores in these capsules serve as food for *Myrmica ruginodis* (Figure 39) and *Formica picea* (Figure 5). Photo by David T. Holyoak, with permission.



Figure 5. *Formica picea* on *Sphagnum*. This ant species feeds on the spores of *Diphyscium foliosum*. Photo by Barbara Thaler-Knoflach, with permission.

Loria and Herrnstadt (1980) found that in the Negev desert the harvester ant (*Messor*, Figure 6) ate capsules of *Aloina aloides* (Figure 7-Figure 8), *Crossidium crassinerve* (Figure 9), and *Bryum bicolor* (Figure 10) in winter when other food was not available. The ants climbed the seta of *C. crassinerve*, chewed off the capsules, and carried them to their nests, forming a parade 15 m long. An average of 30 capsules per minute arrived at the nest! Longton (1984) considered this behavior to be opportunistic because capsules are not available every year in the desert climate. It is possible that this behavior is advantageous for the mosses as well – the ants are likely to place the capsules in places more suitable for spore maturation in this environment where such sites are rare. However, Loria and Herrnstadt (1980) emphasized that mosses do not seem to derive any advantage from this harvesting process.



Figure 6. *Messor barbarus*, member of the genus that eats moss capsules in the Negev Desert. Photo by Valter Jacinto, through Creative Commons.



Figure 7. *Messor* on capsules of *Bryum bicolor* in Negev desert. Photo courtesy of Ilana Herrnstadt.

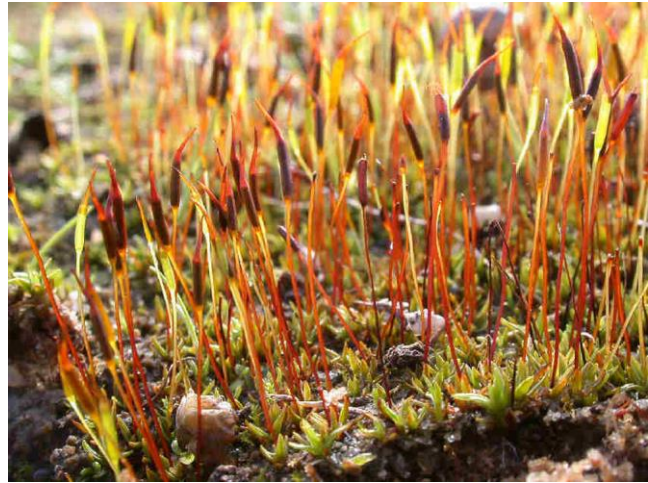


Figure 8. *Aloina aloides* with capsules. Capsules of this species serve as food for *Messor* in the Negev Desert. Photo by David Holyoak, with permission.



Figure 9. *Crossidium crassinerve* with capsules. Capsules of this species serve as food for *Messor* in the Negev Desert. Photo by Michael Lüth, with permission.



Figure 10. *Bryum bicolor* with capsules. Capsules of this species serve as food for *Messor* in the Negev Desert. Photo by Jonathan Sleath, with permission.

Bear feces are known to contain mosses, with one study reporting 50-90% mosses, primarily *Pleurozium schreberi* (Figure 30) (Dalen *et al.* 1996). But when the

feces contained 15% *Brachythecium reflexum* (Figure 11), Dalen and coworkers concluded that it was unlikely that the mosses were eaten by choice. Rather, they probably came along with its inhabiting food organisms – the ants.



Figure 11. *Brachythecium reflexum*, a moss where ants can dwell and the moss seems to be eaten by bears along with the ants. Photo by Michael Lüth, with permission.

The Green Salamander, *Aneides aeneus* (Figure 12), is a well-known moss-dwelling insectivore. At Cooper's Rock in West Virginia, USA, the gut consisted of 53% ants, but also included moss fragments (Lee & Norden 1973). It is likely that this is another case of a moss inhabitant getting mosses along with its intended prey. Gunzburger (1999) likewise concluded that mosses in the gut of the Red Hills Salamander *Phaeognathus hubrichti* (Figure 13) got there in the process of eating moss inhabitants, including ants.



Figure 12. *Aneides aeneus*, a moss-dwelling salamander that eats a lot of ants. Photo by Mike Graziano, with permission.



Figure 13. *Phaeognathus hubrichti*, another moss dweller that eats ants among mosses and consumes part of the moss along with them. Photo by Danté B. Fenolio, with permission.

Anthills

Anthills range in size from those tiny volcanoes in the cracks in the sidewalk to massive structures that rival termite mounds (Figure 1). And some are simple entrances to a series of underground tunnels. In British chalk grasslands, King (1977) found that anthills have shorter vegetation, more rabbit dung, drier soil, smaller structural aggregates, lower bulk density, and more temperature extremes than the surrounding pasture. Several of these factors also lead to less moisture.

Eiseman and Charney (2010) report mosses on the abandoned anthill mounds of *Formica exsectoides* (Figure 14). Des Callaghan (Bryonet 3 August 2014) recently visited Finland and photographed a giant ant nest. The ants had cleared the nest of its tracheophytes, but, as he put it, they appear to have a fondness of leafy liverworts. Several species of liverworts [*Barbilophozia hatcheri* (Figure 15), *B. floerkei* (Figure 16), *Tritomaria quinquedentata* (Figure 17), *Lophozia ventricosa* (Figure 18)] cover one of the mounds. In addition the mound served as substrate for the ubiquitous *Pohlia nutans* (Figure 19).



Figure 14. *Formica exsectoides* mound. Photo by Greg Schechter, through Creative Commons.



Figure 15. *Barbilophozia hatcheri*, a colonizer on anthills of *Formica exsectoides*. Photo by Michael Lüth, with permission.



Figure 16. *Barbilophozia floerkei*, a colonizer on anthills of *Formica exsectoides*. Photo by Hermann Schachner, through Creative Commons.



Figure 17. *Tritomaria quinquedentata*, a colonizer on anthills of *Formica exsectoides*. Photo by Malcolm Storey, through DiscoverLife.



Figure 18. *Lophozia ventricosa*, a colonizer on anthills of *Formica exsectoides*. Photo by Michael Lüth, with permission.



Figure 19. *Pohlia nutans*, a colonizer on anthills of *Formica exsectoides*. Photo by Michael Lüth, with permission.

Pekka Punttila (pers. comm.) explained the mound nests of the two species that may be inhabiting the mounds photographed by Des Callaghan (Figure 1). *Formica lugubris* (Figure 20) is **monogynous** (has only one queen in a mound). The longevity of this queen and her colony lasts typically only about 20 years. This loss opens the mound to invasion by other species or simply to die off if something happens to the queen. *Formica aquilonia* (Figure 21-Figure 23), on the other hand, is **polygynous**, meaning it has more than one queen in a mound. That strategy permits the species to maintain its nest for a long time. Furthermore, if many mounds are present, it is likely to be that of *F. aquilonia*, a **polydomous** species. These mounds may reach dozens or even hundreds in an area. *Formica lugubris* typically builds single mounds.



Figure 20. *Formica* cf. *lugubris*, a monogynous species that builds single mounds. Photo by Richard Bartz, through Creative Commons.



Figure 21. *Formica aquilonia* mound. Photo by Villak, through Creative Commons.



Figure 22. *Formica aquilonia* on moss. Photo by Brian Eversham, with permission.



Figure 23. *Formica aquilonia*, attacking its prey. Photo by Brian Eversham, with permission.

The monogynous species such as *Formica lugubris* (Figure 20) are able to disperse during their nuptial flight, temporarily parasitize other nests, and establish in young forests or older forest fragments (Punttila 1996). The polygynous species, including *F. aquilonia* (Figure 21-Figure 23), disperse primarily by "nest budding," permitting them to form large colonies of cooperative nests. These are found in older forests and larger old forest fragments.

Anthills create microhabitats of their own. This is evidenced by the moss *Pseudoscleropodium purum* (Figure 24). This species predominates on the north-facing sides of anthills constructed by *Lasius flavus* (Figure 25-Figure 26) (King 2003). King experimented with survivorship of the moss by rotating the anthills either 360° or 180°. Hence, half the anthills were now facing south. For those mosses facing south, over half the shoots turned white at the tips and up to 20 mm from the apex. Those rotated 360°, thus still facing north, remained green and healthy. Nevertheless, most of the mosses on the south side survived. Those on the north side grew faster and King concluded that it may be more difficult for the fragments to establish on the south side due to the longer periods that were dry and unfavorable for growth. Carl

Farmer found anthills of this species in Scotland completely covered by mosses while the ants thrived inside.



Figure 24. *Pseudoscleropodium purum*, a moss that lives on the north sides of anthills of *Lasius flavus*. Photo by Michael Lüth, with permission.



Figure 25. *Lasius flavus*, an ant that makes mounds where one can find *Pseudoscleropodium purum* on the north side of the mound. Photo by Anki Engström <www.krypinaturen.se>, with permission.



Figure 26. *Lasius flavus* tending aphids. Photo by Anki Engström <www.krypinaturen.se>, with permission.

In acidic grasslands, bryophytes may be confined to anthills. King (1981) found that the acrocarpous mosses *Dicranum scoparium* (Figure 27), *Polytrichum juniperinum* (Figure 28), and *Polytrichum piliferum* (Figure 29), all colonizers, were almost confined to the anthills in the Gower Peninsula of South Wales. King considered dispersal ability and ability to withstand burial to be primary factors to favor these mosses over surrounding tracheophyte plants, downplaying the importance of soil chemical and physical factors. *Lasius flavus* (Figure 25-Figure 26) builds mounds that are 15-20 cm high and 50-70 cm in diameter. In these acidic habitats, King found that *Pleurozium schreberi* (Figure 30), like *Pseudoscleropodium purum*, is abundant on the north-facing sides of the mounds. On the other hand, *Polytrichum juniperinum* and *Polytrichum piliferum* are more frequent at the summit of the mound than at the periphery, but *P. piliferum* is more frequently on the south side, a location consistent with its habitation of more exposed, xeric habitats. *Polytrichum juniperinum* has its base 15 cm below the soil, suggesting that it grew up through the anthill as the anthill increased in size.



Figure 27. *Dicranum scoparium*, a species that is common on anthills in South Wales. Photo by Janice Glime.



Figure 28. *Polytrichum juniperinum*, a species that is common at the summit of anthills. Photo by Janice Glime.



Figure 29. *Polytrichum piliferum*, a species that is frequent at the summit of anthills, but mostly on the south side. Photo by David Holyoak, with permission.



Figure 30. *Pleurozium schreberi*, a moss that grows on north-facing slopes of anthills made by *Lasius flavus*. Photo by Michael Lüth, with permission.

Des Callaghan (Bryonet 10 May 2017) has seen *Buxbaumia viridis* (Figure 31) living on the ant hills of the wood ant, *Formica rufa* (Figure 53-Figure 55). Many Bryonettors have reported what appears to be herbivory on this species of *Buxbaumia*, but thus far there is no direct evidence that these are consumed by ants.



Figure 31. *Buxbaumia viridis* capsules, a species that can inhabit wood ant (*Formica rufa*) nests. Photo by Hermann Schachner, through Creative Commons.

For mosses in deciduous forests, anthills provide a substrate that rises above the forest floor. This permits the leaf litter to fall downward, keeping the anthill exposed and preventing burial of the bryophytes by leaf litter.

Ants as Gardeners

In several tropical areas, ants make ant gardens (Ule 1901; Blüthgen *et al.* 2001). These aerial gardens usually consist of plants, started as seeds by the ants, and used as a matrix in which soil is placed to construct a nest. But Ule reported only flowering plants in these ant gardens. In 1985, Frahm reported risk of life to collect a nest 15 cm in diameter with a yellow-green center surely of moss. The escapade began when he and Rob Gradstein chopped down the tree holding the nest, using machetes. But alas, the tree fell, only to land within the arms of another tree, with the nest still out of reach. Again, the second tree was cut in like manner, but it fell 10 meters deep into the river, thus drowning the ants in their nest! Not to be discouraged from their quest, the two bryologists then had to cross the river, as the tree was accessible only down a steep and rocky slope and to the other side of the valley. Attempts to raise the nest to the bridge with a rope destroyed most of it, but they were able to rescue the moss, determined as *Brachymenium columbicum* (Figure 32), a moss known also from Colombia and Ecuador, and now, for the first time, from Peru.



Figure 32. Ant garden, primarily of *Brachymenium columbicum* (and seedlings), from a tree in Peru. Photo by Jan-Peter Frahm, with permission.

Blüthgen *et al.* (2001) suggested the importance of these aerial ant gardens. Nutrients are scarce in the canopy. Some plants are adapted by producing **adventitious** roots (roots that arise from stems and other non-root axis points) that are able to grow and penetrate animal debris, bromeliad tanks, bryophytes, and plant cavities. But some lack the ability to take advantage of these nutrient sources. Among these some are able to form commensalistic associations. The association between ants and epiphytes is one such association. The ants carry seeds that they imbed in the garden. The ants then care for the garden by protecting it and providing a stable germination and establishment state. As noted by Frahm (1985), some of these gardens, as already noted, have bryophytes that can further help by maintaining moisture and trapping airborne dust and nutrients.

The leafy liverwort *Nardia* sp. (Figure 33) is a pioneer on volcanic ash, forming layered deposits up to 15 cm thick (Jongmans *et al.* 2001). These growths are able to adhere to vertical cliffs and to form bridges between volcanic boulders, facilitating the establishment of vascular plants.

These carpets sometimes are invaded by ants and other insects that help to keep the liverworts clean and bring seeds and spores to continue the garden. In Costa Rica ants took up residence among the fronds of the hanging garden liverwort *Nardia succulenta* on the ash of volcano Arenal (Jongmans *et al.* 2001).



Figure 33. *Nardia scalaris*. *Nardia* is a genus that forms bridges between volcanic boulders and is maintained by ants. Photo by Hermann Schachner, through Creative Commons.

Gibson (1993a, b) found that ants placed seeds of the cow wheat (*Melampyrum lineare*, Figure 34-Figure 36) more frequently under *Polytrichum* (Figure 28-Figure 29) than expected by chance, based on its relative cover (Figure 37). In the oak-pine forest of the New Jersey Pinelands, Gibson and Good (1987) found that the seeds of *Melampyrum lineare* were restricted to mossy patches. Ants gather these seeds and store them, later using the oily and nutrient-rich eliasome (Figure 36) as a food source without damaging the seed to which it is attached (Gibson 1993a, b). Litter and lichens were also used, but *Polytrichum* seemed to be highly selected. *Dicranum* (Figure 27) and *Pleurozium* (Figure 30), although more abundant than the *Polytrichum*, attracted far fewer ants to store seeds. This behavior afforded the seeds a safe place where mice did not eat them and they retained sufficient moisture to survive. These seeds have low survival if they dry out and will die if they fall to the soil and remain exposed. If they remain in the capsules until evening, the mice will eat them.



Figure 34. *Melampyrum lineare*, a hemiparasite whose seeds are dispersed by ants. These seeds are often deposited under mosses and lichens. Photo by Janice Glime.



Figure 35. *Melampyrum lineare* fruits. Photo by Keir Morse at <gobotany.newenglandwild.org>, with permission.



Figure 36. *Melampyrum lineare* moist seeds. Note the white eliasome. If the seeds drop to the ground they will dry out and turn black. Photo by Keir Morse at <gobotany.newenglandwild.org>, with permission.

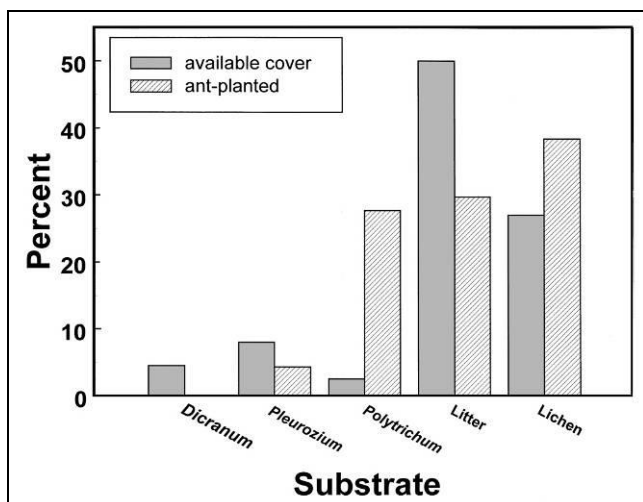


Figure 37. Percent frequency of *Melampyrum lineare* seeds stored by ants under various available substrates near Houghton, Michigan, USA. Modified from Gibson 1993a.

Forest Ants

I have found little literature on forest floor bryophytes and their ant inhabitants. Ward (2000) reviewed some of these from leaf litter communities. Wilson and Hölldobler (2005) included bryophytes among the sites offering the desirable small spaces to ponerine ants on the forest floor. While these species are relatively abundant in the tropical and warm-temperate forests, they are scarce in the cool-temperate forests, deserts, and arid grasslands.

Myrmica rubra (Figure 38), *M. ruginodis* (Figure 39), and *Formica lemani* (Figure 40-Figure 41) are widespread among forest mosses (Stenhouse 2007). The latter nests in stumps. *Myrmica rubra* is the most moisture-loving of the *Myrmica* species, preferring moist, shady forests (Kupianskaya *et al.* 2000). It builds its nests in decaying stumps and logs, under mosses, and other moist locations. *Myrmica ruginodis* is the most abundant of the red ants in the North Vidzeme Biosphere Reserve, Latvia (Gluhovs 2013). Gluhovs determined that soil pH, bryophyte cover, and coarse woody debris did not have a significant effect on the ant communities in the forest.



Figure 38. *Myrmica rubra* workers drinking from a water droplet on a leaf. Photo by Richard Becker at <www.bwars.com>, through open source permission.



Figure 39. *Myrmica ruginodis* worker carrying pupa. This species is common among forest mosses in Europe. Photo by Brian Eversham, with permission.



Figure 40. *Formica lemani* queen on moss. Photo by Brian Eversham, with permission.



Figure 41. *Formica lemani* worker carrying pupa across moss. Photo by Brian Eversham, with permission.

In addition to *Myrmica rubra*, it is likely that moisture is important to other species and may account for vertical distribution of species and location of nesting sites. Billings and Drew (1938) demonstrated that bryophytes created a microhabitat that held six times as much water as the bare bark of old-growth tulip trees (*Liriodendron tulipifera*) in Tennessee.

Myrmica lobifrons and *Dolichoderus pustulatus* are the dominant ants in bogs in New England, USA (Gotelli & Ellison 2002). In fact, *M. lobifrons* seems to specialize in bogs and other humid habitats.

In forest sites in the Czech Republic, the **Formicidae** were among the most abundant taxa in the biggest bryophyte samples (400 cm²) (Božanić 2011). *Lasius brunneus* (Figure 42) was abundant among epiphytic mosses on trees with a diameter of 60-110 cm, especially on old oak trees.



Figure 42. *Lasius brunneus* adult, an inhabitant of old oak trees where it lives among epiphytic mosses. Photo by Stanislav Krejčík, through Creative Commons.

Božanić (2008) examined the aspects of forest mosses that made them suitable environments for invertebrates. He suggested that ants may live there or go to mosses to search for food or shelter or to lay eggs. The microclimate, especially in retaining moisture, provides a haven for forest dwellers. On the other hand, the invertebrates help the bryophytes by spreading spores. Using heat extraction with a Tullgren funnel, Božanić extracted invertebrates from 66 moss samples. The richest fauna of invertebrates, including **Formicidae**, occurred with the moss *Brachythecium curtum* (Figure 43). The most important factors for number of taxa were type of substrate, height above ground, and moss sample area. The species were affected by the type of substrate, height above ground, and tree diameter.



Figure 43. *Brachythecium curtum*, a preferred moss for habitation by members of **Formicidae**. Photo by Janice Glime.

Božanić *et al.* (2013) investigated the factors that affected invertebrate communities among bryophytes in forests of the Czech Republic. The dominant bryophyte was *Hypnum cupressiforme* (Figure 44) and Božanić and coworkers reported on 13 invertebrate groups, encompassing 45 species. Of these classes, orders, and families, 4 species of **Formicidae** (ants) were present. Height above ground was an important parameter in describing the **Formicidae** communities. But unlike the epiphyte communities in Costa Rica described by Longino and Nadkarni (1990) discussed below, Božanić *et al.* found that the **Formicidae** preferred habitats on the ground or

close to it. It is likely that the epiphyte cover in the Czech Republic is much less developed and protective compared to that in the cloud forests of Costa Rica.



Figure 44. *Hypnum cupressiforme*, a dominant bryophyte in forests of the Czech Republic and home to ants there. Photo by Michael Lüth, with permission.

Epiphyte Communities

As seen above, Blüthgen *et al.* (2001) have demonstrated one importance of ants as epiphyte gardeners. Yanoviak *et al.* (2007) likewise considered the epiphytic mats as important habitats. In Costa Rica, these mats were thinner and exhibited less structural diversity in secondary forests compared to undisturbed forests. But for ants, the diversity was significantly greater in the secondary forests, especially *Solenopsis* spp. (subterranean fire ants). During the dry season, arthropod diversity declined among the epiphytes.

Nadkarni and Longino (1990) used the Winkler sifting apparatus to extract arthropods from Costa Rican canopy soils. They found that ants were among the dominant invertebrate groups in these habitats. In fact, the ants were the only group that did not have higher densities on the ground than in the canopy.

Longino and Nadkarni (1990) demonstrated a vertical zonation of ants in these Costa Rican cloud forests. The genera were similar in the canopy (litter and humus that include mosses) to those among the ground litter, but represented a subset of those genera. But at the species level, the two habitats were distinct with rare overlap in species between the two. Surprisingly, their new find was on the ground, where *Stenamma* JTL-3 (see Figure 62) was nesting under moss mats.

Ant activity in the tropical forests seems to be greater in the canopy than on the ground. Yanoviak and Kaspari (2000) used bait defense to determine these differences. The bait indicated more defense in the canopy (60%) than in the litter (32%), independent of tree species and bait type. It also indicated higher activity in defending protein baits than carbohydrate baits. Furthermore, the litter and canopy had no species in common.

Epiphylls as Defenders

Not all bryophytes favor the ants. The leafcutter ant *Atta cephalotes* (Figure 45) is repelled by epiphylls,

including bryophytes, on citrus leaves. Mueller and Wolf-Mueller (1991) removed the epiphylls from citrus leaves and found 2-3 times as much herbivore damage from ants compared to leaves with epiphylls intact. These epiphylls consisted of leafy liverworts and crustose lichens. They suggested that the epiphylls increased the cutting effort, or that secondary compounds in the liverworts might have been major contributors to the antiherbivory (see Swain 1977). A further possibility is that the epiphylls inhibited the growth of the fungi that served as food for these ants.

Coley *et al.* (1993) looked at the relationship from a different perspective. They found that long-lived tracheophyte leaves have better defenses against herbivores and pathogens than those with deciduous leaves. They suggested that liverworts may provide protection of the leaves, citing the rich concentration of terpenoids in liverworts. It takes only two years to cover leaves with species that have rapid colonization rates.



Figure 45. *Atta cephalotes*, a leaf cutter ant that is repelled by epiphylls such as leafy liverworts. Photo by Scott Bauer, through public domain.

Dispersal

The busy ants run all over their habitats and the tiny, widely spaced hairs on their bodies would seem to provide ideal locations for some sizes of dispersal units. Rudolphi (2009) set out to discover if such a hypothesis was indeed viable. He reasoned that both ants (*Lasius platythorax*, Figure 82) and mosses, *Aulacomnium androgynum* (Figure 46) in particular, occurred on the same dead wood in Swedish forests. Therefore, it is reasonable that the gemmae (Figure 47) of this moss might be transported by the ants. First he tested whether the gemmae would adhere to the ants. He put one tuft of moss in each of eight Petri dishes and released eight ants into each dish, repeating the experiment 8 times. Once the ants ran across the moss (at least 30 seconds), they were removed by letting them crawl into a bottle. Ants were frozen and examined for adherence of gemmae. As many as six gemmae did, in fact, adhere, with 1/3 of the ants having gemmae within less than two minutes of exposure. He found that while moisture on the moss did not influence time the ant spent on the moss (42 sec wet vs 48 sec dry), the adherence was five times as great on the dry mosses (mean 0.94) vs wet (mean 0.19).



Figure 46. *Aulacomnium androgynum* showing gemmae that adhere to ants that share the same dead wood. Photo by Michael Lüth, with permission.



Figure 47. *Aulacomnium androgynum* gemmae. Photo by Des Callaghan, with permission.

Rudolphi (2009) followed this with a second experiment to determine residence time of the gemmae on the ants. Using nine ants in each of five time periods (0, 1, 2, 4, 8 hours), he attached two gemmae to the dorsal abdomen and let the ants run around. Ants were then frozen and examined for gemmae. Each time interval experiment was again repeated 8 times. After two hours, ants averaged retention of one gemma. After eight hours, 24% of the ants still had at least one gemma attached, suggesting that ants could be an effective dispersal agent of these gemmae.

But why more dry propagules? Wet gemmae tend to stick together, making the dispersal unit larger and heavier, thus easier to dislodge. This greater success of dry gemmae is actually advantageous because the ants are more active when the weather is dry (Elchuk & Wiebe 2003).

Now we just need to watch the ants to see if they traverse the mosses on the logs and if they drop the propagules in suitable sites for successful establishment. Surely both of these conditions are met at least some of the time.

Ants are able to make trails – trails that we can see and follow. They do this by cutting vegetation that slows them down, and that includes cutting bryophytes. This activity provides an opportunity for dispersal. Korpelainen *et al.* (2011) explored the importance of this role in the leafy liverwort *Barbilophozia attenuata* (Figure 48). Using microsatellite markers, they showed significant kinship relationships up to 8 m. After that the relationship coefficients approached 0, then decreased to negative correlations. At more than 25 m they again approached 0, indicating random distribution. They suggested that the large gemmae permit effective establishment more easily than do spores. Gemmae were favored over spores along the ant trails (and are more likely in other areas of disturbance). Nevertheless, the researchers concluded that ants do not have a large role as dispersal agents, and the physical structure of the ant trails likewise does not lead to greater dispersal. Rather, the trails provide colonization sites available to this liverwort.



Figure 48. *Barbilophozia attenuata*, a liverwort with gemmae that are distributed by ants. Photo by Andrew Spink, with permission.

Spain (2012a) puzzled over a section of moss lawn where the mosses exhibited a trail (Figure 49). It ended at the base of a tree, ruling out a watering hose as the causal factor. Finally he observed the trail long enough to see carpenter ants (*Camponotus* sp.; Figure 50) following the trail (Figure 49) in both directions, one after the other. The ants had apparently removed thousands of moss plants to make the trail, hence making travelling easier (Figure 52). They no longer needed to climb up and down across the stems (Figure 51). Although the trail was only 10 m long, by ant lengths it was equivalent of the length of more than 7 football fields traversed by a human. This trail had actually been cut to remove the obstructing branches. Spain suggests if you want to get rid of the ants, give the nests frequent disturbance, such as hosing them, or fill the entrance with disturbing powders such as cinnamon, diatomaceous earth, or cloves (Spain 2012b).



Figure 49. Moss-trail by made by carpenter ant. Photo from Moss and Stones Garden, with permission.



Figure 50. Carpenter ant (*Camponotus* sp.) that made the moss trail. Photo from Moss and Stones Garden, with permission.



Figure 51. Here the busy ants appear to be dancing on a mound of moss, but its rough nature slows them down on their trail. Photo from Moss and Stones Garden, with permission.



Figure 52. Ant trail showing cut through mosses. Photo from Moss and Stones Garden, with permission.

Recognizing the importance of bryophyte fragments, Heiken *et al.* (2007) sampled nesting material from 25 *Formica rufa* (Figure 53-Figure 55) group nest mounds in five different forest types in Germany. In these nests they found numerous fragments of 20 bryophyte species occurring on almost all sampled mounds. Although both lichens and bryophytes occurred in the nests, 20 species represented bryophytes, whereas only 10 were lichens. The choices indicated some specificity. Those used were the abundant ones – no surprise there, but life form seemed to matter. Weft bryophytes accumulated on the mounds, but tall turfs seemed to be ignored. *Hypnum cupressiforme* (Figure 44) was the most abundant on the nests, appearing in 16 of the 25 samples and comprising 67.5% of the fragments detected. Other common flora were *Pleurozium schreberi* (Figure 30) and species of *Brachythecium* (Figure 63-Figure 64, Figure 43). Certain life forms (weft bryophytes, reindeer lichens) accumulate on mounds, while others (tall turfs, cup-type *Cladonia* spp.) discriminate, reflecting fragmentation features of the species.



Figure 53. *Formica rufa* nest in which bryophyte fragments are incorporated. Photo through public domain.



Figure 54. *Formica rufa*, an ant that is known to use at least 20 species of mosses in its nests. Photo by Brian Eversham, with permission.



Figure 55. *Formica rufa*, ready to bite or fire chemical weapons in its defense. Photo by Brian Eversham, with permission.

Some bryophytic nest contents were restricted by forest type (Heiken *et al.* 2007). *Pohlia nutans* (Figure 19) and *Polytrichum piliferum* (Figure 29) occurred in *Cladonio-Pinetum* nests; *Pleurozium schreberi* (Figure 30) in *Leucobryo-Pinetum*; *Polytrichastrum formosum* (Figure 56) and *Rhytidiadelphus squarrosus* (Figure 57) in spruce forests; *Campylopus pyriformis* (Figure 58) in low-mountain ranges; *Plagiothecium* spp. (Figure 59) in *Calamagrostio-Piceetum*.



Figure 56. *Polytrichastrum formosum* with frost. This species is found in ant nests in spruce forests. Photo by Aimon Niklasson, with permission.



Figure 57. *Rhytidiadelphus squarrosus*, a species found in ant nests in spruce forests. Photo by Michael Lüth, with permission.



Figure 58. *Campylopus pyriformis*, a moss used in ant nests in low mountain ranges. Photo by Michael Lüth, with permission.



Figure 59. *Plagiothecium laetum*. Several species of this genus are ant nest components in the *Calamagrostio-Piceetum*. Photo by Michael Lüth, with permission.

Heiken *et al.* (2007) concluded that the ants were important dispersal agents by dropping fragments during transport and providing a colonization site on the mounds, especially those that were abandoned.

Anthills are not friendly bryophyte sites. The outer part of the nest dries faster than the forest floor (Heiken *et al.* (2007). Nests are frequently disturbed by ants, birds, and wild boar, suppressing the growth of the bryophytes. Heiken and coworkers determined that at least 25,000 fragments of bryophytes and lichens were carried to ant nests in one year. That is no guarantee they will grow.

Nesting

Ants build elaborate nests in trees or underground (Figure 60-Figure 61) (Wikipedia 2016). They typically maintain the nest at a temperature that is ideal for development of the larvae. They do this by choosing the location, materials, ventilation, and solar radiation. The worker and activity and metabolism help to contribute to heat control. In moist nests, microbial activity helps to control the temperature.



Figure 60. Ant nest under *Dicranum scoparium*. Photo courtesy of Serhat Ursavas.



Figure 61. Ant nest under *Dicranum scoparium* showing closer view of the ants. Photo courtesy of Serhat Ursavas.

Longino (2005) examined nesting behavior of two species of the neotropical *Stenamma* (**Formicidae**; Figure 62). By comparing ants on soil banks, he found that they are absent from new (unvegetated) banks. They are very abundant on the banks at the intermediate stage that has only a sparse covering of small bryophytes. But when the mosses become abundant, the abundance of ants decreases greatly.

Ants use bryophytes to varying degrees to construct nests (Figure 63-Figure 65). Some nest under them (Figure 66). Some incorporate small bits of bryophytes in nest construction. And some use bryophytes almost exclusively. General collecting by Longino and Nadkarni (1990) in Monteverde and other highland sites in Costa Rica has revealed that *Stenamma* (Figure 62) makes nests under moss mats in the forest understory.



Figure 62. *Stenamma brevicorne*, a species that lives under mosses, litter and similar protected sites, in this case carrying a grub. Photo by Galpert, through Creative Commons.



Figure 63. These ants have included *Brachythecium* (Figure 64) and *Hypnum* (Figure 65), among other things, in their nest. Photo by Janice Glime.



Figure 64. *Brachythecium* sp., a genus incorporated into ant nests. Photo by Janice Glime.



Figure 67. *Formica* on *Sphagnum* nest that makes this hummock in Michigan, USA. Photo by Janice Glime.



Figure 65. *Hypnum imponens* and *H. jutlandicum*, mosses than can be incorporated into ant nests. Photo by Michael Lüth, with permission.



Figure 68. *Formica* on *Sphagnum* nest in Michigan, USA. These ants are busy repairing the nest as it is being blown apart by wind. Photo by Janice Glime.

Abandoned nests can become the site of moss invasions, as seen in Figure 69.



Figure 66. *Polydesmus angustus* nest under moss, Crowle Moors, UK. Photo by Brian Eversham, with permission.

The Neotropical frog *Agalychnis saltator* (Hylidae) makes nests and lays its eggs among mosses on lianas (vines) (Roberts 1994). Among the dangers to these eggs are cohabiting ants. As adults these frogs are able to escape quickly by parachuting.

My own experience is watching ants repair an ant nest mound made of *Sphagnum* during heavy winds (Figure 67- Figure 68). Bits were flying off the mound as fast as the ants could repair it. Ants are fairly common in bogs, and grabbing a handful of *Sphagnum* can result in an arm full of ants.



Figure 69. Ant hill with moss. Photo by Annette Schimming, with permission.

If you have ever trudged through a peatland with hummocks and hollows, you know how difficult walking can be. It is easy to twist your ankle on the uneven substrate. What you may not know is that ants can be

responsible for some of that rough terrain. They are clever engineers and in the peatlands they build elaborate nests, as you have just seen. But in natural hummocks formed by *Sphagnum* growth, ants can play a role in the changes in microtopography (Luken & Billings 1986). Due to their tunneling behavior, it appears that when the mosses die, hummock retrogression is accelerated by the tunnelling of the ants. In fact, some of these collapsed hummocks can eventually form hollows.

Ants, *Sphagnum* Collars, and Aphids

Robin Stevenson (Bryonet 17 June 2015) reported moss collars around the bases of pine (Figure 70-Figure 73) and birch (Figure 74) trees. "The lower part of the 'trunk' was covered in little bits of dried *Sphagnum* (Figure 78), and the whole plant was swarming with lots of ants. We didn't see the ants actually moving any of the *Sphagnum*, but they did look as if they were coming up from underneath it. We got the impression that it was the ants who were responsible."



Figure 70. Ants, aphids, and *Sphagnum* sleeves on sapling in bog. Photo courtesy of Robin Stevenson.



Figure 71. Ants and basal sleeve of *Lasius platythorax* in bog. Photo courtesy of Robin Stevenson.



Figure 72. Ant (*Lasius platythorax*) *Sphagnum* sleeves on pine. Photo courtesy of Robin Stevenson.



Figure 73. Partial sleeve made by *Lasius platythorax* around branching point in Durham Bog. Photo courtesy of Robin Stevenson.



Figure 74. Birch sleeve of *Sphagnum* built by *Lasius platythorax*. Photo courtesy of Robin Stevenson.

I have several hypotheses for the *Sphagnum* ant nests:

1. The ants are just beginning a nest and the pine serves as a central support column.
2. The nest has been mostly destroyed and the ants are repairing it.
3. The *Sphagnum* is tucked into the pine to maintain higher moisture for laying eggs. (I doubt that is the case.).
4. There is some commensal/symbiotic relationship going on, probably aphids, and the ants are improving conditions for aphids or other insects that will serve as food.

Stevenson returned to the site and found three more of these constructions (pers. comm. 22 June 2015). Not all were at the bases, but rather formed collars farther up the sampling trunk (Figure 75). The ants were scurrying about, on, and through, the moss collars (Figure 76). These collars were made of a variety of the materials available (Figure 77), but mostly of *Sphagnum fallax* (Figure 78) and *Aulacomnium palustre* (Figure 79-Figure 80), but also included leaves of *Polytrichum commune* (Figure 81), *Erica tetralix*, and *Calluna vulgaris*. Much of the composition was *A. palustre* tomentum (Figure 80). *Sphagnum* was tucked in among the leaves of the pine, well above the substrate (Figure 75).



Figure 75. Partial sleeve by *Lasius platythorax* at branching point on pine. This nest is at some distance from the tree base. Photo courtesy of Robin Stevenson.



Figure 76. *Lasius platythorax* in nest where they are running about. Photo courtesy of Robin Stevenson.



Figure 77. Sleeve material of *Lasius platythorax* collars that house aphids. Photo courtesy of Robin Stevenson.



Figure 78. *Sphagnum fallax*, a moss used by ants to make collars housing aphids on saplings of pines and birches. Photo by Michael Lüth, with permission.



Figure 79. *Aulacomnium palustre*, a common moss in ant-made moss collars in UK bogs. Photo courtesy of Robin Stevenson.

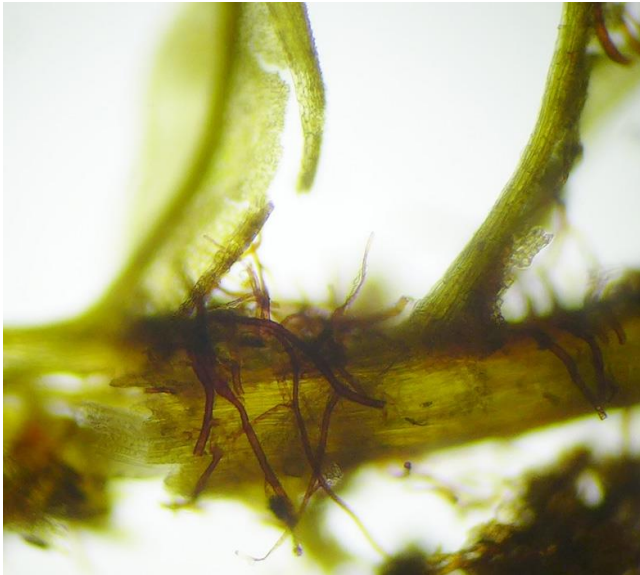


Figure 80. *Aulacomnium palustre* showing tomentum from ant nest at Durham Bog. Photo courtesy of Robin Stevenson.



Figure 81. *Polytrichum commune* fragments from nest of *Lasius platythorax*. Photo courtesy of Robin Stevenson.

So let's return to the moss collars to shed more light on these hypotheses. On another return visit, Stevenson had a "good look to see what the ants were up to: lots of scurrying about, and a few interactions with aphids – of which there didn't seem to be too many. However... when I broke a bit of sleeve off, there were a lot of aphids all huddled together underneath. So, it looks as if the ants are herding them under the cover of the sleeve – or might they shelter there of their own volition? Herding sounds more likely – but how does that work? I'd have thought that pine bark was a bit tough, even for an aphid's mouth parts, and they would have been better off up among the leaves?"

The ants were ultimately identified as *Lasius platythorax* (Figure 82-Figure 83) (Wells 2015). The aphids provide **honeydew** (Figure 84-Figure 85) for the ants, and the ants, in turn, police the stems with the nests (Figure 83, Figure 86), warding off a number of kinds of predators. Interestingly, the aphids are species-specific. That is, the birch aphids are *Symydobius oblongus*,

whereas those on the pine are *Cinara pini* (Figure 84-Figure 86).



Figure 82. *Lasius platythorax*, an ant that makes moss sleeves around saplings in bogs to cultivate aphids. Photo by April Nobile, through Creative Commons.



Figure 83. Ants (*Lasius platythorax*) and free aphids (*Cinara pini*) on pine stem at Durham Bog, UK. Photo courtesy of Robin Stevenson.



Figure 84. *Cinara pini* with honeydew drop at anus. This one is on *Pinus sylvestris*. Photo from <Influentialpoints.com>, through Creative Commons.

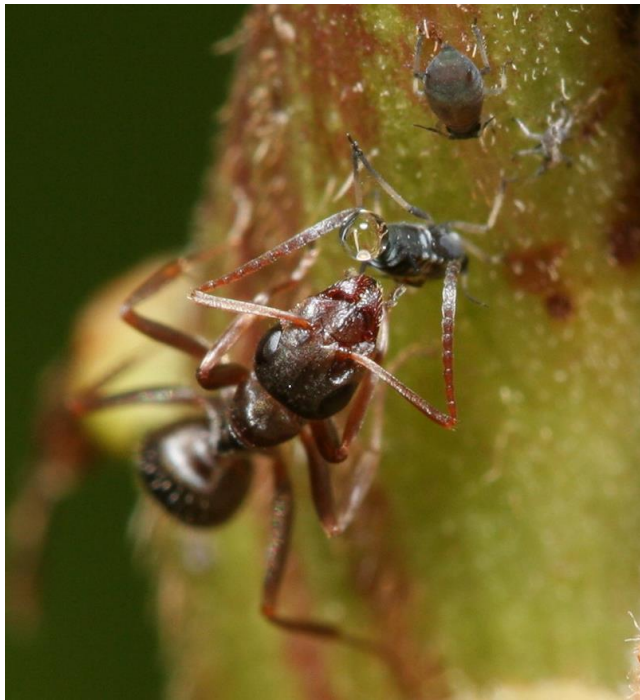


Figure 85. Ant feeding on aphid honeydew. Photo by Jmalik, through Wikipedia Commons.

Bauer-Dubau (2000) found that *Cinara pini* (Figure 84-Figure 86) produces more offspring when attended by ants. In Germany, the aphids on several pine species are heavily attended by the ant *Lasius fuliginosus* (Figure 87). The density of ants increased from 10-20 to 26-48 ants per colony in one generation. Without the ants, the aphid anus becomes covered with honeydew and the colony disperses.

Beattie (1985) reviewed ant service to aphids. That review demonstrated that the ants provide not only protection, but also sanitation and transportation, decrease their development time, and increase the colony growth rate, survivorship, and fecundity (Kennedy & Stroyan 1959; El-Ziady 1960; Banks 1962; Way 1963; Banks & Macauley 1967; Bristow 1982). Furthermore, the ants reduce parasitism by wasps (27.4-98.4% reduction) by preventing the egg-bearing female parasites from landing

on the aphids and ovipositing there (Bartlett 1961). Disturbance by ants resulted in 27.4% to 98.4% reduction in parasitism, depending on the parasite species. Ants even place aphids in areas that give them better access to the phloem that provides their food source (Banks 1962; Way 1963). The ants build shelters that protect them from rain and enemies, using soil, vegetation, and other materials (Andrews 1929; Levieux 1967; Duviard 1969; Duviard & Segeren 1974).



Figure 86. The aphid *Cinara pini* being attended by the wood ant *Formica rufa* on *Pinus sylvestris* at Flatropers Wood. Photo from <influentialpoints.com>, through Creative Commons.



Figure 87. *Lasius fuliginosus*, a species that attends the aphid *Cinara pini* on pines in Germany. Photo by Ab H Baas, with permission for non-commercial use.

Ants are known for feats of strength and strong societal behavior. In one recent study in Israel, Gelblum *et al.* (2015) describe their seemingly undirected behavior while carrying a Cheerio. The ants doing the carrying can't see what is ahead and often get off course. But navigator ants (scouts) occasionally enter the scene and direct the Cheerio carriers back on course. The communication between the scout and the carrier ants seems to be through the changed direction felt through the Cheerio. It would be interesting to observe whether similar carriers and scout leaders exist in the movements of mosses to make the mounds observed in bogs and fens or the collars around birch trees.

Bogs and Fens

One must be careful when reaching deep into a moss hummock to collect the moss because a swarm of ants may soon be on its way up one's arm! I have experienced this in several locations in North America. Rosengren (1969) and Collingwood (1979) relate the commonness of ants among *Sphagnum* turfs in Central Europe, where such ants as *Formica uralensis* (Figure 88) likewise carve nests (Figure 89) out of the peat (Stankiewicz *et al.* 2005) and hibernate under mosses in winter (Collingwood 1979). This species is restricted mostly to *Sphagnum* habitats. Matthey (1971) reported that both *Myrmica ruginodis* (Figure 39) and *Formica picea* (Figure 5) make nests in *Sphagnum*. As mentioned above, I have observed nests made of *Sphagnum* (Figure 90), but I was unable to identify the species. Blank Shaw found a similar nest in Maine (Figure 91).



Figure 88. *Formica uralensis*, an ant that nests in *Sphagnum* in Europe. Photo by Ruth Ahlburg, with permission.



Figure 89. Nest of *Formica uralensis*, made of *Sphagnum*. Photo by Ruth Ahlburg, with permission.



Figure 90. These ants are busy repairing their nest in this *Sphagnum* hummock on a windy day in Michigan's Upper Peninsula. Photo by Janice Glime.



Figure 91. Ant nest made of *Sphagnum rubellum* in Maine. Photo by Blanka Shaw, with permission.

Šteffek and Wiezik (2008) reported 11 species of ants in a peat bog at Hrabušice, N Slovakia. *Myrmica scabrinodis* (Figure 92) is dominant there in patches with the highest humidity. They build their colonies among the thick mosses. In Switzerland, the inhabiting *Myrmica ruginodis* (Figure 39) and *Formica picea* (Figure 5) form nests among the *Sphagnum* (Matthey 1971).



Figure 92. *Myrmica scabrinodis*, a dominant ant in peat bogs of northern Slovakia. Photo by Tim Faasen, with permission.

Certainly many insects are housed in mosses, but one of the most distinctive nests is the smooth dome built by ants in a fen. I watched these industrious creatures groom

their mound of *Sphagnum* continuously on a windy day, weaving each loose fragment of moss back into the construction (Glime, personal observation). They could barely move against the wind and often were moved backward by its force.

Lesica and Kannowski (1998) reported that the ants *Formica podzolica* (Figure 93), *Myrmica fracticornis* (Figure 94), and *M. incompleta* (Figure 95) are common in large rich fen complexes of Montana, USA. All three of these species build nests there. *Formica podzolica* nests are much larger than nests of the two species of *Myrmica* and occur in the hummock-hollow complex. The nests are about the size of a hummock, and likewise have elevated levels of K, PO_4^- , Mg, and Na similar to those of hummocks. Lesica and Kannowski (1998) suggested that the hummocks were actually abandoned ant mounds. Even here, the *Formica podzolica* gains most of its nutrition by tending the aphids that feed on the shrubs. And the shrubs are provided a rich habitat for establishment when they germinate in the mounds. Because of this germination relationship, the ants become ecosystem engineers that permanently change the structure and composition of the rich fen vegetation. But there is a feedback mechanism in which the ants benefit from the increase in host plants for the aphids.



Figure 93. *Formica podzolica* adult, a species that nests in large, rich fen complexes in Montana, USA. Photo by Tracy Barbaro, through Creative Commons.



Figure 94. *Myrmica fracticornis* adult, a species that nests in large, rich fen complexes in Montana, USA. Photo by Dan Kjar <www.discoverlife.org>, through Creative Commons.



Figure 95. *Myrmica incompleta* adult, a species that nests in large, rich fen complexes in Montana, USA. Photo by Tom Murray, through Creative Commons.

In a Norway mire, Collingwood (1976) found even greater diversity. Using pit-fall traps, Collingwood recorded 18 species in 13 mires habitats at Eidskog. Among these, *Formica forsslundi* and *F. transcaucasica* are ture mire species. Among the most abundant species were *Myrmica scabrinodis*, *M. ruginodis*, *F. transcaucasica*, and *Leptothorax acervorum*.

Ants can influence the distribution of other invertebrates in peatlands. Antonovic *et al.* (2012) suggested that the higher diversity of terrestrial isopods could in part be the result of predator pressure by *Myrmica* ants (and lycosid spiders).

Bees

Bees are disappearing in alarming numbers, so anything new we can learn about them may be important in saving them. It may surprise you to learn that a number of bees use mosses for various purposes.

Guy Brassard (Bryonet 31 March 2016) reported that bees on Ellesmere Island in the Canadian High Arctic use bryophytes in their nests! He identified more than 50 species of mosses and about 8 species of liverworts among the 47 nests, with an average of 6-7 species per nest. Some of the moss species were present in more than 25 nests and some in very few nests, suggesting that the bees are selective about the bryophytes chosen.

Annie Martin (Bryonet 31 March 2016) reported observations of honey bees, wasps, and butterflies gathering on mosses at her Mossery. They would sit for up to half an hour instead of just a quick stop. A beekeeper explained that worker bees gather water and take it back to the hive or nest. Given the choice between a puddle or larger water body compared to moss colonies, the bees seem to prefer the moss option! There didn't seem to be any species preference.

And if you are a moss gardener, beware. Martin also has found yellow jackets, carpenter bees, wasps, ants, and termites making their homes in giant *Polytrichum commune* (Figure 81) colonies.

Apidae – Honey Bees, Bumblebees, Carder Bees, etc.

Honey Bee

The small red dwarf honey bee, *Apis (Micrapis) florea* (Apidae; Figure 96-Figure 98) has a mysterious habit of collecting "something" from mosses. Sunil Chaturvedi observed this species probing the pots with mosses, whereas they were not doing this in nearby pots of similar moisture but no mosses (Bryonet 26 February 2011). Daniel McConnell, a US Forest Service botanist, reported seeing this behavior for many years (probably with a different honey bee species), and observed that it seemed to be much more common on calcareous mosses (Bryonet 27 February 2011). Wolfgang Hofbauer (Bryonet 28 February 2011) stated that "bees love to take in water at open moist places. For this purpose moss cushions seem to be very suitable. In spring beekeepers even offer them moistened moss cushions near their beehives."



Figure 96. *Apis florea* adult, a species that collects something, probably water, from bryophytes. Photo by John Ascher <www.discoverlife.org>, through Creative Commons.



Figure 97. *Apis (Micrapis) florea* on moss, apparently getting water, but perhaps not. Photo by Sunil Chaturvedi, with permission.

In their blogspot, the Hive Honey Shop recommends providing bees with water in summer (Beekeeping 2013). They warn not to use fresh water because the bees will not touch it. Rather, they prefer mature mineral-rich water.

Provide them with a number of places where they can land to get water without drowning. They suggest putting moss around the edges or in the water dish not only for safe footing, but also to filter the water and prepare it for drinking (Figure 98).



Figure 98. Close-up of *Apis (Micrapis) florea* on *Pohlia*, apparently getting water, or is it simply attracted by UV reflectance by the bulbils of the *Pohlia*? Photo by Sunil Chaturvedi, with permission.

But what draws the bees to the mosses? Sunil Chaturvedi suggested that the mosses may bring more bees to the area because of UV reflectance, hence increasing pollination of crop plants. These observations recalled to my mind the interesting observations of Gisela Nordhorn-Richter that demonstrated UV reflectance of *Pohlia* bulbils (Figure 99). Could it be that the bees are attracted to some bryophytes by UV waves, seen by bees but not by humans? Jon Shaw (pers. comm.) noted that the mosses observed by Sunil Chaturvedi appeared to be *Pohlia* with abundant bulbils (Figure 99). In any case, the mosses seem to be important sources of seasoned water for the bees.



Figure 99. *Pohlia bulbifera* bulbils. These fluoresce under ultraviolet light and could possibly attract bees. Photo by Des Callaghan, with permission.

Annie Martin (2015) reports that honey bees rest on the mosses in her moss garden, simply sitting quietly for a period of time. These bees drink the water on the leaves of the mosses. Beekeepers have suggested that the bees prefer moss water, possibly because of antibiotics in the water (Adventures in Natural Beekeeping 2017). This needs to be verified.

Grdović and Sabovljević (2008) also observed bees visiting bryophytes in beehive yards. They suggested that the bryophytes influence the humidity, maintaining a milder microclimate for the flowering plants and enabling those plants to remain moist longer and grow better. The same moisture provides a water source for the bees.



Figure 100. Honey bee (*Apis* so.) on *Sphagnum* cf. *palustre*, where it is able to get a drink of water and rehydrate. Photo courtesy of J. Paul Moore.

One could pose several hypotheses for this bee activity on mosses. Tom Thekathyl stated that bees and wasps often "imbibe water" from the surfaces of mosses and suggested that the mosses may have tiny pools of free water that are not available on the bare soil. This is a reasonable hypothesis, given the tiny capillary spaces on mosses that typically hold water longer than the soil surface. The straw-like mouth parts (Figure 101) of the honey bees would permit them to extract water from these tiny droplets.



Figure 101. Honey bee proboscis. Photo from <www.MzePhotos.com>, through Creative Commons.

Another hypothesis is that the water quality might be different on the mosses. On calcareous soil, high concentrations of carbonates might deter the bees, whereas the capillary water of the mosses could be altered by the cation exchange on the moss surface, or by the addition of oxygen from photosynthesis. This suggestion is supported by the observations at the Hive Honey Shop (Beekeeping 2013).

Water certainly seems to be a likely motivator. Bashir Yusuf Abubakar, Bryonet 28 February 2011, pointed out that water is a prime requirement of bees in culture such

that they are always available in moistened areas. One can even find them surrounding a dripping tap. The water retention capacity of mosses varies between mosses and could account for differences in visitation frequencies.

The bee mouthparts facilitate the use of tiny drops of water such as those on bryophytes. The proboscis (Figure 101) uses capillary action and suction to draw a fine stream of liquid to the mouth (Krenn *et al.* 2005).

Bumblebees

Guy Brassard (Bryonet 1 June 2010) identified bryophytes from 47 bumblebee nests, primarily *Bombus polaris* (Figure 102) and *Bombus hyperboreus* (Figure 103) on northern Ellesmere Island, in the Canadian High Arctic (Richards 1973). The use of mosses helps to insulate the nests, permitting these two bees to survive farther north than other bumble bees (Heinrich 2004). But then, *B. hyperboreus* is a parasite on *B. polaris*. Hence, the behavior of *B. polaris* determines the temperature control for both species.

Bombus polaris sometimes takes advantage of the activities of rodents, building their own nests in lemming and other burrows, but these locations are too cold. Instead, most build their nests in meadows and marginal pools on flat areas, in depressions, and beside small hummocks of mosses or other vegetation. Entrances typically faced the sun during the daily temperature peak, and rearranging the mosses to suit their needs (Richards 1973). The female pulls the moss with her mandibles and forelegs, pushing it under her body with her mid- and hind legs to the desired position. The queens and assisting workers continue to rearrange the bryophytes as the colony expands. Guy Brassard (pers comm. 1 April 2016) reported to me that an individual nest typically had 2-14 species of bryophytes and an average of about 6 or 7 species per nest. These comprised at least 56 species of mosses and 6 species of liverworts overall (see Richards 1970). Only one of the nests lacked any bryophytes. Bryophytes were typically intermixed with dried sedge leaves to cover the nest and create a thick, tight surface of insulation. The most frequent bryophyte species were all common in the region. The following were the most often found (with total number of nests out of 47): *Campylium arcticum* (33) (Figure 107); *Orthothecium chryseum* (29) (Figure 109); *Drepanocladus revolvens* (28) (Figure 108); *Distichium capillaceum* (21) (Figure 105); *Ditrichum flexicaule* (19) (Figure 106); also *Bryum* sp. (38 – tiny unidentifiable scraps) (Figure 10). The three pleurocarpous species were usually dominant or abundant; the others were often very minor components.



Figure 102. *Bombus polaris*, a species that uses mosses in its nest. Photo by J. C. Schou, with permission.



Figure 103. *Bombus hyperboreus* adult, a species that uses mosses in its nest. Photo by Marko Mutanen, through Creative Commons.



Figure 106. *Ditrichum flexicaule*, one of the species used in bee nests. Photo by Michael Lüth, with permission.



Figure 104. *Apoidea* nest uncovered from mosses, showing bees in the nest. Photo by Panoramedia, through Creative Commons.



Figure 107. *Campylium arcticum*, one of the species used in bee nests. Photo by Michael Lüth, with permission.



Figure 105. *Distichium capillaceum*, one of the species used in bee nests. Photo by Michael Lüth, with permission.



Figure 108. *Drepanocladus revolvens*, one of the species used in bee nests. Photo by Kristian Peters, with permission.



Figure 109. *Orthothecium chryseum*, nesting material for bees. Photo by Michael Lüth, with permission.

Bumblebees (*Bombus*; Figure 110) can use abandoned mouse nests in areas with tussock grass or moss (Saunders 2015). Goulson (2010) found that suitable sites for nesting provided insulating materials for the nest. Such materials include mosses, feathers, hair, and grass. Harvey (2015) echoed this advice for rearing bees, including the need for attracting mice and voles to create nesting sites. In fact, Sladen (2014) reported that a carder bee may build its own nest when moss is abundant instead of occupying abandoned nests of small animals.



Figure 110. *Bombus* sp. adult, a genus that uses abandoned mouse nests that often contain mosses. Photo by Yann, through Creative Commons.

Fussell and Corbet (1992) found that nesting sites differed significantly among color groups of British bumblebees. These involved position of the nest relative to ground level, time of day at which direct sunlight reached the nest, and nature of the immediate environment of the nest.

Bumblebee visits to bryophytes may be facultative (Grdović & Sabovljević 2008). These researchers did find that a relationship of the bees with the bryophytes was supported statistically, suggesting that humidity and a milder microclimate supported the relationship.

Even bumblebees that do not build nests of mosses may find them useful for overwintering. *Bombus lucorum* (white-tailed bumblebee; Figure 111), *B. lapidarius* (Figure 112), and *B. hortorum* (garden bumblebee; Figure

113) spend their winter in mosses (Alford 1969). *Bombus pratorum* (early bumblebee; Figure 114) uses mosses facultatively – overwintering sometimes in moss, sometimes underground.



Figure 111. *Bombus lucorum* adult, a bee that overwinters among mosses. Photo by James K. Lindsey, with permission.



Figure 112. *Bombus lapidarius* adult, a bee that overwinters among mosses. Photo by Beate & Heinz Beyerlein, through Creative Commons.



Figure 113. *Bombus hortorum* adult on protonemata on soil. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 114. *Bombus pratorum* adult sometimes overwinters in mosses and sometime underground. Photo by Aiwok, through Creative Commons.

Carder Bees

Carder bees include the moss carder bee, *Bombus muscorum* (Figure 115). These bees are so-named because they cleanse/comb the mosses before inserting them into the nest construction (Smith 1876). They typically build the nest entirely of moss, working it with their feet into a compact mass that resists the weather (Cuthbert 1895). If mosses are abundant, the nest may be made entirely of mosses, but if mosses are scarce, they may build nests with no mosses. The nest is comprised of a series of cells connected by coarse brown wax (Cuthbert 1895).



Figure 115. *Bombus muscorum* adult, a species that uses mosses to build its nest. Photo by J. C. Schou <www.biopix.com>, through Creative Commons.

Rennie (1857) describes the nest-building of *Bombus muscorum* (Figure 115) as a series of backward pushes. The bees establish a line of up to 6 bees to transport the moss from the source to the nest. The last bee in the file grabs some moss with her mandibles, disentangling it and carding it with her forelegs into a small bundle. She pushes this bundle under her body to the next bee, who passes it to the next with the same under body move, and so forth.

The nest has a long, arched passageway that is formed by a variety of mosses, wide enough to permit free passage for the bees (Smith 1876). The final nest has a dome of 10-15 cm above the ground (Rennie 1857). Wax from the bees forms the ceiling, repelling rain and preventing high winds from carrying away the nest. During the day, the top of the dome may be opened more than 2.5 cm, apparently to ventilate the nest. It is not used for entry, and it is closed again at night. Instead, there is an entrance passage at the bottom of the nest that is about 30 cm long and 1.2 cm

wide. The larvae spin cells. When the grubs are ready to emerge, it is the older bees that chew off the cover to free them. One of these spheres may house 3-30 eggs. Rennie found that the adults were of a color similar to the moss they used.

Bombus muscorum (Figure 115) carders collect mosses and dry grass, constructing the nests on or just under the ground (Wikipedia 2015a). The mosses and grass are used to cover the nest. Once the nest is completed, the bee aggressively protects it, attacking intruders by biting and stinging them simultaneously.

The carder bees differ from other members of *Bombus* that nest underground (Carvell 2002). The partially above ground nesting by carder bees seems to necessitate the grass-moss habitat to maintain warmth. Nevertheless, there is a negative relationship between number of carder bees and depth of moss. On the other hand, Jukes (2008) reported that *Bombus muscorum* (Figure 115) in Sussex made its nest in deep moss in exposed places.

Iles (2010) listed the carder bees *Bombus humilis* (Figure 116), *B. sylvarum* (Figure 117), and *B. muscorum* (Figure 115) as species that require tall grassland with "plenty of leaf litter or moss" to use as nesting material. *Bombus pascuorum* (Figure 118) appears to be more flexible, as indicated by its many habitats. Similarly, *Bombus ruderarius* (Figure 119) builds its nest at the surface or just below, using grass and mosses, and likewise often utilizing an abandoned mouse or vole nest (Benton 2008).



Figure 116. *Bombus humilis* adult, a species that uses mosses to build its nest. Photo by Tim Faasen, with permission.



Figure 117. *Bombus sylvarum* adult, a species that uses mosses to build its nest. Photo by James K. Lindsey, with permission.



Figure 118. *Bombus pascuorum* adult, a species that uses mosses in its nests, but that occupies a variety of habitats. Photo through Creative Commons.



Figure 119. *Bombus ruderarius* adult, a species that nests under mosses and grasses. Photo by James K. Lindsey, with permission.

The common carder bee, *Bombus pascuorum* (Figure 118), is widespread in Europe, living in meadows, waste ground, ditches, embankments, roads, gardens, parks, and forests (Wikipedia 2015b). Like the moss carder bee *B. muscorum*, this species also collects mosses and grasses, constructing a small, hollow sphere. Walls of this sphere are bonded with wax and sealed off. Inside they form a large bowl (5 mm diameter) of brown wax filled with pollen. They deposit 5-15 eggs, then close the cell. They fill a second chamber (20 mm high) with nectar to provide a food reserve for days when weather is not suitable for foraging. Larvae hatch in 3-5 days, then spend only a week to mature as they feed on the food reserves.

Braconidae – Parasitic Wasps

In New Zealand, a new genus, *Shireplitis*, was described as mostly in moss, litter, or tussock grasslands (Fernández-Triana *et al.* 2013). *Parolitis wesmaeli*, also **Braconidae**, from Europe, is a parasitic wasp that uses larvae of *Scoparia basistrigalis* (Pyralidae) and *Bryotropha umbrosella* (Gelechiidae) (both **Lepidoptera**) as hosts. Larvae of both of these hosts feed from their silken tube or tent, grazing on mosses and grasses. Four of the *Shireplitis* species (*e.g.* Figure 120) were themselves collected from mosses and may likewise live on moss-eating **Lepidoptera**. Fernández-Triana *et al.* considered the robust body and legs with shortened antennae of these

Braconidae to be adaptive for moving among "litter" while searching for hosts. See Chapter 12-14 for further discussion of the **Lepidoptera** hosts.



Figure 120. *Shireplitis bilboi* adult, an inhabitant of *Sphagnum* and grasses. Photo through Creative Commons.

Cynipidae and Mimicry

Some members of the **Cynipidae** take advantage of mosses in a different way. *Diplolepis rosae* (Figure 121) causes a gall formation that resembles a moss to house its eggs and larvae (Callan 1940).



Figure 121. *Diplolepis rosae* gall, a mimic of real mosses. Photo by Björn Appel, through Creative Commons.

Diprionidae – Conifer Sawflies

Jarmo Holopainen (pers. comm. 16 September 2011) found that in experiments pupae of pine sawflies (*Neodiprion sertifer* – **Diprionidae**; Figure 122-Figure 125) had a higher emergence rate when kept in *Sphagnum* peat. He suggested that the antibiotic properties of peat helped to increase wasp survivorship.



Figure 122. *Neodiprion sertifer* female and male adults, a species that has a higher emergence rate when kept among *Sphagnum*. Photo by Jarmo Holopainen, with permission.



Figure 123. *Neodiprion sertifer* larva and eggs, a species that survives better when cultured in *Sphagnum*. Photo by Jarmo Holopainen, with permission.



Figure 124. *Neodiprion sertifer* larvae, a species that survives better when cultured in *Sphagnum*. Photo by Jarmo Holopainen, with permission.

Ichneumonidae

Among the **Ichneumonidae**, twelve genera are able to overwinter as adults (Duffield & Nordin 1970). These take advantage of the insulating properties of logs, rocks, and mosses to endure the extreme conditions of winter. Those that overwinter accumulate glycerol and sorbitol when

subjected to cold temperatures of winter. Dana <Abundantnature.com> tells of lifting a clump of moss from a rock and discovering not one, but two, species of *Ichneumon* hibernating there as adults (Figure 126-Figure 128).



Figure 125. *Neodiprion sertifer* pupa, a species that has higher emergence rates when cultured in *Sphagnum*. Photo by Jarmo Holopainen, with permission.



Figure 126. Habitat of *Ichneumon cf mendax* hibernating adults. Photo by Dana <Abundantnature.com>, with permission.



Figure 127. *Ichneumon cf mendax* and a second species, hibernating adults under mosses. Photo by Dana <Abundantnature.com>, with permission.



Figure 128. *Ichneumon cf mendax* hibernating adult that has been disturbed. Photo by Dana <Abundantnature.com>, with permission.

Lungu-Constantineanu and Constantineanu (2014) found the importance of mosses as hibernation sites for at least 10 species of **Ichneumonidae** in the Bârnova Forest Massif, Romania. They found six types of hibernation sites, two of which required mosses. Ten of these sites were between the cracks of bark covered by moss. Others were in dense carpets of mosses on stones. They found that pollution reduced the moss cover, resulting in the disappearance of large ichneumonid clumps with dozens of hibernating individuals. Instead, the hibernating ichneumonids were mostly isolated individuals. The mosses that contributed to the large number of habitats for ichneumonid hibernation between cracks of bark of old but living trees were *Anomodon attenuatus* (Figure 130-Figure 131), *A. viticulosus* (Figure 132-Figure 133), *Brachythecium salebrosum* (Figure 134), *Hypnum cupressiforme* (Figure 44), *Platygyrium repens* (Figure 135), and *Porella platyphylla* (Figure 136). These ichneumonids under mosses in the cracks in tree bark were *Apaeleticus mesostictus*, *Deloglyptus pictus*, *Diadromus troglodites* (Figure 137), *Herpestomus brunnicornis* (Figure 138), *Heterischnus truncator*, (Figure 139),

Ichneumon balteatus (Figure 140), *Ichneumon simulans* (Figure 141), *Rhadinodonta flaviger* (Figure 142), and *Tycherus cephalotes* (= *Phaeogenes cephalotes*). Only one species of ichneumonid (*Cinxaelotus erythrogaster*) hibernated on the rocks, where *Mnium stellare* (Figure 143) covered them.

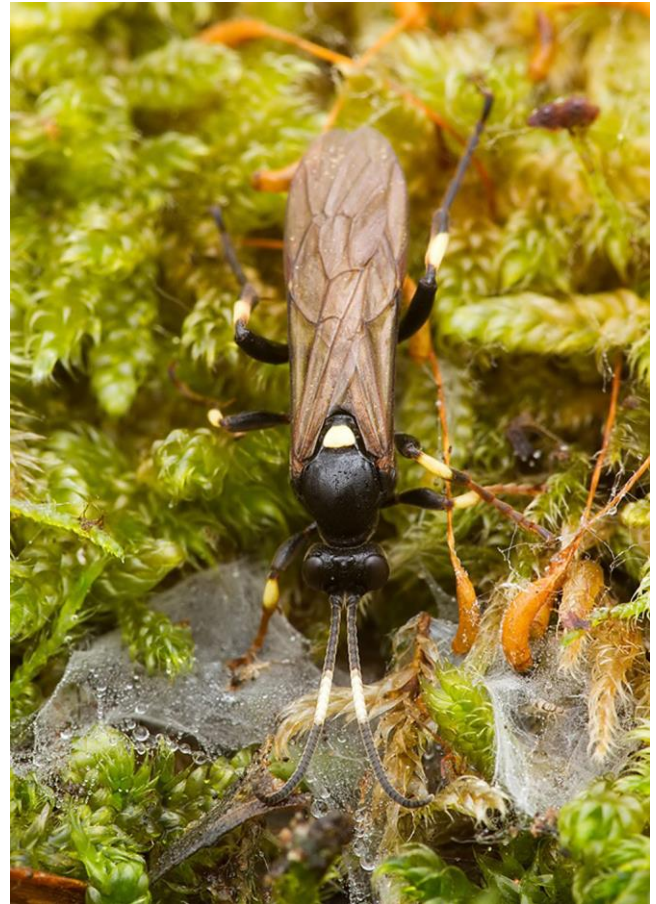


Figure 129. *Ichneumon stramentor* adult on moss, a species that hibernates as an adult under mosses. Photo by Ladislav Tábi, with permission.



Figure 130. *Anomodon attenuatus* on tree base, covering cracks in the bark where ichneumonid adults overwinter. Photo by Bob Klips, with permission.



Figure 131. *Anomodon attenuatus*, a moss that provides insulation for ichneumonids overwintering in cracks and under bark. Photo by Michael Lüth, with permission.



Figure 132. *Anomodon viticulosus* covering cracks in bark where ichneumonids overwinter. Photo by Michael Lüth, with permission.



Figure 133. *Anomodon viticulosus*, overwintering home for adult ichneumonids in cracks in bark. Photo by Michael Lüth, with permission.



Figure 134. *Brachythecium salebrosum* covering broken bark where ichneumonids overwinter. Photo by Michael Lüth, with permission.



Figure 135. *Platygirium repens* on bark, covering cracks where ichneumonid adults overwinter. Photo by Dick Haaksma, with permission.



Figure 136. *Porella platyphylla* on bark, overwintering home for adult ichneumonids in cracks in bark. Photo by Michael Lüth, with permission.

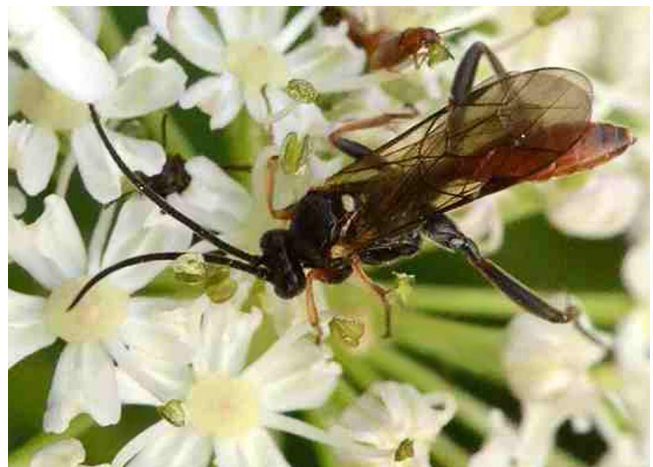


Figure 137. *Diadromus troglodytes* adult, a species that hibernates in cracks in bark under mosses. Photo by James K. Lindsey, with permission.



Figure 138. *Herpestomus brunnicornis* adult, a species that hibernates in cracks in bark under mosses. Photo by Marko Mutanen, through Creative Commons.



Figure 141. *Ichneumon simulans* adult, a species that hibernates under mosses in cracks in bark. Photo by James K. Lindsey, with permission.



Figure 139. *Heterischnus truncator* adult, a species that lives in cracks in tree bark under mosses. Photo by Jonas Lutz, through Creative Commons.



Figure 142. *Rhadinodonta flaviger* adult, a species that hibernates in cracks in bark under mosses. Photo by Stefan Schmidt, through Creative Commons.



Figure 140. *Ichneumon balteatus* adult, a species that hibernates in cracks in bark under mosses. Photo by Stefan Schmidt, through Creative Commons.



Figure 143. *Mnium stellare* on rock outcrop, providing an overwintering habitat for *Cinxaletus erythrogaster*. Photo by Michael Lüth, with permission.

But overwintering is not the only use they make of mosses. Sarah Lloyd caught one in the act of ovipositing among mosses (Figure 144).



Figure 144. Ichneumonid wasp ovipositing on moss. Photo courtesy of Sarah Lloyd.

Pompilidae

Bees and wasps do not seem to be usual active inhabitants of bryophytes, but the rare spider wasp, *Anoplius caviventris* (Pompilidae; Figure 145) in Sweden lives in a *Sphagnum* habitat (Berglind 1993). In Sweden, this species was found in 1991 and 1993 in a reed swamp (*Phragmites communis*) where it was living on mosses, primarily *Sphagnum* in three different mires.



Figure 145. *Anoplius caviventris* adult, a *Sphagnum* dweller in Sweden. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Scelionidae

It appears that among the **Hymenoptera**, the ants are the only ones with well-developed relationships in peatlands. However, Austin (1988) did find a new genus of wasps in the **Scelionidae** to be associated with mosses in New Zealand. Austin (1988) described this new genus, based on *Neobaeus novazealandensis*. Austin found that collection data indicate this species lives on moss-covered ground, with 80% of the specimens collected by putting mosses in Berlese funnels. This species differs from *Baeus* in having a micropterous (short-winged) male. Austin suggested that wings would hinder movement in this mossy habitat.

Sphecidae

O'Brien (1987) observed *Tachysphex aethiops* (Sphecidae; Figure 146) digging at the bases of clumps of moss on sand. They inspected the burrow entrances throughout the day at various times. Females of this species typically nest in mossy sand slopes where they use pre-existing burrows made by other kinds of insects. One female intermittently removed sand from a burrow, raking the sand onto the nest mound after carrying several loads out of the nest.



Figure 146. *Tachysphex aethiops* adult, a species that nests in mossy sand slopes. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Vespidae – Wasps

The yellow jackets [*Vespa* (Figure 147) and *Dolichovespa* (Figure 148); **Vespidae**] are best known for their papery aerial nests (Figure 149). But they also can inhabit mosses such as *Polytrichum* (Figure 28-Figure 29) with at least 15-20 cm of soil attached, where they constantly go in and out (Annie Martin, pers. comm. 6 October 2013).



Figure 147. *Vespula germanica* worker, a species that sometimes lives under mosses. Photo by James K. Lindsey, with permission.



Figure 148. *Dolichovespula arenaria* adult, member of a genus that sometimes lives under mosses. Photo by Gilles Gonthier, through Creative Commons.



Figure 149. *Vespula vulgaris* nest showing the interior intricacies of this papery nest. Photo by Richerman, through Creative Commons.

A Calyptra Mimic

This story lacks a critical detail – the name of the wasp. But it is too interesting to omit, and perhaps someone can shed light on the wasp involved.

Györfy (1952) tells of checking out the twin capsules on the seta of *Polytrichum strictum* (Figure 150). Upon

closer examination, he found that these were not Siamese twins, but rather a capsule with its calyptra and a wasp cocoon, both perched on a single seta. In one of his favorite haunts in Austria, Györfy had seen these "twin capsules" among the "billions" of plants of this moss species in the harvested peat bogs. In this exploration, what he found was that the second twin was a lemon yellow cocoon closely adjacent to the calyptra, and from these cocoons deep black larvae hatched. Mimicry of a calyptra by Hymenoptera – or any other invertebrate – seems to be reported only here. Györfy concluded that such mimicry protected the larvae from cocoon-eating birds as they would prefer to do their "gymnastics" on tree branches.



Figure 150. *Polytrichum strictum* capsules with calyptrae – a structure mimicked by the egg cocoon of a wasp. The insect shown here appears to be an orthopteran – also somewhat resembling the covered capsules. Photo by Michael Lüth, with permission.

Summary

Ants have flexible bodies that permit them to maneuver among the bryophytes. The ants are able to chew and move the bryophytes, permitting them to build trails through the bryophytes, making their foraging easier. They defend themselves with strong mandibles, stings, and chemical sprays. They keep their nests clean. Some remove the tracheophytes around their nests, thus creating space where bryophytes can grow.

Bryophytes provide insulation that maintains a buffered temperature and moisture. For some ants such as *Messor*, bryophytes also provide food, especially the capsules, but some are also known to eat the leafy plants. Bryophytes also provide a suitable habitat for some of their predators such as salamanders. Even bears may forage in the bryophytes for ants. As the ants move about, spores, fragments, and gemmae may be trapped between the body hairs and get transported to a new location.

Some bryophytes are prone to growing on ant hills, possibly taking advantage of the higher concentration of nutrients or being raised above the forest floor where

they can avoid burial by leaf litter. They also avoid competition. Some take advantage of the north-facing slope to reduce desiccation.

A number of ant species use bryophytes in building nests. *Sphagnum* in particular is used, in some cases to make a nest for aphids that provide honeydew for the ants. Ants may be responsible for the hummocks in some peatlands. Some ants create arboreal gardens, using mosses and planting seeds among them. Others place seeds under mosses on the ground, providing them with a suitable protected germination site.

Bryophytes in the environment provide sites for finding drops of water and seeking cover. Others use them for finding food or laying eggs. Epiphylls on leaves, especially in tropical forests, may produce compounds that discourage herbivory on the leaves.

Honeybees appear to use bryophytes for obtaining water from that resting on the bryophytes. Beekeepers often place bryophytes near hives to provide watering sites, but species such as *Pohlia* spp. may attract more bees by reflecting UV light.

Bumblebees use bryophytes in their nests. Some species overwinter under the bryophytes. Carder bees build elaborate nests, partly above ground, lined with bryophytes.

Some species of the parasitic wasps in **Braconidae** are consistently associated with mosses because their lepidopteran hosts live there. One member of the **Cynipidae** mimics mosses with the galls it makes. For some **Hymenoptera**, the peat helps survival, possibly through antibiotic properties. A number of **Ichneumonidae** overwinter in and under mosses and some may oviposit there. Some members of **Pompilidae** live in *Sphagnum* habitats. The scelionid *Neobaeus novaezealandensis* lives on moss-covered ground. Even the wasps sometimes nest under mosses such as *Polytrichum*.

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CHAPTER 12-11

TERRESTRIAL INSECTS:

HOLOMETABOLA – TRICHOPTERA

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CHAPTER 12-11

TERRESTRIAL INSECTS:

HOLOMETABOLA – TRICHOPTERA



Figure 1. *Eniocyba pusilla* larva, the most common terrestrial caddisfly and often a moss dweller. Photo by John Bingham, with permission.

The adults of caddisflies are terrestrial, but most caddisflies have aquatic larvae. Nevertheless, a few have adapted to living in wet places on land. And mosses can provide those wet places. For example, Sleight (1913) described one member of **Limnephilidae** in mosses at tree roots, but not in the water.

Some aquatic larvae are able to feed near the surface of water. The aquatic *Pycnopsyche guttifera* (Figure 2) will sometimes eat terrestrial mosses, but this occurs when the mosses are just below the water line (Williams & Williams 1982).



Figure 2. *Pycnopsyche guttifera* larva, a larva that eats terrestrial mosses when they become submersed. Photos by Tom Murray, through Creative Commons.

Larvae

We now know that there are three species of terrestrial *Enoicyla* (**Limnephilidae**; Figure 1) in Europe, and that larvae of these live in the humid and temperate mosses of deciduous forests and rock crevices (Crampton 1920; Meidl & Molenda 2000), often far from water (Crampton 1920). Perhaps the best known of these terrestrial larvae are those of *Enoicyla pusilla* (Figure 3-Figure 5). These larvae build cases from fine grains of sand and vegetable matter among mosses (Butler 1886). In Britain, *Enoicyla pusilla* is restricted to woodlands, and Harding (1998) suggested that it may have been accidentally introduced from the European continent. This species has five larval instars, becoming more scarce by late summer. Eggs hatch in October and November, and larval success may depend on rainfall during those months. The larvae of this species typically occur among mosses and leaf litter.



Figure 3. *Enoicyla pusilla* larvae, a species that inhabits mosses and leaf litter. Photo by Ernest van Asseldonk, through Creative Commons.



Figure 4. *Enoicyla pusilla* larva feeding on a slime mold. Photo by John Bingham, with permission.



Figure 5. *Enoicyla pusilla* adult, a species whose larvae live among terrestrial mosses. Photo by James K. Lindsey, with permission.

Green (1997) reported that in the UK the larvae of *Enoicyla pusilla* (Figure 3) feed on the soft tissues of dead leaves, mosses, and algae. In one observation, 50 or more individuals were actively climbing up logs and apparently browsing on black slime molds (Green 2012). Their requirement for nearly 100% humidity limits their terrestrial habitats. They have no gills and must rely on cutaneous respiration. If they get too wet, they climb upward and "hang themselves out to dry." When the humidity decreases to 70%, they drop again to the ground. Sometimes many larvae occur together on the surfaces of mosses and liverworts on stream banks after a rain (Green & Westwood 2005; Green 2012).

Flint (1958) considered that *Ironoquia pusilla* in northeastern United States closely resembled *Enoicyla pusilla* in its pupal stage. He reported that the larvae of *I. parvula* left the water and climbed to land where they spent their pupal stage among the leaf litter.

Another genus of caddisfly that lives on land as larvae is *Manophylax* (**Apataniidae**) (Chuluunbat *et al.* 2010). *Manophylax futabae* larvae can be found on the vertical sides of large rocks 10-30 m from mountain streams, as well as on vertical rocky outcrops. Chuluunbat and coworkers found that these larvae were often covered with mosses and lichens, but assumed that their only water usually came from precipitation. *Manophylax alascensis* and *M. annulatus* both construct their cases (4.0-9.8 mm) from fine rock fragments with attached moss and algal fragments dorso-laterally.

It may be that the movement of Trichoptera to land began with species that moved there to feed. *Desmona bethula* (**Limnephilidae**) is one such species (Erman 1981). When it reaches its fifth instar, it adventures from the water to feed on semiaquatic plants. But for this species, inclusion of bryophytes is not known.

Oviposition

If there are larvae on land, then there must be oviposition on land, at least for species that are not adjacent to water. It is interesting that the information I have found on the terrestrial caddisflies is not well linked. We know about the larvae of *Enoicyla* (Figure 3-Figure 5) feeding on bryophytes, but I have found no discussion of their oviposition. On the other hand, I have found information on egg-laying in the **Leptoceridae**.

Leptorussa darlingtoni (**Leptoceridae**) females become active in late afternoon in oviposition (Towns 1983). In Australia, most had congregated in damp mosses near the water surface, with 30 adults along an 80-cm line at 10-20 cm above the water. *Leptorussa darlingtoni* deposits its egg masses in communities above the water, whereas *Lectrides varians* (Figure 6), also in the **Leptoceridae**, deposits a single egg mass at 65-95 cm above the water. For *Leptorussa darlingtoni*, the egg masses are placed in small crevices, but they are always near extensive moss cover. Nevertheless, the moss moisture does not seem to be important as the eggs survive in these same locations when the mosses are dry in years with little rainfall. Towns suggested that the terrestrial deposition may be an avoidance of the fluctuating oxygen levels in the water. In fact, when Towns attempted to rear the eggs on damp mosses in the laboratory, fungal infections caused death of the eggs. Towns asserted that *Leptorussa darlingtoni* is the only species of caddisfly that has communal oviposition and hatching without water.

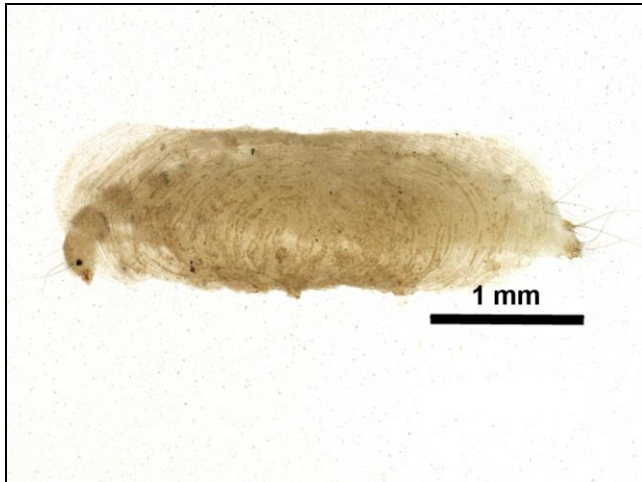


Figure 6. *Lectrides varians* larva, a species that deposits its eggs where there are lots of mosses. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Pupation

Most of the aquatic larvae of **Trichoptera** remain in the water to pupate, emerging onto vegetation or rocks to climb out of the water as adults. But if larvae can live on land, we can assume that their pupae, and perhaps pupae of others, may survive terrestrial life. Erman (1984) suggested that terrestrial pupation in this group evolved as an adaptation to living in intermittent streams. Some larval members of **Limnephilidae** leave the water in the final instar to pupate on land. *Limnephilus peltus* (see Figure 7) leaves spring streams shortly after the snow melts in the Sagehen Creek basin, California, USA, to burrow into the mosses at the edges of fen streams. If the spring flow ends too early and the mosses dry, some pupae may die without any adult emergence.

Another caddisfly, in the **Goeridae**, *Archithremma ulachensis*, spends its larval days in a layer of *Sphagnum* (Figure 8) on a springbank (Levanidova & Vshivkova 1984). Its pupa seems to be adapted to this dense terrain. It lacks long setae and projections used by other pupae in

the family to clean the silk disks that close the case. The first abdominal segment lacks posterior rugosity, and there are no swimming legs. The larvae, however, live in water courses that have cold summer temperatures (3-5°C). The authors consider these cold brooks to have less food competition, thus favoring the larvae of this species.



Figure 7. *Limnephilus* sp. larva; *L. peltus* burrows into mosses to pupate. Photo by Jason Neuswanger, with permission.



Figure 8. *Sphagnum capillifolium*; *Sphagnum* is home for the larvae of *Archithremma ulachensis*. Photo by Bernd Haynold, through Creative Commons.

Hayashi *et al.* (2008) cite the terrestrial habits of the limnephilid *Nothopsyche*. This genus has species in which both pre-pupae and pupae are entirely terrestrial. Their mitochondrial data indicate that this genus was originally aquatic and that just one lineage became terrestrial in the pre-pupal and pupal stages. In this terrestrial lineage, *Nothopsyche montivaga* became completely terrestrial. The terrestrial line also exhibit a switch in case materials from plant matter to sand.

Bogs

For an order of insects evolving from water to land, bogs would seem to be the ideal place to begin. The mosses wick water upward, remaining moist most of the year. Furthermore, water can often be reached by moving downward.

Buczyńska *et al.* (2012) searched for the rare *Hagenella clathrata* (Phryganeidae; Figure 9-Figure 10) in Poland. This species is associated with bogs, making it even more threatened due to habitat destruction. This research team was able to collect larvae in the mountain area using Barber pitfall traps, indicating their mobility in terrestrial habitats.



Figure 9. *Hagenella clathrata* larva, a species that lives in bogs. Photo by Marko Mutanen, through Creative Commons.



Figure 10. *Hagenella clathrata* adult, a bog dweller. Photo by Rob Felix, through Creative Commons.

Summary

Few of the caddisfly larvae have adapted to terrestrial living, and even fewer use bryophytes for their terrestrial adventures. Several of the bryophyte associates are in the **Limnephilidae**. *Pycnopsyche guttifera* sometimes eats terrestrial mosses that extend below water. *Limnephilus peltus* burrows into mosses to pupate. But the best known example is that of *Enoicyla pusilla*, larvae that live terrestrially and include mosses in their varied diet.

Larvae of *Manophylax* (Apataniidae) may include mosses in their cases. *Leptorussa darlingtoni* (Leptoceridae) lays eggs near water in damp mosses, but the eggs can dry safely and thus may not require mosses. Larvae and pupae of *Archithremma ulachensis* (Goeridae) live among *Sphagnum*. *Hagenella clathrata* (Phryganeidae) likewise live in bogs.

Acknowledgments

Thank you to those photographers who gave me permission or placed their images in Creative Commons. For this chapter, I would welcome additional images!

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CHAPTER 12-12

TERRESTRIAL INSECTS:

HOLOMETABOLA – LEPIDOPTERA

BIOLOGY AND ECOLOGY

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CHAPTER 12-12

TERRESTRIAL INSECTS:

HOLOMETABOLA – LEPIDOPTERA

BIOLOGY AND ECOLOGY



Figure 1. These **Lepidoptera** seem to be on these epiphytic bryophytes for a reason, but often we don't know why. Photo by Janice Glime.

Lepidoptera

I was surprised to find that in one study in Romania Dincă (2005) found that 1.8% of the approximately 1000 Macrolepidoptera taxa were "moss" consumers. Pierce (1995) stated that larvae that live in mosses have an environment that is close to aquatic. But few **Lepidoptera** live in the water, so we can expect that these terrestrial insects may have other reasons for visiting or living in bryophytes. On the other hand, the **Trichoptera** and **Lepidoptera** are closely related (Crampton 1920; Shields 1988; Britannica 2008), and most **Trichoptera** larvae are aquatic. Shields contends that the **Lepidoptera** evolved from aquatic **Trichoptera**, so it is therefore predictable that some have strong needs for moisture. This divergence

most likely occurred in the late Triassic at a time when many streams were dry and water was scarce, eliminating many insects that were dependent on water.

Klok and Chown (1997) report that water balance is important for the sub-Antarctic caterpillar, *Pringleophaga marioni* (**Tineidae**; Figure 2). But these moths seem to have no mechanisms for preserving or regulating their water, hence requiring moist habitats. One of these habitats for the larvae is in the mire moss *Sanionia uncinata* (Figure 3) (Burger 1978). These moths are wingless as adults and thus have a limited distribution on Marion Island.



Figure 2. *Pringleophaga marioni* adult, a sub-Antarctic moth with no known mechanism to regulate water. Photo by S. L. Chown, B. J. Sinclair, H. P. Leinaas, and K. J. Gaston, with permission.

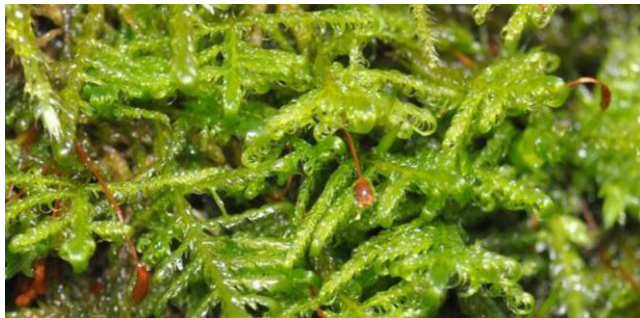


Figure 3. *Sanionia uncinata* with capsules. This species is home for *Pringleophaga marioni* on Marion Island in the sub-Antarctic. Photo by Andrew Hodgson, with permission.

Like all creatures, adult **Lepidoptera** need water. Bryophytes collect water and it often stays at leaf bases and other capillary spaces where cohesion keeps it from rolling away. These water droplets are suitable for the tube-feeding adult **Lepidoptera** to get a drink of water (Figure 4). Martin (2015) has observed butterflies and moths pausing for a drink of water from the moss leaves in her moss garden.



Figure 4. Butterfly on *Palustriella commutata*, a place where one can often find water droplets. Photo by Serhat Ursavas, with permission.

Life Cycle

All stages of **Lepidoptera** (egg-larva-pupa-adult) are known from bryophytes. The adult females of bryophyte-feeding larvae often lay eggs there. Several families include members whose larvae live in and feed on bryophytes, a number of which specialize on liverworts. These bryophyte-feeding larvae are often in primitive families that originated before flowering plants.

Eggs

For those **Lepidoptera** that use the bryophytes for egg-laying, the bryophytes provide a safe haven for emerging larvae. This is the case for the hemlock looper (*Lambdina fiscellaria*; Figure 5) (an inchworm; **Geometridae** – see Chapter 12-13), which is a serious conifer pest (Shepherd & Gray 1972).



Figure 5. The hemlock looper (*Lambdina fiscellaria*) larva hiding in moss in autumn. Photo from USFS, through public domain.

Some females create cocoons in which they lay eggs (Figure 6-Figure 7). Timea Deakova sent me images of a cocoon of eggs from the moss *Climacium dendroides* in Oregon, USA. The larvae eat moss and grass.



Figure 6. Moth cocoon on *Climacium dendroides*. Photo courtesy of Timea Deakova.

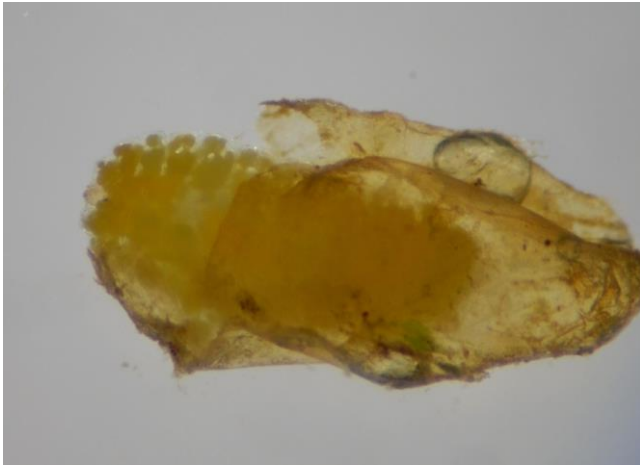


Figure 7. Cocoon from *Climacium dendroides*, with eggs emerging. Photo courtesy of Timea Deakova.



Figure 8. Moth caterpillar on moss in *Polytrichum juniperinum* in Oregon, USA. This larva developed and hatched into the adult in Figure 9. Photo courtesy of Timea Deakova.



Figure 9. Adult that hatched from the above larva on mosses. The ragged wings are due to hungry larvae feeding on them in captivity. Photo courtesy of Timea Deakova.



Figure 10. Moth hatched from larva on moss. Photo courtesy of Timea Deakova.

Larvae

Larvae of **Lepidoptera** can be recognized by the presence of **crochets** (hooks; Figure 11) on their **prolegs** (fleshy short legs on the abdomen). Some **Lepidoptera** spin their cocoons in mosses or use bits of mosses or liverworts as part of the cocoon (Figure 12-Figure 13). Buchanan (1971) reported this behavior for *Pyrusta cingulata* (Crambidae; Figure 13-Figure 14), *Phycis subornatella* (Pyralidae), and *Eana penziana* (Tortricidae; Figure 15) near Perth, Australia. Buckler (1871) reported silken cocoons of larvae of *Acronicta myrica* (Noctuidae; see Figure 16-Figure 17) covered with moss.



Figure 11. *Cossus cossus* larval prolegs showing crochets. Photo by Anki Engström <www.krypinaturen.se>, with permission.



Figure 12. **Lepidoptera** larval cocoon of the liverwort *Riccardia filicina*. Although the larva has left its cocoon, the liverwort fragments are still alive. Photo courtesy of David Glenney.



Figure 13. *Pyrausta cingulata* larva with bits of its cocoon. Photo by Bob Heckford, with permission.

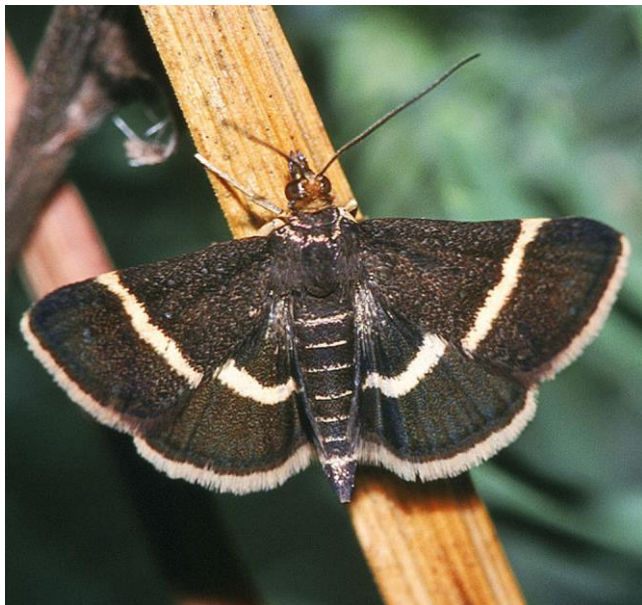


Figure 14. *Pyrausta cingulata* adult, a species that spins its cocoon on mosses. Photo by Olaf Leillinger, through Creative Commons.



Figure 15. *Eana penziana* adult. Larvae of this species build cocoons on mosses. Photo by Kurt Kulac, through Creative Commons.



Figure 16. *Acrionicta euphorbiae* larva, a species related to the moss user *Acrionicta myricae*. Photo by Harald Süpfle, through Creative Commons.



Figure 17. *Acrionicta* sp. adult. *Acrionicta myricae* builds cocoons on mosses. Photo by Olaf Leillinger, through Creative Commons.

Pupation

Bryophytes offer a safe site for pupation of **Lepidoptera** (Figure 18-Figure 20). It is likely that a number of **Lepidoptera** pupate among the bryophytes, but this stage is difficult to identify and is easily overlooked. Hence the records of this stage may not be truly representative of the usage of mosses for overwintering and escape from desiccation. Nevertheless, I have been pleasantly surprised not only by the number of records, but by the identification of the bryophytes involved for both larvae and pupae.



Figure 18. **Lepidoptera** pupal shell in moss. Photo courtesy of Sarah Lloyd.



Figure 19. **Lepidoptera** pupal shell in moss. Photo courtesy of Sarah Lloyd.



Figure 20. **Lepidoptera** pupa on moss. Photo by Vinicius Santana Orsini Brazil.

Some **Lepidoptera** pupae, for example the privet hawk moth *Sphinx ligustri* (**Sphingidae**; Figure 21-Figure 24), survive winter in rotting logs covered with mosses, but the necessity for the moss has not been assessed (Brackenbury 1994).



Figure 21. *Sphinx ligustri* adult, a species that survives winter as pupae in logs covered with mosses. Photo by Olaf Leillinger, through Creative Commons.



Figure 22. *Sphinx ligustri* larva. Photo by Georg Slickers, through Creative Commons.



Figure 23. *Sphinx ligustri* pupating, an activity it commonly does in moss-covered logs. Photo ©entomart, through Creative Commons



Figure 24. *Sphinx ligustri* mature pupa, the overwintering stage in logs covered with mosses. Photo from ©entomart, through Creative Commons.

Food Sources

Gerson (1982) reviewed what could be found regarding bryophytes as food sources for **Lepidoptera**. He reported that the larvae of **Meessiinae** feed on both lichens and mosses, but they also incorporate the fragments of these two groups of organisms in their cases. *Nudaria mundana* eats both saxicolous lichens and liverworts (Forster & Wohlfahrt 1960). Some larvae have a safe haven while they feed on the bryophytes. The *Sabatinca* larva is a liverwort mimic with its greenish color and large setae (Tillyard 1922; Yasuda 1962; Gerson 1982; Holloway 1993).

Feeding on Leafy Gametophytes

As I worked on this chapter, I became amazed at the number of **Lepidoptera** that feed on bryophytes. Most feed on the leafy plants (Figure 25). Some of them feed on mosses and others feed exclusively on liverworts.



Figure 25. Caterpillar feeding on the moss *Fabronia leikipiae*. The caterpillar has an ideal color and pattern to blend in with the bryophyte branches. Photo by Min Petiot.

As early as 1894, Chapman noted that some **Lepidoptera** larvae feed on mosses, especially in the primitive families. We now know that some are bryophyte

specialists. Robin Stevenson shared his image with me to demonstrate feeding on mosses (*Tortula truncata*) by **Lepidoptera** larvae (Figure 26).



Figure 26. *Tortula truncata* showing feeding damage by larval **Lepidoptera**. Photo courtesy of C. Robin Stevenson.

A number of **Lepidoptera** larvae feed on the leafy gametophytes of bryophytes. Members of the primitive lepidopteran suborder **Zeugloptera** are moss feeders (Chapman 1894; Tillyard 1926), suggesting that the advent of flowering plants opened new food sources for them. Among these bryophyte feeders is *Micropterix calthella* (**Micropterigidae**; Figure 27-Figure 28) (Chapman 1894).

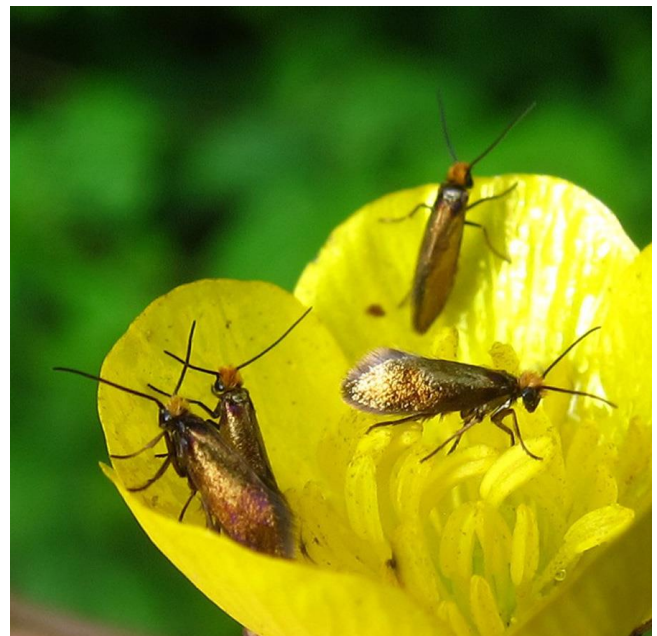


Figure 27. *Micropterix calthella* adult, a bryophyte feeder in its larval stage. Photo by Wouter Bosgra, through Creative Commons.



Figure 28. *Micropterix calthella* adult of a larval bryophyte feeder. Photo by Tom Deroover, through Creative Commons.

Feeding on Capsules

Fang and Zhu (2012) reviewed accounts of **Lepidoptera** feeding on bryophyte capsules. They found that the known feeding habits of lepidopteran larvae included capsules in only four families: **Micropterygidae** (Gerson 1969), **Mnesarchaeidae** (Grehn 1984), **Arctiidae** (as **Lithosiidae**) (Liu 1989), and **Geometridae** (Maciel-Silva & dos Santos 2011). Thus, theirs is the first record of **Noctuidae** larvae that feed on mosses. *Agrotis* sp. (**Noctuidae**; Figure 29) larvae commonly feed on capsules of *Haplocladium microphyllum* (Figure 30) in Shanghai in the spring (Fang & Zhu 2012).



Figure 29. *Agrotis* feeding on capsules of *Physcomitrium sphaericum*. Photo by Rui-Liang Zhu, with permission.



Figure 30. *Haplocladium microphyllum* capsules and setae where capsules have been completely eaten by a species of *Agrotis*. Photo by Rui-Liang Zhu, with permission.

Butterflies

"Among those groups of butterflies that feed on plants, none is known to feed on bryophytes or on Psilopsida, Lycopsida, or Sphenopsida, nor is any known from ferns" (Ehrlich & Raven 1964). This statement surprised me because I had already found a number of **Lepidoptera** that feed on bryophytes. But I soon realized these are almost entirely moths. However, there are exceptions (see **PAPILIONOIDEA** in Chapter 12-14) in the **Lycaenidae** (Callaghan 1992), **Nymphalidae** (Singer & Mallet 1986; Hamm 2015), and **Rionidae** (DeVries 1988). It is interesting that two of these exceptions are butterfly larvae that feed on the epiphylls that live on tracheophyte leaves.

It is not unusual for **Lepidoptera** to eat plants, but it is unusual among the butterflies. While bryophytes are not a main fare, some satyrid butterflies do consume bryophytes (Singer & Mallet 1986). In Japan, the primitive *Sabatinca* (Figure 31) and *Neomicropteryx nipponensis* (both in **Micropterigidae**; Figure 32) feed on liverworts (Figure 33) (Yasuda 1962).



Figure 31. *Sabatinca congruella* larva on a leafy liverwort, demonstrating its cryptic form and color. Photo by George Gibbs, with permission.



Figure 32. *Neomicropteryx nipponensis* larva feeding on *Conocephalum conicum*. Photo by Yume Imada, with permission.



Figure 33. *Conocephalum conicum*, food for *Sabatinca* and *Neomicropteryx nipponensis* in Japan. Photo by Hermann Schachner, through Creative Commons.

Epiphylls as Food

Bodner *et al.* (2015) found that in southern Ecuador the caterpillar assemblages often did not feed on their expected hosts. Rather, they chose foliose lichens, dead leaves, and the epiphylls, including bryophytes.

Invertebrates on the Menu

One normally thinks of caterpillars, the larvae of the **Lepidoptera**, as plant eaters. But Murawski (2003) describes "killer" moths that are carnivores, usually on soft-bodied insects and spiders. They use camouflage, seductive odors, and armor shields to enable them to sneak up on their prey. Some (*Maculineaalcon* – **Lycaenidae**; Figure 34) visit flowers to obtain a waxy cover of hydrocarbons that smell like *Myrmica* (Figure 35-Figure 36) ant larvae, enabling them to enter the ant nest. They then trick the ants into accepting them and feeding them while they attack the ant larvae! The ants whose nests are invaded include *Myrmica scabrinodis* (Figure 35), *Myrmica ruginodis* (Figure 36), and *Myrmica rubra* (Figure 37). All three of these ant species are associated with mosses, often nesting under them, hence the **Lepidoptera** live under mosses as well.



Figure 34. *Maculineaalcon* adult; larvae of this species trick ants into accepting them and feeding them. These ants typically associate with mosses, hence, so does the *Maculineaalcon*. Photo by Joris Egger, through Creative Commons.



Figure 35. *Myrmica scabrinodis*, an ant that is mimicked in smell by the larvae of *Maculineaalcon*. Photo by Tim Faasen, with permission.



Figure 36. *Myrmica ruginodis* adult on moss, an ant species that is fooled by the odors of *Maculineaalcon* and takes care of their larvae. Photo by James K. Lindsey, with permission.



Figure 37. *Myrmica rubra* workers, a species whose nests are invaded by *Maculineaalcon*. Photo by Gary Alpert, through Creative Commons.

Some **Lepidoptera** that are indeed carnivorous caterpillars take advantage of the mosses to gain their food in a quite different way. In Hawaii, these carnivores are camouflaged as leaf litter, lichens, twigs, or mosses (Figure 38), permitting them to stalk their invertebrate prey (Murawski 2003).



Figure 38. *Adelpha serpa celerio*, a moss-mimicking caterpillar from Panama, but in this case, not a carnivore. Photo by Arthur Anker, with permission.

Antiherbivory

The limitation of **Lepidoptera** larvae primarily to leaves of seed plants may be due to antiherbivore compounds. Wada and Manakata (1971) demonstrated that some liverwort terpenoids inhibit feeding by **Lepidoptera** larvae. Ottosson and Anderson (1983) showed that fewer species were associated with ferns than with other tracheophytes and provided evidence that the wide range of chemical defenses in the ferns discouraged many insects from eating them. Nevertheless, the **Lepidoptera** seemed able to exhibit spatiotemporal adaptations that permitted them to avoid the unfavorable biochemistry of the ferns.

Krishnan and Murugan (2013) investigated feeding by **Lepidoptera** on bryophytes, using 20 species. They chose two species [corn earworm, *Helicoverpa zea* (Figure 39) – Noctuidae, and armyworm, *Spodoptera litura* (Figure 40) – Noctuidae]] that do not eat bryophytes. They compared the effects of protein extracts from bryophyte species with those from the normal food plant *Glycine max* (Figure 41) cultivar using bioassays. In these experiments, protein extracts from four species [*Octoblepharum albidum* (Figure 42), *Fissidens virens* (see Figure 43), *Bryum argenteum* (Figure 44), and *Marchantia linearis* (Figure 45)] caused the greatest decrease in damage in leaf-disk assays and in insect larval growth. They also caused a reduction in efficiency of digestion and food conversion. Further discussion of antiherbivory in **Lepidoptera** is in the following subchapters.



Figure 39. *Helicoverpa zea* larva, a species that does not eat bryophytes and avoids extracts of them. Photo by R. L. Croissant, through Creative Commons.



Figure 40. *Spodoptera litura* adult, a species whose larvae do not eat bryophytes and avoid extracts of them. Photo by Merle Shepard, Gerald R. Carner, and P. A. C. Ooi, through Creative Commons.



Figure 41. *Glycine max*, a normal food plant of larvae of *Helicoverpa zea* and *Spodoptera litura*. When bryophyte extracts were applied to these leaves, the larvae of these two species reduced feeding on it. Photo by Pancrat, through Creative Commons.



Figure 42. *Octoblepharum albidum*, a species that deters at least some **Lepidoptera** larvae from eating it. Photo by Niels Klazenga, with permission.



Figure 43. *Fissidens dubius*; *F. virens* deters at least some **Lepidoptera** larvae from eating it. Photo by Kurt Stüber, through Creative Commons.



Figure 44. *Bryum argenteum*, a species that deters at least some **Lepidoptera** larvae from eating it. Photo by Martin Hutten, with permission.



Figure 45. *Marchantia linearis*, a species that deters at least some **Lepidoptera** larvae from eating it. Photo by Manju C. Nair, through Creative Commons.

Adaptations

Bryophytes can provide a number of characteristics that are favorable for small invertebrates. They absorb water rapidly, reduce evaporation, and provide insulation against extremes of temperature and wind (Gerson 1982).

Most adult **Lepidoptera** associated with bryophytes do not have morphological adaptations for the bryophytic habitat, but rather blend with the flowers they visit. Others, however, are dull grays and browns that permit them to blend with the bark where they rest.

Larvae, on the other hand, are usually colored with browns, grays, and greens, and have tubercles or spines. Some have behaviors that cause them to include bryophytes in the construction of cocoons or cases. Their biggest adaptation, however, seems to be the ability to eat and digest the bryophytes. On the other hand, for at least some families, this is a primitive trait (Powell *et al.* 1999; Hashimoto 2006).

Some of the larvae, but few of the adults, have color patterns that would camouflage them among the bryophytes (Figure 46-Figure 47). Intermixed greens, browns, and black would make it easy for the larvae to hide among bryophytes, but these colors do not always coincide with known uses. Is this just our lack of sufficient observations, or are they adapted to walking among the mosses on their way from one location to another?



Figure 46. Caterpillar on moss, showing greens, black, and a brown head capsule. But does it live there? Photo by Carrie Andrew, with permission.



Figure 47. Moth adult on bryophytes, showing cryptic coloration. Photo courtesy of Sarah Lloyd.

One type of mimicry that seems not to be reported elsewhere is that reported by Györfy (1952). He relays his adventures in checking out twin capsules, only to discover that one was not a capsule at all. On the setae of *Atrichum undulatum* (Figure 48) he found not only a capsule, but also a cocoon. He reared the cocoon successfully to its maturity, from which emerged a moth. He did not describe it in this case, so it is not clear if it truly resembled a capsule of the moss, but especially noticeable as the animal it was.



Figure 48. *Atrichum undulatum* with capsules, home for some **Lepidoptera** pupae on the setae. It is easy to see how a pupa might be inconspicuous among these capsules. Photo by Michael Lüth, with permission.

Habitats

In their altitudinal study in Australia and New Zealand, Andrew *et al.* (2003) collected bryophytes and extracted invertebrates using the kerosene phase separation method. They identified these to family and found only one family of **Lepidoptera**. Nevertheless, bryophyte-dwelling **Lepidoptera** are more common than most of us might suspect in the forests and peatlands.

Forests

Diversity of **Lepidoptera** in forests is related to, but not limited to, the layers of the forest, disturbance, and management (Thorn *et al.* 2015). These researchers found that abundance of moth larvae of the **saproxylic** (pertaining to decaying wood) and detritus-feeding guilds was higher under a regime of natural disturbance and in multi-layered

stands. Larvae of moss-feeding moths, on the other hand, was lower in multi-layered stands.

Some of the relationships may be indirect, but nevertheless, important. *Liphyra brassolis* (**Lycaenidae**; Figure 49-Figure 51) is a rarely found species, protected as larvae from ant bites by a leathery "hide." Larvae of this species enter green tree ant (*Oecophylla smaragdina* – **Formicidae**; Figure 52) nests (Figure 53) to feast on larvae. These don't involve bryophytes, but similar behavior in aerial moss nests of ants is possible (See Chapter 12-10). It is certainly worth looking for them.



Figure 49. Ventral view of *Liphyra brassolis* larva, an insect that invades ant nests and is protected from attack by its leathery covering. Photo by Martin Lagerwey, with permission.



Figure 50. *Liphyra brassolis* larva showing head view, an insect that invades ant nests and is protected from attack by its leathery covering. Photo by Martin Lagerwey, with permission.



Figure 51. Dorsal view of *Liphyra brassolis* larva, showing its thick, leathery covering that protects it from ant attacks. Photo by Martin Lagerwey, with permission.



Figure 52. Tree-dwelling *Oecophylla smaragdina* carrying a grub. Photo by Zlouemark, through Creative Commons.



Figure 53. Aerial nest of *Oecophylla smaragdina* where caterpillars of *Liphyra brassolis* go to feed. Photo by J. M. Garg, through GNU Free License.

Epiphytes

In the tropical tree canopy, bryophyte and other epiphyte assemblages can be important food sources. Yanoviak *et al.* (2004). observed that larvae of the **Lepidoptera** on bryophytes occurred exclusively in the green fraction. The distribution of small epiphytes is influenced by the gross epiphyte morphology and location (Martin 1938; Gerson 1982).

Events such as hurricanes can have a severe impact on the epiphytic flora, including bryophytes, and the fauna living among them (Loope *et al.* 1994). Loss of bryophytes may not only be a loss of food and cover, but the **Lepidoptera** that live among them may be dispersed during the hurricane, but not necessarily to a suitable habitat.

But not all leaf dwellers feed on the leaves they inhabit. Some species of **Lepidoptera** occur regularly in the canopy leaf habitat and feed on the epiphylls, including bryophytes, algae, lichens, and fungi (Lucking 2000). Some are broad spectrum feeders, but the larvae of **Lepidoptera** seem to specialize on either the lichens or bryophytes.

Pettersson *et al.* (1995) found that larger invertebrates (>2.5 mm) served as food for foraging perching birds. These food invertebrates are higher in number in natural

forests and include **Lepidoptera** among the dominant species. Their number and biomass relate to the abundance of lichens. This suggests that it would be worthwhile to look for similar relationships with bryophytes.

Bogs and Wetlands

Peatlands can be ideal habitats for many butterflies and moths. Spitzer and Jaroš (1993) found 569 **Lepidoptera** species in a single peat bog in Central Europe! Jaroš *et al.* (2014) found 1040 species of moths and butterflies in just five peat bogs in the Třeboň Basin up to the montane/subalpine zone of the Bohemian Forest. These included 33 relict species of cold-adapted **tyrphobionts** [species living only in peat bogs and mires (Peus 1928)] and 74 **tyrphophilous** species that prefer peatlands. Spitzer and Jaroš (2014) contend that the bogs are refugia for northern **Lepidoptera** species by creating a climate that is suitable. The *Sphagnum* (Figure 54) is responsible for temperature-buffered microclimates that are suitable for these northern relict species of **Lepidoptera**.

Väisänen (1992) used a belt transect to sample butterflies and day-active moths in a raised bog in southeastern Finland. The species richness was higher in the adjacent mineral land, with the highest number of both species and individuals on the **lagg** [nutrient-enriched zone that grades to land (Paradis *et al.* 2015)] and marginal slope. The **Lepidoptera** communities were related primarily to the structural characteristics of the bog, including tree height and undergrowth floristic characteristics (Väisänen 1992).



Figure 54. *Sphagnum magellanicum*, dominant *Sphagnum* in a raised bog that has 11 tyrphobiontic and 14 tyrphophilous **Lepidoptera**. Photo by James K. Lindsey, with permission.

A number of butterflies (**Lepidoptera**: especially **Lycaenidae**, **Nymphalidae**, and **Satyridae**) complete their entire life cycle within peatland habitats of the Lake Superior drainage basin in northwestern Wisconsin (Nekola 1998). Nekola surveyed 70 peatlands in the drainage basin. The highest number of taxa occur in the muskeg sites, including five species that do not occur in other peatlands. In both the muskegs and kettlehole peatlands, butterfly species richness correlates highly with habitat size. These sites provide the southernmost locations for these northern species.

Chapman (1894) noted that some moth caterpillars in bogs use *Sphagnum* (Figure 54) for nests. And some eat the *Sphagnum*. But more commonly, the *Sphagnum*

provides a suitable habitat for the host plant. For example, one species, *Nola aerugula* (**Nolidae**; Figure 55), seems to be present as a dominant in a number of bogs, at least in Lithuania (Dapkus 2004a, b). It occurs throughout most of Europe, east to Japan. The larvae feed on *Trifolium* (Figure 56) and *Lotus corniculatus* (Figure 57), but also on *Betula* (Figure 58), *Salix* (Figure 59), and *Populus* (Figure 60) species, indicating its wide habitat distribution, but not indicating any direct use of the bryophytes.



Figure 55. *Nola aerugula* adult, a species that is often dominant in Lithuanian bogs. Photo by André den Ouden, through Creative Commons.



Figure 56. *Trifolium repens*, a genus that is food for *Nola aerugula*. Photo by Forest and Kim Starr, through Creative Commons.



Figure 57. *Lotus corniculatus*, food for *Nola aerugula*. Photo by David G. Smith <www.delawarewildflowers.org>, with online permission.



Figure 58. *Betula populifolia* leaves, in a genus that is food for *Nola aerugula*. Photo by Richtid, through Creative Commons.



Figure 59. *Salix cinerea* leaves, in a genus that is food for *Nola aerugula*. Photo by Sten Porse, through Creative Commons.



Figure 60. *Populus tremula* leaf, in a genus that is food for *Nola aerugula*. Photo by Treetime, through Creative Commons.

Dapkus (2000) compared **Lepidoptera** in two peatlands and a raised bog in Lithuania. The raised bog was dominated by *Sphagnum magellanicum* (Figure 54) and exhibited true tyrphophilic and tyrphobiontic species, but none was present in the two peatlands that had been affected by disturbance due to peat extraction. In all, the raised bog had 11 tyrphobiontic and 14 tyrrophilous **Lepidoptera**, whereas the Balodža peatland had 4 tyrphobiontic and 9 tyrrophilous **Lepidoptera** species. The Palios peatland fared even worse with only 3 tyrrophilous and no tyrphobiontic **Lepidoptera** species.

Spitzer and Jaroš (1993) conducted an extensive survey of the **Lepidoptera** of a bog in southern Bohemia. They noted that all the tyrphobionts feed on peat bog plants. But for some of the tyrrophilous species, mosses are on the dinner table. These include *Bryotropha boreella* (Gelechiidae; Figure 61-Figure 63), *Phiaris micana* (Tortricidae; Figure 64-Figure 65), and *Phiaris palustrana* (Tortricidae; Figure 66-Figure 67). In addition, *Thumatha senex* (Erebidae; Figure 68) feeds on both mosses and lichens.



Figure 61. *Bryotropha boreella* adult on *Sphagnum*, a food source for its larvae. Photo by Stephen Palmer, with permission.



Figure 62. *Bryotropha boreella* larva on its food source, a moss. Note the net surrounding the larva. Photo © Bob Heckford, with permission.



Figure 63. *Bryotropha boreella* pupa on moss. Photo © Bob Heckford, with permission.



Figure 64. *Phiaris micana* larva, a moss eater in bogs. Photo by James K. Lindsey, with permission.



Figure 65. *Phiaris micana* adult, a bog species with larvae that eat mosses. Photo by James K. Lindsey, with permission.



Figure 66. *Phiaris palustrana* adult, a bog species with larvae that eat mosses. Photo by Donald Hobern, through Creative Commons.



Figure 67. *Phiaris palustrana* larva, a moss eater in bogs. Photo by Bob Heckford, with permission.



Figure 68. *Thumatha senex* adult, a species whose larvae feed on mosses and lichens. Photo by James K. Lindsey, with permission.

The question remains, why are bogs important to these tyrphobiotic and tyrphophilous species? What is the role of the bryophytes? Do they simply provide the habitat needed by tracheophyte food plants, or are they necessary to survive in some stage of the life cycle?

So far, it appears that few studies indicate that any bog species feed on the bryophytes. In New Zealand Grehan and Patrick (1984) found that the larvae of *Cladoxycanus minos* (Hepialidae; Figure 69) build feeding tunnels in the moss, extending to 300 mm deep and under the water. This species eats *Sphagnum cristatum* (Figure 70). Two other unidentified species of Hepialidae likewise make tunnels into the moss mat. In the same bog *Wiseana umbraculata* (Hepialidae; Figure 71) occurs on saturated mosses that are in close contact with the soil surface.



Figure 69. *Cladoxycanus minos* male adult; this species builds larval feeding tunnels in mosses. Photo from Landcare Research, Manaaki Whenua, with online permission.



Figure 70. *Sphagnum cristatum*, food for *Cladoxycanus minos* in New Zealand. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.



Figure 71. *Wiseana umbraculata* male adult, a species that occurs on saturated mosses. Photo from Landcare Research, Manaaki Whenua, with permission.

Sunny peatlands seem to be suitable for the mustard white butterfly, *Pieris oleracea* (Pieridae; Figure 72). But where *Sphagnum* (Figure 54) grows, danger often lurks. Chew (1978) observed one of these butterflies stuck to the sticky hairs of sundew leaves (Figure 73) in Vermont, USA, quite dead. And this species is not alone in being snared by bog-dwelling sundews (Figure 73). As these butterflies and moths struggle to get free, they only get further entangled in the sticky hairs.



Figure 72. *Pieris oleracea* adult, a bog resident that gets trapped by sundews. Photo by D. Gordon E. Robertson, through Creative Commons.



Figure 73. *Drosera rotundifolia* that has caught a bog butterfly. Photo by Noah Elhardt, through Creative Commons.

Disappearing Species

Local species extinctions have been occurring at a high rate, and members of **Lepidoptera** are no exception (Franco *et al.* 2006). Both climate change and habitat loss account for these losses. Typically, the species retract northward. Franco and coworkers concluded that mountain and northern species may be in jeopardy due to climate warming.

By contrast, Nöske *et al.* (2008) compared moths in **Geometridae** and **Arctiidae** (**Erebidae**?) in mature and recovering forest and in open vegetation of the montane belt in Andes of Ecuador. There was no uniform pattern of change in species richness with increasing disturbance. Rather, species richness of geometrid moths was significantly higher in the recovering forest than in the mature forest or the open habitats. The **Arctiidae** were also most species-rich in the recovering forest, but also in the open vegetation compared to the mature forest.

Any recovery of species following logging depends on the availability of colonists (Niemelä 1997). Butterflies, in particular, suffer from logging of old-growth forests, as do bryophytes (Hydén & Sjökvist 1993), and sometimes the **Lepidoptera** may suffer because of loss of bryophytes.

Maelfait *et al.* (2007) reported the loss of the butterflies *Aricia agestis* (**Lycaenidae**; Figure 74-Figure 77) and *Issoria lathonia* (**Nymphalidae**; Figure 78-Figure 79) from Dutch coastal dunes. This loss was attributed to loss of the varied vegetation structure that included patches of mosses and bare sand, both of which disappear when tall grasses expand coverage (Brouwer *et al.* 2005).



Figure 74. *Aricia agestis* adult, a species that lives where there are bryophytes in the habitat. Photo by Hectonichus, through Creative Commons.



Figure 77. *Aricia agestis* larva, a species that disappears when bryophytes disappear from its habitat. Photo by Jérôme Albre, with permission.



Figure 75. *Aricia agestis* adult, a species that lives where there are bryophytes in the habitat. Photo by Jérôme Albre, with permission.



Figure 78. *Issoria lathonia* larva, a species that seems to depend on mosses in the dunes. Photo by Wolfgang Wagner, with permission.

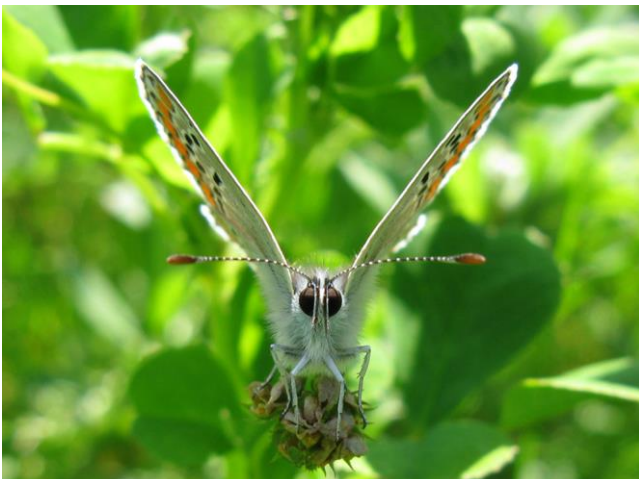


Figure 76. *Aricia agestis* adult showing its antennae and eyes. Photo by Jérôme Albre, with permission.



Figure 79. *Issoria lathonia* adult, a species that disappears when dune mosses are replaced by grasses. Photo by Korall, through Creative Commons.

Schtickzelle and Baguette (2004) expressed the importance of demographic parameters in fragmented landscapes. For the bog fritillary butterfly (*Proclossiana eunomia* – *Nymphalidae*; Figure 80), a specialist glacial relict, density dependence seemed to be related to parasitism of the larvae. Dispersal was dependent on the ability to move between patches of suitable bog habitat.

Hence, destruction of bogs can easily lead to the demise of this species, in part due to crowding and increased parasitism.



Figure 80. *Proclossiana eunomia*, a bog dweller. Photo by Gilles San Martin, through Creative Commons.

Because of their vulnerability due to changes in drainage, bogs are disappearing habitats. Murdock (1994) claims that one-third of the threatened and endangered species in the USA live in wetlands. In the Southern Appalachian Mountains, USA, bogs and fens house many rare and unique species that occur in no other habitats. Among these is the rare Baltimore butterfly, *Euphydryas phaeton* (Nymphalidae; Figure 81-Figure 83).



Figure 81. *Euphydryas phaeton* (Baltimore butterfly) larva, a rare bog inhabitant in the Southern Appalachian Mountains, USA. Photo by Pennsylvania Department of Conservation and Natural Resources, through Creative Commons.



Figure 82. *Euphydryas phaeton* adult, a rare bog species in the Southern Appalachian Mountains, USA. Photo by Alison Hunter, through Creative Commons.



Figure 83. *Euphydryas phaeton* adult, a rare bog species. Photo by D. Gordon E. Robertson, through Creative Commons.

Many examples, such as those reported by Pescott *et al.* (2015), attest to the effect of changing air quality in causing the disappearance of bryophytes. They provided the first evidence for the indirect association between returning air quality and the increase of lichenivorous moths.

Changing climate can put life cycle stages out of sync. Food plants may mature at the wrong time for developing larvae. Males and females may respond to different stimuli, causing them to be ready for mating at different times. The Earth's mean global temperature has increased by about 0.6°C in the past century (Walther *et al.* 2002). Migrant butterflies are arriving at their spring destinations earlier and breeding earlier than times recorded before the 20th century. Bryophytes may play a role in retaining moisture as the climate dries.

Summary

The **Lepidoptera** are primarily plant eaters as larvae, and for some this includes bryophytes. This appears to be a relict trait from the early **Lepidoptera** that appeared at about the same time as bryophytes became abundant. Many of these bryophyte dwellers have similarities to their sister group, the **Trichoptera**, including case making, wings that rest like a pup tent, and hairs on the wings. Larvae often have appendages and coloration that help them to blend with the bryophytes. They are holometabolous, having eggs, larvae, pupae, and adults in their life cycle.

Pupae develop in bryophytes in some taxa. Adults use the bryophytes for resting sites, in some cases having coloration that camouflages them. Some lay their eggs among bryophytes. Butterflies are less represented than moths and few feed on them.

Although most of the lepidopteran bryophages eat the leaves, some are specialists on capsules. And some eat only liverworts, especially the thallose liverwort *Conocephalum conicum*. Others specialize on epiphyllous bryophytes and some eat the periphyton on the bryophytes. But some bryophytes seem to be inedible, presenting terpenoids and other compounds that serve as chemical defense. A few larvae are carnivorous and ambush prey by resembling bryophytes and hiding there to attack.

Many of the bryophyte dwellers have poor or no flying ability and therefore have limited dispersal ability and distribution. This makes them susceptible to extinction as forests and bogs are destroyed. While peatlands can have a huge number of species, some of these are very rare and easily extirpated as these relict habitats disappear. Bog drainage, climate change, peat harvesting, pollution, and logging all contribute to the losses of these rare species.

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CHAPTER 12-13

TERRESTRIAL INSECTS:

HOLOMETABOLA – LEPIDOPTERA:

MICROPTERIGOIDEA – GELECHIOIDEA

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CHAPTER 12-13

TERRESTRIAL INSECTS:

HOLOMETABOLA – LEPIDOPTERA:

MICROPTERIGOIDEA – GELECHIOIDEA



Figure 1. Upper altitude limit of *Sabatinca chrysargyra* (Micropterigidae). Photo by George Gibbs, with permission.

MICROPTERIGOIDEA

Micropterigidae – Mandibulate Archaic Moths

As flowers rapidly expanded into numerous colors, sizes, and shapes, so did the **Lepidoptera** (see Powell *et al.* 1999). But these new flowers fed the adults, not the larvae.

This family is an ancient group, so it is not surprising that there are bryophyte specialists among them. Among these is the rarely collected *Epimartyria* sp. in the moth family **Micropterigidae** (Loren Russell pers. comm. Jan. 2008). The *Epimartyria* (Figure 11-Figure 16) larvae feed on *Conocephalum conicum* (Figure 2) and other liverworts in mountain springs, as well as on *Pellia neesiana* (Figure 3-Figure 4), the leafy liverworts *Scapania bolanderi* (Figure 5), and the *Calypogeia-Riccardia* association on logs, and once on *Porella navicularis* (Figure 6), an epiphyte.



Figure 2. *Conocephalum conicum*, home and food source for members of *Epimartyria*. Photo by Janice Glime.



Figure 3. *Pellia neesiana* showing the habitat that is home and food for *Epimartyria* larvae. Photo by C. & C. Johnson, with permission.



Figure 4. *Pellia neesiana* with antheridia, home and food for *Epimartyria* larvae. Photo by C. & C. Johnson, with permission.



Figure 5. *Scapania bolanderi*, home and food for species of *Epimartyria*. Photo by Matt Goff, with permission.



Figure 6. *Porella navicularis*, home and food for species of *Epimartyria*. Photo by Tonya Yoder, through Creative Commons.

In the lab, *Epimartyria* sp. survived feeding on *Riccardia latifrons* (Figure 7) and the leafy liverworts *Calypogeia fissa* (Figure 8), *Jungermannia obovata* (Figure 9), and *J. rubra* (Figure 10) (Loren Russell pers. comm. Jan. 2008). Russell found them to be most abundant in wet seepage zones with abundant *Pellia neesiana* and *Conocephalum conicum*.



Figure 7. *Riccardia latifrons*, food for species of *Epimartyria*. Photo by Kristian Peters (Korseby Online), with permission.



Figure 8. *Calypogeia fissa*, food for species of *Epimartyria*. Photo by David T. Holyoak, with permission.

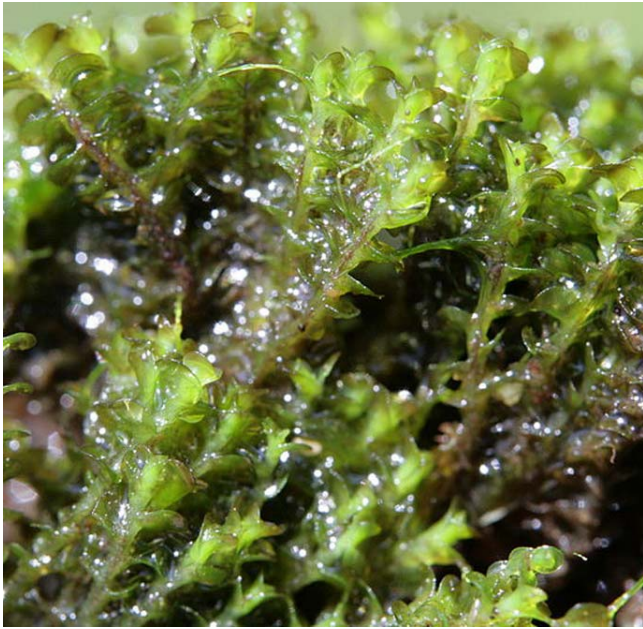


Figure 9. *Jungermannia obovata*, food for species of *Epimartyria*. Photo by Hermann Schachner, through Creative Commons.



Figure 10. *Jungermannia rubra* with perianth, food for species of *Epimartyria*. Photo by Ken-Ichi Ueda, through Creative Commons.

In northeastern USA and Canada, *Epimartyria auricrinella* (Figure 11) lives in shaded locations of wet, swampy woods, boggy ditches, and streamsides where leafy liverworts are abundant (Gibbs 2010). One of its food plants is the leafy liverwort *Bazzania trilobata* (Figure 12-Figure 13) (Davis & Landry 2012). *Epimartyria bimaculella* (Figure 14), in the northwestern USA and Canada (Gibbs 2010), likewise feeds on leafy liverworts, including *Lepidozia* (Figure 15) (Davis & Landry 2012). Davis and Landry (2012) successfully reared them in the lab from larvae that were provided with only the leafy liverwort *Jungermannia obovata* (Figure 9). The larvae have a plastron mechanism (see Chapter 11-10) that permits them to survive short periods of flooding.



Figure 11. *Epimartyria auricrinella* adult, a species whose larvae live among and eat moist leafy liverworts. Photo by Jim Vargo, through Creative Commons.



Figure 12. *Bazzania trilobata* on a log where *Epimartyria auricrinella* was found. Photo by D. R. Davis and J-F. Landry, through Creative Commons.



Figure 13. *Bazzania trilobata*, home and food of *Epimartyria auricrinella*. Photo by Michael Lüth, with permission.



Figure 14. *Epimartyria bimaculella* adult, a species whose larvae feed on leafy liverworts. Photo by Donald R. Davis and Jean-Francois Landry, through Creative Commons.



Figure 15. *Lepidozia reptans*, home for *Epimartyria bimaculella*. Photo by David T. Holyoak, with permission.

In 1989, Gibbs considered the **Micropterigidae** and **Mnesarchaeidae** to be similar in their habitats and seasonal requirements, often occurring together in New Zealand. But the **Micropterigidae** have a distribution around the Pacific rim, whereas the **Mnesarchaeidae** are endemic to New Zealand. Gibbs also considered the larvae of both families to live in the "periphyton layer" of their bryophytic habitat. In this often moist layer the larvae can find algae, bacteria, and fungi that provide suitable food.

The basal lineage of **Lepidoptera** – many as members of the **Micropterigidae** – continued their habit of feeding on cryptogams as larvae (Powell *et al.* 1999; Hashimoto 2006). Powell and coworkers pointed out that in East Asia there are about 25 endemic species that exclusively eat the thallose liverwort *Conocephalum conicum* (Figure 2). Nevertheless, the worldwide distribution of this family is patchy (Imada *et al.* 2011a). Its greatest species diversity is in Japan and Taiwan (greater than 25 spp.), New Caledonia (greater than 20 spp.), New Zealand (20 spp.), and Madagascar (ca 15 spp.) (Gibbs 2010). The **Micropterigidae** of Japan represent the largest radiation of

herbivorous insects known from a single host taxon (Imada *et al.* 2011a).

Epimartyria pardella (Figure 16) is one such example of the dispersal limitations. This species lives in northern California to northern Oregon, USA (Tuskes & Smith 1984). Its flight is very sporadic, and on those occasions when it does fly, it fails to go more than 21 cm! These moths are day-active as adults and associate closely with liverworts [*Conocephalum* (Figure 2) and *Pellia* (Figure 3-Figure 4)]. They frequent canyon walls and streamsides. When they are protected from the wind, they often perch on the upper surfaces of fern fronds, but always near liverworts. When it is windy or dry, they remain among the moist bryophytes such as *Hookeria lucens* (Figure 17), *Atrichum undulatum* (Figure 18), and *Conocephalum conicum* (Figure 2). But unlike the Japanese members of this family, larvae of this species prefer the thallose *Pellia* for food. Young larvae are active both day and night, but older larvae become night active. They typically do not damage the margin of the thallus. Instead, they feed on the underside of the thallus, removing it but not chewing through the upper surface.



Figure 16. *Epimartyria pardella*, a dweller among moist bryophytes and liverwort feeder with limited dispersal ability. Photo by Donald R. Davis and Jean-Francois Landry, through Creative Commons.



Figure 17. *Hookeria lucens* with capsules, habitat for *Epimartyria pardella*. Photo by Matt Goff <www.sitkanature.org>, with permission.



Figure 18. *Atrichum undulatum* with capsules, habitat for *Epimartyria pardella*. Photo by Mejdlowiki, through Creative Commons.

The poor dispersal ability of this group with its limited flying ability has created localized populations where the liverwort is available, creating geographic isolation that has resulted in this high diversity of endemic *Conocephalum* (Figure 2, Figure 19) specialists. In fact, larvae of the modern species in this family feed on either detritus or bryophytes (Kristensen 1999; Powell & Opler 2009).

The **Micropterigidae** in Japan illustrate the species radiation of this family, and it goes beyond *Epimartyria*. In the Japanese archipelago, 17 species of **Micropterigidae** are present (Hashimoto 2006). These species are typical of moist riverine environments, a habitat suitable for lush growths of bryophytes and ferns. Kobayashi and Ando (1981) demonstrated that both larvae and eggs of *Neomicropteryx nipponensis* (Figure 19-Figure 21) are easily harmed by drought stress. Four [*Palaeomicroides* (Figure 21), *Neomicropteryx*, *Kurokopteryx* (Figure 22), *Issikiomartyria* (Figure 23)] of these five genera feed exclusively on *Conocephalum conicum* (Figure 2) (Yasuda 1962; Imada *et al.* 2011a). This is in habitats where as many as 14 other bryophyte species commonly co-occur. It is interesting that despite their specificity on this species, these larvae do not discriminate (Imada *et al.* 2011b) among the three cryptospecies (Akiyama & Hiraoka 1994; Miwa *et al.* 2009) of *C. conicum*. Only *Paramartyria* (Figure 24) uses several liverworts as food: *Makinoa crispata* (Figure 25), *Heteroscyphus coalitus* (Figure 26), and *Conocephalum conicum*.



Figure 19. *Neomicropteryx nipponensis* larva feeding on *Conocephalum conicum*. Note the darkened necrotic areas where the outer cells have been removed. Photo by Yume Imada, with permission.



Figure 20. *Neomicropteryx nipponensis* adult, a species whose larvae eat *Conocephalum conicum*. Photo by Yume Imada, with permission.



Figure 21. *Palaeomicroides obscurella* adult, a species whose larvae feed exclusively on *Conocephalum conicum*. Photo from BIO Photography Group, Biodiversity Institute, Ontario, through Creative Commons.



Figure 22. *Kurokopteryx dolichocerata* adult, a genus whose larvae feed exclusively on *Conocephalum conicum*. Here the adult is resting on that liverwort. Photo by Yume Imada, with permission.



Figure 23. *Issikiomartyria* sp. adult, a genus whose larvae feed exclusively on *Conocephalum conicum*. Photo by Yume Imada, through Creative Commons.



Figure 24. *Paramartyria semifasciella* adult, in a genus that feeds on several species of thallose liverworts. Photo by Yume Imada, through Creative Commons.



Figure 25. *Makinoa crispata*, food for larvae of *Paramartyria*. Photo through Creative Commons.

These genera are spatially separated (**allopatric**) (Imada *et al.* 2011a; Imada & Kato 2018). Among these, *Issikiomartyria* (Figure 23) occurs only in the snow-rich

area facing the Sea of Japan. *Kurokopteryx* (Figure 22) occurs only in south central Japan, facing the northwest Pacific Ocean. Yet their diets are the same, representing the "largest radiation of herbivorous insects that does not accompany any apparent niche differentiation" (Powell *et al.* 1999). These five genera [*Palaeomicroides* (Figure 21), *Neomicropteryx* (Figure 19-Figure 20), *Kurokopteryx* (Figure 22), *Issikiomartyria* (Figure 23), *Paramartyria* (Figure 24)] of larvae feed on the thalli of *Conocephalum conicum* (Figure 2) by grazing the surface, with no apparent differences in feeding mode among these micropterigid species (Imada *et al.* 2011a).



Figure 26. *Heteroscyphus coalitus*, food for larvae of *Paramartyria*. Photo by Jiadong Yang, through Creative Commons.

In Japan and New Caledonia, the larvae of the endemic *Sabatinca* live (Harris 2012) and feed on bryophytes (Figure 1) (Yasuda 1962; Holloway 1993). *Sabatinca* larvae have cryptic coloration that is greenish with large setae that help to camouflage them among the liverworts (Tillyard 1922). On Mt. Cargill, N. Z., *Sabatinca quadrijuga* (Figure 27-Figure 28) lives on leafy liverworts as larvae (Harris 2015). Most of the adults of *Sabatinca* are day-active and feed mostly on fern spores, but they also eat club moss (Lycopodiaceae) spores or pollen from sedges and other flowers (Gibbs & Lees 2014). The adult still has an affinity for bryophytes, however. It "hops" around on the mosses on rocks (flying close to the ground), but only when the sun is shining (Harris 2015).



Figure 27. *Sabatinca quadrijuga* eggs. This species is a leafy liverwort inhabitant and feeder. Photo by George Gibbs, with permission.



Figure 28. *Sabatinca quadrijuga* adult, a species that lives among and eats liverworts as larvae and hops around on mosses as an adult. Photo by George Gibbs, with permission.

Sabatinca caustica (Figure 29-Figure 31) illustrates the bryophytic adaptations of this genus. The hunch-backed caterpillars (Figure 29) are camouflaged by their pigments (Gibbs & Lees 2014). Like all members of *Sabatinca*, they feed on leafy liverworts and are known as **exposed feeders** because they feed on the surface.



Figure 29. *Sabatinca caustica* larva, illustrating bryophytic adaptations. Note the hunched back, bryophytic coloring, and projections that resemble bryophyte leaves. Photo by George Gibbs, with permission.



Figure 30. *Sabatinca caustica* adult, a species whose larvae eat leafy liverworts. Photo by George Gibbs, with permission.



Figure 31. Habitat with mosses and liverworts where one can find *Sabatinca caustica*. Photo by George Gibbs, with permission.

Gibbs (2014) described four new species of *Sabatinca* in New Zealand. All 19 of the New Zealand species are confirmed liverwort feeders. The life cycle of this genus is typically annual. Larvae grow throughout the winter and the pupal stage is short. The larvae exhibit cryptic coloration (Figure 32), but the adults instead often have brilliant iridescent colors (Figure 33, Figure 36, Figure 38). Nevertheless, the adult coloration helps to conceal these small moths in the spotty light of their wooded and streamside habitats. *Sabatinca calliarcha* (Figure 32-Figure 33) and *S. doroxena* (Figure 35-Figure 36), and a number of other *Sabatinca* species, exhibit on the upper forewing (at rest) a black patch with several brilliant white spots in it (Figure 33, Figure 36). Gibbs speculated that these might serve as mimics of one of their main predators, a jumping spider in the *Salticidae* (Figure 34).



Figure 32. *Sabatinca calliarcha* larva showing adaptations to the bryophyte habitat, shown here on a leafy liverwort. Photo by George Gibbs, with permission.



Figure 33. *Sabatinca calliarcha* adult showing black area with white spots on wings. Photo by George Gibbs, with permission.



Figure 35. *Sabatinca doroxena* larva, a recently described liverwort feeder from streamsides in New Zealand. Photo by George Gibbs, with permission.



Figure 34. *Maratus volans* (Salticidae) showing color patterns and black spots (eyes) that seem to be mimicked by some species of *Sabatinca*. Photo by Jurgen Otto, with permission.

Gibbs (2014) was able to name specific larval hosts, mostly leafy liverworts, for a number of the New Zealand *Sabatinca* (Table 1). Larvae of *Sabatinca* on *Plagiochila* not only feed there, but they roll the leaves or otherwise use them to form a cocoon (David Glenney, pers. comm.; Figure 45).



Figure 36. *Sabatinca doroxena* adults copulating, a recently described liverwort dweller from streamsides in New Zealand. Photo by George Gibbs, with permission.

Table 1. Larval hosts for some of the New Zealand members of *Sabatinca*, based on Gibbs (2014).

<i>S. aurella</i>	Figure 37-Figure 38	<i>Heteroscyphus normalis</i>	Figure 39
<i>S. bimacula</i>	Figure 40	possibly <i>Plagiochila intertexta</i>	
<i>S. chalcophanes</i>	Figure 41	<i>Bazzania involuta</i>	
		<i>Hymenophyton flabellatum</i>	Figure 42-Figure 43
		variety of foliose liverworts	Figure 43
<i>S. doroxena</i>	Figure 35-Figure 36	<i>Heteroscyphus normalis</i>	Figure 39
<i>S. heighwayi</i>	Figure 45-Figure 47	<i>Plagiochila circumcincta</i>	Figure 48
<i>S. weheka</i>	Figure 49-Figure 50	<i>Plagiochila deltoidea</i>	Figure 51-Figure 53



Figure 37. *Sabatinca aurella* larva on a leafy liverwort. Photo by George Gibbs, with permission.



Figure 40. *Sabatinca bimacula* larva, a species that lives on *Bazzania involuta*. Photo by George Gibbs, with permission.



Figure 38. *Sabatinca aurella* adult, a species whose larvae feed on *Heteroscyphus normalis*. Photo by George Gibbs, with permission.



Figure 41. *Sabatinca chalcophanes* adult, a liverwort feeder as larvae. Photo by Neville Hudson, through Public Domain.



Figure 39. *Heteroscyphus* cf. *normalis*, a leafy liverwort eaten by *Sabatinca aurella* larvae. Photo by Andrew Hodgson, with permission.



Figure 42. *Hymenophyton flabellatum*, home and food for *Sabatinca chalcophanes*. Photo by Niels Klazenga, with permission.



Figure 43. *Sabatinca* habitat where one can find *S. aurantissima* (Figure 44), *S. aurella*, *S. aemula*, *S. chalcophanes*. Photo by George Gibbs, with permission.



Figure 44. *Sabatinca aurantissima* larva, an inhabitant of bryophytes. Photo by George Gibbs, with permission.



Figure 45. Pupa of *Sabatinca heighwayi* showing leaves of *Plagiochila* cf. *fasciculata*. Photo by George Gibbs, with permission.



Figure 46. Pupa of *Sabatinca heighwayi* removed from its cocoon. Photo by George Gibbs, with permission.



Figure 47. *Sabatinca heighwayi* male adult, a species whose larvae feed on *Plagiochila circumcincta*. Photo by George Gibbs, with permission.



Figure 48. *Sabatinca* habitat with *Plagiochila circumcincta*, host of *S. heighwei*. Photo by George Gibbs, with permission.



Figure 49. *Sabatinca weheka* larva, a species that feeds on *Plagiochila deltoidea*. Photo by George Gibbs, with permission.



Figure 50. *Sabatinca weheka* male adult, a species whose larvae feed on *Plagiochila deltoidea*. Photo by George Gibbs, with permission.



Figure 51. *Plagiochila deltoidea*, host of *Sabatinca weheka*. Photo by George Gibbs, with permission.



Figure 52. *Plagiochila deltoidea*, food and home for *Sabatinca weheka*. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.



Figure 53. *Sabatinca* habitat where one can find *S. weheka*, *S. aurella*, *S. chrysargyra* (Figure 54), and *S. chalcophanes* in New Zealand. Photo by George Gibbs, with permission.



Figure 54. *Sabatinca chrysargyra* larva on *Plagiochila*. Photo by George Gibbs, with permission.

But not all members of the **Micropterigidae** are bryophyte feeders. Some are not able to eat bryophytes and choose other food sources (Lorenz 1961; Luff 1964). Instead, these larvae eat fungi, detritus, and flowering plant green leaves (Kristensen 1998). For example, *Micropterix calthella* (Figure 55) and *M. aruncella* (Figure 56-Figure 57) ate the flowering plant *Stellaria* spp. in the lab and refused both mosses and liverworts (Carter & Dugdale 1982). But Shield (1856) recorded them from mosses and Meyrick (1895) found that both live on wet mosses in the British Isles, claiming that the genus feeds on mosses. Likewise, Chapman (1894) found that they eat mosses. Later, Coutin (2004b) stated that the larvae of *M. calthella* feed on mosses and liverworts. Perhaps they are choosy about the mosses they eat.



Figure 55. *Micropterix calthella* adult, a member of **Micropterigidae** whose larvae bryophytes sometimes, but refuse them at other times. Photo by Tom Deroover, through Creative Commons.



Figure 56. *Micropterix aruncella* adult, a species of **Micropterix** that sometimes refuses to feed on bryophytes. Photo by Marko Mutanen, no rights reserved.



Figure 57. *Micropterix aruncella* adult, a species of **Micropterix** may eat bryophytes but at other times refuses to feed on them. Photo by Marko Mutanen, no rights reserved.

Gibbs (1983) noted that in Australia the evolution of the **Micropterigidae** is paralleled by the evolution of the eastern Australian rainforests. In other locations, particularly in New Caledonia, the developing lineages seem to mirror the development or disappearance of different land masses.

Recently, Imada and Kato (2018) discovered four new species of *Issikiomartyria* [*I. catapasta* (Figure 58), *I. hyperborea*, *I. leptobelos*, *I. trochos* (Figure 59-Figure 60)], and a new genus (*Melinopteryx*) in the subalpine zone in Japan. These species of *Issikiomartyria* and the new *Melinopteryx bilobata* (Figure 61) are all associated with *Conocephalum conicum*, which serves as the food source for larvae. How many more undescribed species and genera are hiding inside liverwort thalli?



Figure 58. *Issikiomartyria catapasta* adult; larvae feed on *Conocephalum conicum*, Tachimata-keikoku, Akita Pref., Japan. Photo by Yume Imada, with permission.



Figure 59. *Issikiomartyria trochos* adult, a new species whose larvae feed on *Conocephalum conicum* at Mahirudake-rindo, Iwate Pref., Japan. Photo by Yume Imada, with permission.



Figure 60. *Issikiomartyria trochos*, a new species whose larvae feed on *Conocephalum conicum* at Jintsu-kyo, Yamagata Pref., Japan. Photo by Yume Imada, with permission.



Figure 61. *Melinopteryx bilobata* adult, a new species whose larvae feed on *Conocephalum conicum* at Ushikubi-touge, Shizuoka Pref., Japan. Photo by Yume Imada, with permission.

MNESARCHAEOIDEA

Mnesarchaeidae – New Zealand Primitive Moths

When the **Micropterigidae** emerged, the New Zealand endemic **Mnesarchaeidae** likewise was becoming established. *Mnesarchaea acuta* (Figure 62) can occur in large numbers on the damp moss-covered banks of streams in a variety of New Zealand forests and at a wide range of altitudes (Gibbs 1979). But it is the **periphyton** (algae and **Cyanobacteria** – Figure 63) layer on the mosses and liverworts that serves as their food. Their fecal matter indicates that they ingest pieces of both live and dead moss leaves, liverwort leaves and rhizoids, fern sporangia, fungal spores and hyphae, and filamentous algae. This is an unusually diverse diet for any lepidopteran. When the females are placed in vials with sufficient periphyton on mosses and liverworts, *M. loxoscia* (Figure 64) and *M. acuta* lay their eggs on the bryophytes. The suitable bryophytes live on rotting logs, tree trunks, and soil in the damp portions of the forests.



Figure 62. *Mnesarchaea acuta*, a species with larvae that eat the algae and *Cyanobacteria* on the bryophytes and adults lay their eggs there. Photo by George Gibbs, with permission.

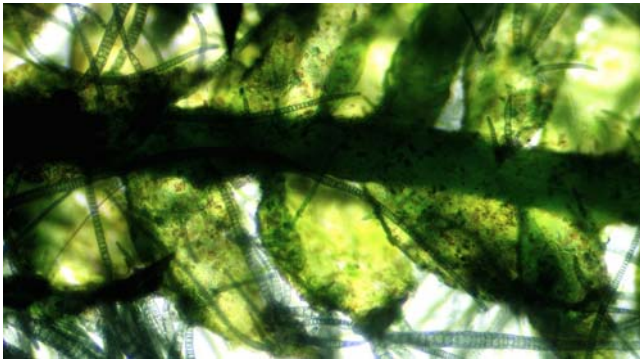


Figure 63. *Cyanobacteria* on moss, food for *Mnesarchaea acuta*. Photo by Nat Tarbox, through Creative Commons.



Figure 64. *Mnesarchaea loxoscia*, a species whose larvae eat the algae and *Cyanobacteria* on the bryophytes and females lay their eggs there. Photo by George Gibbs, with permission.

HEPIALOIDEA

Hepialidae – Ghost Moths

The **Hepialidae** can be considered indicators of the ancient fauna of New Zealand (Patrick 1988). Their larvae are common in bogs among the mosses. They have poor

dispersal ability because the females generally either have short wings or are reluctant to fly. Even with mobile males, reproduction in a distant location is not possible.

Grehan (1989) considered the mosses to be among the food sources for the **Hepialidae** larvae. Grehan suggested that this family was originally fungivorous (feeding on fungi) and that its change to primarily tracheophytes resulted from suppression of mycophagy. But in pastures and grassland species mosses may be important food sources, whereas liverworts seem to be ignored. Among these moss feeders is *Korscheltellus gracilis* (Figure 65- Figure 67) (Brower 1984). Larvae of this species feed above ground in thick mosses.



Figure 65. *Korscheltellus gracilis* larva, a species where larvae feed above ground under mosses. Photo by Johnathan Leonard, with permission.



Figure 66. *Korscheltellus gracilis* host tree where larvae live under mosses. Photo by John Grehan, with permission.

Larvae of *Korscheltellus gracilis* (Figure 65) typically take two years to mature, following an egg development of 16-19 days at 22°C. Pupation occurs on the forest floor in the second year. These require another month to develop before the adult (Figure 67) emerges. It is the larval stage that is of interest to us. These larvae are **polyphagous** – that is, they eat a variety of foods, including leaf litter, fungi, mosses, and below ground tissues of ferns and seed plants.



Figure 67. *Korscheltellus gracilis* adult, a species that emerges from pupae on the forest floor. Photo by Matthew Priebe, with permission for educational purposes.

Korscheltellus gracilis (Figure 65-Figure 67) has an interesting mating behavior that may give insight into other members of the family. Using wind tunnel experiments, Kuenen *et al.* (1994) found that when light intensity was reduced to 11-25 lux after a 16-hour photophase of 450 lux, females initiated wing fanning. Males downwind of them began wing fanning, rapid walking, or both, and flew upwind toward the female soon afterwards. If the hind wings of the females were removed, the fanning activity of the females failed to evoke a male response. Hence, Kuenen and coworkers concluded that the hind wings emit a pheromone that elicits the male's mating behavior.

Bogs seem to be the best site for bryophyte-feeding members of this family. *Cladoxycanus* (Figure 68) and *Heloxycanus* (Figure 78-Figure 79) both feed on cushion plants in bogs, including both mosses and tracheophytes (Dugdale 1994). *Heloxycanus* larvae eat other mosses as well as *Sphagnum* (Figure 69) by cutting the stems to create fragments. It would be interesting to see if this results in dispersal and establishment. *Cladoxycanus* larvae live at the margins of moss-covered bogs and seepages and feed by cropping the mosses. *Cladoxycanus minos* (Figure 68) larvae live in the bogs but also probably occupy mosses in adjoining forests. These two *Hepialidae* genera are restricted to bogs where they live deep in the *Sphagnum* and keep warm because the *Sphagnum* absorbs heat.



Figure 68. *Cladoxycanus minos* male adult, a bog inhabitant that lives in and feeds on cushion plants, including mosses. Photo by Landcare Research, Manaaki Whenua, with online permission.

For *Cladoxycanus* (Figure 68) and *Heloxycanus* (Figure 78-Figure 79) in New Zealand, growth form seems to be important in food choice. These two genera browse on both mosses and higher plants that have a cushion growth form in moss-bog communities (Dugdale 1994).



Figure 69. *Sphagnum* habitat of *Heloxycanus patricki*. Photo by Hamish Patrick, with permission.

Larvae and pupae of *Cladoxycanus* (Figure 68) live in areas where the *Sphagnum* (Figure 69) is harvested and the larvae contribute to cropping the moss, as do *Heloxycanus* (Figure 78-Figure 79) species (Patrick *et al.* 1987; Barratt *et al.* 1990). Both cut the stems and fragment the *Sphagnum* in a way that could reduce its commercial value.

Larvae of soil and moss-inhabiting larvae in bogs in this family excavate a silk-lined shaft (Figure 71). Typically this shaft has side chambers where fecal pellets are stored, but in *Wiseana* (Figure 73-Figure 75) (Barratt *et al.* 1990), *Aoraia* (Figure 70-Figure 71) (Grehan 1989), *Oncopera brachyphylla* (Figure 72) (in Australia; Elder 1970), and *Eudalaca rufescens* (in South Africa; Joubert 1975), another chamber may be used as a storage room for cut plant material. For those living in bogs [*Cladoxycanus* (Figure 68) and *Heloxycanus* (Figure 78-Figure 79)] the *Sphagnum* (Figure 69) surface absorbs radiant heat and larvae spend the daytime up in that warm chamber. These bog dwellers have larval shafts that reach or even penetrate the water surface (Grehan & Patrick 1984). *Cladoxycanus minos* (Figure 68) occurs in water as deep as 300 mm and eats *Sphagnum cristatum* (Figure 76) (Grehan & Patrick 1984). A similar construction is present for *Wiseana umbraculata* (Figure 74-Figure 75) (Dugdale 1994). This permits it to avoid submersion during high water levels; this species is only known from saturated mosses where it is in relatively close contact with the soil surface (Grehan & Patrick 1984).



Figure 70. *Aoraia enysii* female adult, member of a genus that makes side chambers in its tunnels in bogs. Photo by Birgit E. Rhode, Landcare Research, with permission for non-commercial educational use.

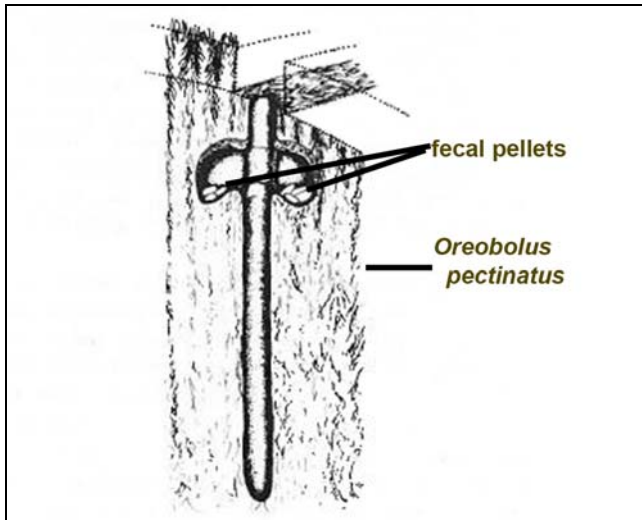


Figure 71. *Aoraia* sp. tunnel under *Oreobolus pectinatus* in bog showing chambers where fecal pellets are deposited. Modified from Grehan 1989.



Figure 72. *Oncopera brachyphylla* female adult, a species whose larvae excavate tunnels in the sedges (*Oreobolus pectinatus*) of bogs. Photo by John Grehan, with permission.



Figure 73. *Wiseana* larva, a genus that lives among mosses. Photo by Phil Bendle, with permission from John Grehan.



Figure 74. *Wiseana umbraculata* female adult; larvae often live among mosses. Photo from Landcare Research, Manaaki Whenua, with online permission.

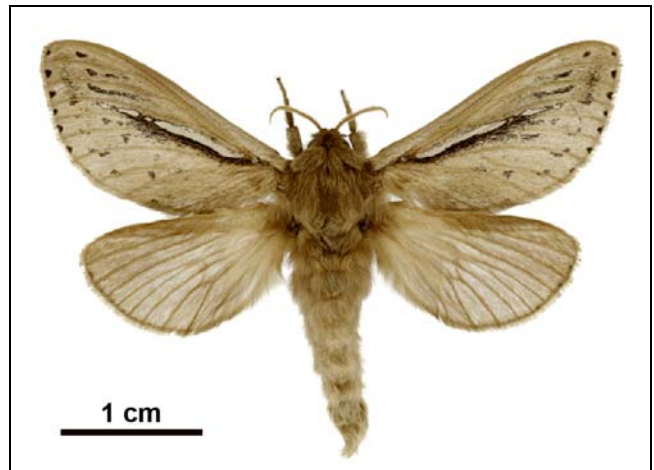


Figure 75. *Wiseana umbraculata* male adult; larvae often live among mosses. Photo from Landcare Research, Manaaki Whenua, with permission.



Figure 76. *Sphagnum cristatum*, a species consumed by *Cladoxycanus minos* in New Zealand. Photo by Jan-Peter Frahm, with permission.

Wiseana (Figure 73-Figure 75) lives among litter and mosses and has a predator in the beetle family Staphylinidae (Eyles 1966). This beetle, *Thyreocephalus chloropterus* (Figure 77), attacks the *Wiseana* and sucks out its fluids. Some of the *Wiseana* larvae may be killed to protect the beetle eggs. Both live in a habitat with plant litter and mosses and are often associated with ants.



Figure 77. *Thyrecephalus chloropterus*, a beetle that attacks *Wiseana* larvae to suck out its fluids. Photo by Ken Walker, Living Atlas of Australia, through Creative Commons.

Heloxycanus patricki (Figure 78-Figure 79) is a New Zealand ghost moth that feeds on *Sphagnum* (Figure 78-Figure 79) (Hamish 2011). It is an endemic and is in danger of extinction as its habitat has become severely fragmented and further suffers from collection for horticulture. Its adults disappear in even-numbered years, presumably indicating that the larvae require two years to develop.



Figure 78. *Heloxycanus patricki* adult on *Sphagnum*, its larval food source. Photo by Hamish Patrick, with permission.



Figure 79. *Heloxycanus patricki* adult on *Sphagnum*. Photo by Hamish Patrick, with permission.

Many of the bryophyte-dwelling larvae in **Hepialidae** spin a web in which they feed or pupate, or both (Figure 80). The larvae of the borer *Aenetus virescens* (Figure 81-Figure 85) live on trees (Grehan 1983). The larva enters its host by positioning itself axially with its head uppermost. It then places silk threads over itself, fastening them to the bark to form a roughly oval web that covers the larva. The larva is still visible through the cover at this stage. Sometimes the larva does this from within a depression so that the cover is nearly flat with the substrate surface. Once this cover is completed, the larva removes the mosses and lichens growing on the surface and places these particles inside the web. This task completed, the larva begins construction of the feeding tunnel by excavating the bark and wood tissue under the top part of the web. These fragments likewise are placed within the net cover, creating a cover that completely hides the larva inside. This chamber becomes filled with wood chips, causing the larva to make an inner silk lining to form a bag-like cavity extending from the entrance to the tunnel. Fecal pellets are placed in the lower third of the cover. *Aenetus virescens* larvae (Figure 81, Figure 83) feed primarily on the fruiting bodies of eight species of wood-inhabiting fungi (Grehan 1984).



Figure 80. Insect pupa inside its web, Kyushu, Japan. Photo by Janice Glime.

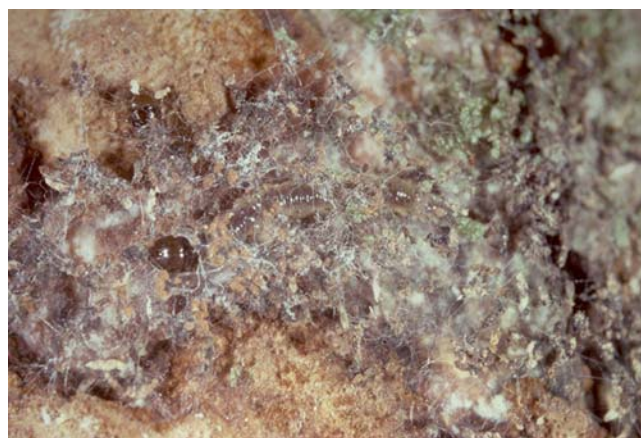


Figure 81. *Aenetus virescens* first instar feeding on fungus. Photo by John Grehan, with permission.



Figure 82. *Aenetus virescens* new tunnel under moss. Photo by John Grehan, with permission.



Figure 85. *Aenetus virescens* adult emerging. Photo by Nga Manu Images NZ, through Creative Commons.



Figure 83. *Aenetus virescens* tunnel in *Nothofagus*. Photo by John Grehan, with permission.



Figure 84. *Aenetus virescens* litter of frass pellets. Photo by John Grehan, with permission.

Aoraia macropis (Figure 86) has been collected from mosses (Dugdale 1994), including those larvae that build shafts in *Sphagnum* (Figure 68) peat (Grehan 1989). Females of this species are **brachypterous** (short-winged), but males are able to fly. This arrangement suggests limited dispersal and brachyptery seems to be a common characteristic for bryophyte-dwelling insects. The genus is endemic to New Zealand.

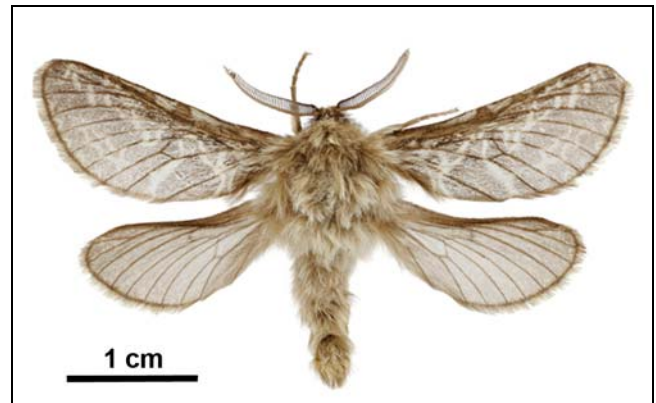


Figure 86. *Aoraia macropis* male adult, a moss dweller that builds shafts in *Sphagnum*. Photo by Birgit E. Rhode, Landcare Research, for non-commercial educational use.

Phymatopus hecta (Figure 87) was originally reported as a feeder on dandelion (*Taraxacum*) (Stainton 1857). But Sterling and Heckford (2005) found the final three larval instars feed on the moss *Mnium hornum* (Figure 89-Figure 90) at the bases of oak trees. Later, Heckford and Stella Beavan found a larva that had spun its silken web over *Mnium hornum* in an open woodland (Grehan 2016). The larva lived in a tunnel in the soil, but it fed on the moss. They also succeeded in rearing the third instar larvae to adulthood with only *Mnium hornum* as a food source. Nevertheless, multiple records indicate that it is also a root feeder.



Figure 87. *Phymatopus hecta* larva amid mosses and litter in Ashurst Wood, Hampshire, U.K. This species feeds on *Mnium hornum* in the final larval instars. Photo © Stella Beavan and Bob Heckford, with permission.



Figure 90. *Mnium hornum*, home for *Phymatopus hecta* larvae. Photo by Tim Waters, through Creative Commons.



Figure 88. *Phymatopus hecta* adult, a larval moss feeder. Photo by Stanislav Krejčík, through Creative Commons.



Figure 89. *Mnium hornum* on tree base, home for *Phymatopus hecta* larvae. Photo by Ján Jad'ud'. PERMISSION PENDING.

Palaeosetidae – Miniature Ghost Moths

Although their small size would suggest that bryophytes could make a suitable home for these ghost moths, few actually are known to live there. Heppner *et al.* (1995) has collected both males and females of *Ogygioses caliginosa* (Figure 91) that were congregating on mossy banks of streams where the mosses were kept wet. The larvae in the lab were provided a variety of food plants, but only the mosses appeared to be eaten. Surely there are other bryophyte associates in this family awaiting our discovery.



Figure 91. *Ogygioses caliginosa* adult, a species in which adults congregate on mosses and the larvae eat them. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

TINEOIDEA

Psychidae – Bagworm Moths, Case Moths

These moths construct cases or bags as larvae (Figure 92-Figure 93). These larvae are mobile, although they may attach when at rest. The bag is later used for pupation and at that time is attached to its substrate.



Figure 92. **Psychidae** case moth on moss. Photo courtesy of Sarah Lloyd.



Figure 93. **Psychidae** case moth on bryophytes, with lichen decorations on case. Photo courtesy of Sarah Lloyd.

Although the case moths usually occur with lichens and algal films, some feed on grass and a few feed on mosses. For example, Dugdale (1987) recommends beating low shrubs and branches covered by bryophytes in order to collect more larvae of *Grypthea* (Figure 94). Sapphire McFish (Bryonet 31 March 2016) reports accidentally collecting some of the case moth larvae in Tasmania. These were on mossy buttresses and logs in a

wet forest gully. The larvae stuck 2-3 mosses in their cases in about the same proportions as the mosses appeared in the area. Among these was *Thuidiopsis sparsa*.



Figure 94. *Grypthea triangularis*, a genus whose larvae live among bryophytes on low shrubs and branches. Picture from America Pink, with online permission for educational use.

Dincă (2005) surveyed the **Macrolepidoptera** at Istrița Hill in Romania and found that *Canephora hirsuta* (Figure 95-Figure 97, a bryophyte feeder, occurs there.



Figure 95. *Canephora hirsuta* larva in case. This species eats bryophytes. Photo through Creative Commons.



Figure 96. *Canephora hirsuta* larva head, the head of a moss eater. Photo by Donald Hobern, through Creative Commons.



Figure 97. *Canephora hirsuta* adult, a species with larvae that feed on mosses. Photo by Jeroen Voogd <info @ butterflies-moths.com>, with permission.

Dr. Peter B. McQuillan of the University of Tasmania described a larva that may be a species of *Narycia* (Figure 98-Figure 99). This larva makes an "untidy case" near the ground. This seems to be an advantage in providing camouflage. The larvae include grasses and mosses and other small plants in their diet.



Figure 98. *Narycia duplicella* larva with a case adorned with lichens. Photo by Patrick Clement, with permission.



Figure 99. *Narycia duplicella* larva with grey lichens adorning its case, blending with the grey lichens on the substrate. Photo by Jeroen Voogd <info@butterflies-moths.com>, with permission.

Tineidae – Fungus Moths

Tinea (Figure 100-Figure 101) is a stone mason caterpillar. The larvae cement together grains of stone, including small fragments of mosses and lichens (Rennie 1857; Zagulyayev 1970). This encasement is carried around much like the cases of the caddisflies.



Figure 100. *Tinea pellionella* larva in case that earned it the name of stone mason. Photo from ©entomart, through Creative Commons.



Figure 101. *Tinea pellionella* adult; larvae sometimes incorporate bryophytes in their cases. Photo from ©entomart, through Creative Commons.

Klok and Chown (1997) looked at temperature tolerance in a member of this family. Using *Pringleophaga marioni* (Figure 102), they found that this moth had a tolerance range from -0.6°C to 38.7°C , a range it might encounter on any day in its larval life in the sub-Antarctic Marion Island. These larvae are able to supercool to -5.0°C , with 100% of the caterpillars surviving freezing to -6.5°C . Their high temperature survival, however, was poor at 35°C and above. Larvae of this species have no osmoregulatory ability. Klok and Chown suggest that they are able to survive by living in damp situations.



Figure 102. *Pringleophaga marioni* adult, a sub-Antarctic species that tolerates temperatures to -6.5°C as larvae. Note reduced wings that seem to characterize many moss dwellers. Photo by Steven L. Chown, through Creative Commons.

Pringleophaga marioni (Figure 102) is a decomposer (Sinclair *et al.* 2004). It often nests in old albatross nests (Haupt *et al.* 2014). Haupt *et al.* suggested that the moths might select habitats that meet their thermal requirements. They choose newly abandoned nests of the Wandering Albatross (*Diomedea exulans*) more frequently than other habitats. But nests are short-lived, so other resources seem to be important. The researchers looked for possible chemosensory and thermal cues among choices in the laboratory, but they found no significant difference in larval preferences for newly abandoned nest material over old nests, the common mire moss *Sanionia uncinata* (Figure 104-Figure 103), or no choice. Larvae commonly occur in this mire moss species (Burger 1978). Although the larvae preferred lower temperatures (5°C) over higher ones (15°C), the researchers concluded that temperature and chemical cues were not the basis for the choice of substrate materials. Furthermore, the caterpillars apparently do not seek the materials that compose the nests, but rather avoid high temperatures.



Figure 103. *Sanionia uncinata* with capsules, nest material for *Pringleophaga marioni*. Photo by David T. Holyoak, with permission.

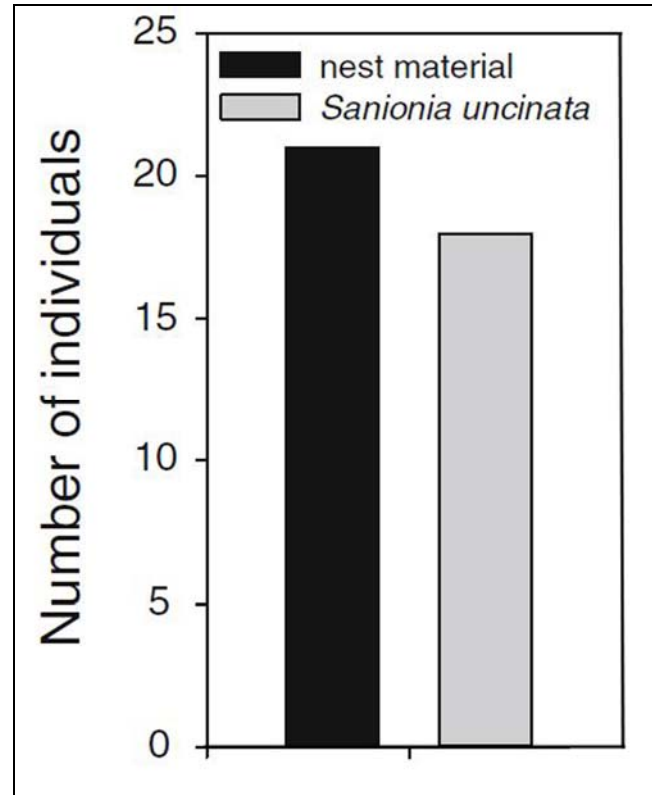


Figure 104. *Pringleophaga marioni* (Figure 102) choice of bird nest material vs the moss *Sanionia uncinata* (Figure 103) for their nests. Adapted from Haupt *et al.* 2014.

GELECHIOIDEA

Gelechiidae – Twirler Moths

This is one of the largest families of **Microlepidoptera** (Powell 1980). They are common in north temperate zones and use mosses and liverworts as their larval food. However, the family includes leaf and needle miners, gall makers, and scavengers. Of these 2% of the records of food are from mosses (18 records). Fewer than 2% of the larvae have multiple host plant species.

The **Gelechiidae** are characterized by being concealed while feeding. Some accomplish this by feeding within tracheophyte leaf tissue. The bryophyte feeders seem to accomplish this by hiding under bark or bryophytes, or by creating their own cover (e.g. *Bryotropha umbrosella* – Figure 105) by making silken tubes or tents (Fernández-Triana *et al.* 2013). Unfortunately, these do not protect them from the parasite *Shireplitis* spp. (**Hymenoptera: Braconidae**; Figure 106) that uses this caterpillar as a host (Fernández-Triana *et al.* 2013).

Kullberg *et al.* (2013) lamented that we know little about the role of mosses for the many **Lepidoptera** species living in the Arctic tundra of European Russia. Yet *Bryotropha* (e.g. Figure 105-Figure 107; originally considered part of *Gelechia*) is one of the most common **Gelechiidae** in the Holarctic (Rutten & Karsholt 2004). The genus *Bryotropha* is among the relatively few **Lepidoptera** known to feed on bryophytes, especially mosses (Heckford & Sterling 2002, 2003; Rutten & Karsholt 2004).



Figure 105. *Bryotropha umbrosella* adult, a larval moss dweller that is subject to parasitism by **Braconidae**. Photo by Janet Graham, through Creative Commons.



Figure 106. *Shireplitis bilboi* adult, member of a genus that is parasitic on *Bryotropha umbrosella*. Photo through Creative Commons.

Kullberg and coworkers (2013) were able to report that *Bryotropha galbanella* (Figure 107) lives on mosses. In Europe, this species lives on the mosses *Dicranum scoparium* (Figure 108) and *Homalothecium lutescens* (Figure 109) as its food source (Rutten & Karsholt 2004). In 1856, Shield reported *Bryotropha desertella* (Figure 110-Figure 111) and *B. umbrosella* (= *B. mundella*; Figure 105) from among bryophytes on sandhills in Europe.



Figure 107. *Bryotropha galbanella* adult, a species whose larvae live among mosses and eat them. Photo by Roy Leverton, with permission.



Figure 108. *Dicranum scoparium*, home and food for *Bryotropha galbanella*. Photo by Dale Vitt, with permission.



Figure 109. *Homalothecium lutescens*, home and food for *Bryotropha galbanella*. Photo by Michael Lüth, with permission.



Figure 110. *Bryotropha desertella* larva on moss, a common substrate for it. Photo by R. J. Heckford, with permission.

In the Netherlands, one can often collect large numbers of adults of these drab *Bryotropha* moths (e.g. Figure 112, Figure 115-Figure 117, Figure 119-Figure 120) (Rutten 1999). Most of them occur in open heaths and dunes, some in forests or urban areas. But all are thought to feed on mosses as larvae. *Bryotropha basaltinella* (Figure 112)

feeds on mosses, especially *Syntrichia ruralis* (Figure 113), on walls and thatched roofs (Britain – Meyrick 1895; Netherlands – Rutten 1999).



Figure 111. *Bryotropa desertella* adult on moss. Photo by Phil Boggis, with permission.



Figure 112. *Bryotropa basaltinella* adult, a species that lives among and eats mosses, including *Syntrichia ruralis*, on roofs as a larva. Photo by Dick Belgers, through Creative Commons.



Figure 113. *Syntrichia ruralis*, home and food for *Bryotropa basaltinella*. Photo by Hermann Schachner, through Creative Commons.

Bryotropa affinis (Figure 114-Figure 115), *B. senectella* (Figure 116-Figure 117), and *B. domestica* (Figure 118-Figure 119) larvae feed on mosses on walls, but they make a silken gallery in which to live and move about, affording them cover and camouflage (Meyrick 1928; Rutten 1999). But for the Netherlands, Rutten was only able to list "possible" food plants for *B. similis* (Figure 120): *Hypnum cupressiforme* (Figure 121), *Brachythecium rutabulum* (Figure 122), *Syntrichia ruralis* (Figure 113), *S. montana* (Figure 123), *Grimmia pulvinata* (Figure 124), *Rosulabryum capillare* (Figure 125), and *Bryum caespitium* (Figure 126) (see also Stainton 1871). Only *Bryotropa basaltinella* has a preference for urban areas, the location of most of the walls covered with mosses. Rutten reminds us that it is easier to locate the larvae on wall mosses and that in non-urban areas the adults are abundant in dry areas with no mosses.



Figure 114. *Bryotropa affinis* larva, a species that makes its silken feeding tunnels on mosses on walls. Photo through Public Domain.



Figure 115. *Bryotropa affinis* adult, a moss dweller in its larval state. Photo by Patrick Clement, with permission.



Figure 116. *Bryotropa senectella* adult, gray form, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Patrick Clement, with permission.



Figure 117. *Bryotropa senectella* adult, brown form, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Patrick Clement, with permission.



Figure 118. *Bryotropa domestica* larva, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo through Public Domain.



Figure 119. *Bryotropa domestica* adult, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Patrick Clement, with permission.



Figure 120. *Bryotropa similis* adult, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Janet Graham, through Creative Commons.



Figure 121. *Hypnum cupressiforme*, home and food for *Bryotropa similis*. Photo by J. C. Schou, Biopix, with permission.



Figure 122. *Brachythecium rutabulum* with capsules, home and food for *Bryotropa similis*. Photo by J. C. Schou <www.biopix.com>, with permission.



Figure 123. *Syntrichia montana*, home and food for *Bryotropha similis*. Photo by Michael Lüth, with permission.



Figure 126. *Bryum caespiticium*, home and food for *Bryotropha similis*, with capsules. Photo by Michael Lüth, with permission.



Figure 124. *Grimmia pulvinata* on wall, home and food for *Bryotropha similis*. Photo by J. C. Schou, Biopix, through Creative Commons.



Figure 127. *Bryotropha boreella* larva in its silken feeding tube on *Rhytidiadelphus squarrosus*. Photo by R. J. Heckford, with permission.



Figure 125. *Rosulabryum capillare* with capsules, home and food for *Bryotropha similis*. Photo through Creative Commons.



Figure 128. *Bryotropha boreella* pupa among mosses. Photo by R. J. Heckford, with permission.



Figure 129. *Bryotropha boreella* adult on *Sphagnum*. Photo by Stephen Palmer, with permission.



Figure 132. *Aulacomnium palustre*, a moss where *Bryotropha boreella* builds silken feeding tubes. Photo by Kristian Peters, with permission.



Figure 130. *Hypnum jutlandicum* with capsules, a moss where *Bryotropha boreella* builds silken feeding tubes. Photo by J. C. Schou, with permission.

Bryotropha terrella (Figure 133-Figure 134) in the British Isles feeds on the moss *Rhytidiadelphus squarrosus* (Figure 131) and the grass *Agrostis capillaris* (Palmer & Palmer 2016b). But elsewhere in Europe it is also known from the mosses *Syntrichia ruralis* (= *S. ruraliformis*; Figure 113), *Hypnum jutlandicum* (Figure 130), and *Calliergonella cuspidata* (Figure 135). Early instars construct a tough, opaque silken tube low among moss or grass, the upper end reaching near the moss surface. The tube is covered with chewed moss fragments and bits of grass. But in the final instar, the larva makes a flimsy, transparent gallery with no attached plant material.



Figure 131. *Rhytidiadelphus squarrosus*, a moss where *Bryotropha boreella* builds silken feeding tubes. Photo by Michael Lüth, with permission.



Figure 133. *Bryotropha terrella* larva, a species that includes mosses in its feeding tube until its last instar, shown here on *Rhytidiadelphus squarrosus*. Photo by R. J. Heckford, with permission.



Figure 134. *Bryotropa terrella* adult, a species whose larvae live among mosses or at the base of grasses. Photo by Steve Palmer, with permission.



Figure 135. *Calliergonella cuspidata*, larval home of *Bryotropa terrella*. Photo by Michael Becker, through Creative Commons.

Larvae of *Bryotropa politella* (Figure 136), also from the British Isles, feeds on *Rhytidiadelphus squarrosus* (Figure 131) (Palmer & Palmer 2016a). But these larvae also can occur under the moss *Schistidium* (Figure 137), although its food relationship to that species is not known (Heckford & Sterling 2003).



Figure 136. *Bryotropa politella* larva on moss. Photo © Bob Heckford, with permission.



Figure 137. *Schistidium apocarpum* with capsules, a moss genus that sometimes provides cover for *Bryotropa politella* larvae. Photo by Hermann Schachner, through Creative Commons.

In the USA and Canada, the genus *Bryotropa* is less common. *Bryotropa gemella* (Figure 138) sometimes occurs on mosses (Rutten & Karsholt 2004). The bryophage *Bryotropa galbanella* is also known from Alaska.



Figure 138. *Bryotropa gemella* adult, a North American species that sometimes lives among mosses as larvae. Photo by Jeremy deWaard, through Creative Commons.

In Russia, Bidzilya and Li (2010) reported that *Agnippe echinuloides* (Figure 139) lives in moss bogs.



Figure 139. *Agnippe echinuloides* adult, a bog species in Russia. Photo by Marko Mutanen, through Creative Commons.

Monochroa tenebrella (Figure 140) lives among mosses in Europe (Shield 1856). *Pseudotelphusa scalella* (Figure 141) larvae feed on mosses, lichens, and *Quercus robur* in Europe (Wikipedia 2015b).

Hoare (2011) found a new species of *Kiwaia* in northern New Zealand. Two specimens were found on the dominant moss *Campylopus introflexus* (Figure 142). Laboratory experiments verified that these larvae could grow to adulthood when only this moss was available as food. On the other hand, *K. jeanae* live on *Raoulia* (Asteraceae; Figure 143-Figure 144) mats, cushions that somewhat resembles a cushion of *Campylopus introflexus*, suggesting that the growth form may be important for moisture conservation.



Figure 140. *Monochroa tenebrella* adult, a species whose larvae live among mosses. Photo by Patrick Clement, Gelechiid Recording Scheme, with permission.



Figure 141. *Pseudotelphusa scalella* adult, a species whose larvae live among mosses. Photo by Donald Hobern, through Creative Commons.



Figure 142. *Campylopus introflexus*, probably home for a species of *Kiwaia*. Photo by J. C. Schou, through Creative Commons.



Figure 143. *Raoulia* sp. in full flower, home for *Kiwaia jeanae*. Photo by Nicola Tilley, through Creative Commons.



Figure 144. *Raoulia* sp. cushion with a few flowers, home for *Kiwaia jeanae*. The cushion suggests a similarity to a moss cushion. Photo from the University of Basel, through Creative Commons.

But food is not the only use this family makes of mosses. The pupal stage of *Teleiodes luculella* (Figure 145-Figure 147) in the Maltese Islands overwinters (Patocka 1987). Sorhagen (1996) found that this stage can occur under mosses or bark (Zerafa 2009).



Figure 145. *Teleiodes luculella* larva, a species that overwinter as pupae under mosses on bark. Photo © Bob Heckford, with permission.



Figure 146. *Teleiodes luculella* adult, a species that overwinters as pupae under mosses and bark. Photo by Peter Clement, with permission.



Figure 147. *Teleiodes luculella* adult, a species that overwinters as pupae under mosses and bark. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Oecophoridae – Concealer Moths

At least some of the **Oecophoridae** (concealer moths) prefer mossy habitats (Coutin 2004a). The larva of the rare *Aplota palpella* (Figure 148-Figure 149) lives among mosses on tree trunks; this species was recorded in England by Phil Sterling and Derek Hallett in Dorset County for the first time since the 19th century! (Butterfly Conservation 2001). *Crassa tinctella* (Figure 150) develops from September to May among the arboreal plant bodies of mosses and lichens, which also serve as its food (Coutin 2004b).



Figure 148. *Aplota palpella* adult, a species whose larvae live among mosses on tree trunks. Photo by Peter Huemer, through Creative Commons.



Figure 149. *Aplota palpella* adult, a species whose larvae live among mosses on tree trunks. Photo by Graham Wenman, with permission.



Figure 150. *Crassa tinctella* adult, a species whose larvae develop among epiphytic bryophytes and lichens and use them for food. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Summary

The Microlepidoptera include the **Micropterigidae** and the **Mnesarchaeidae**, but it is really a group of small Lepidoptera without close phylogenetic ties. The **Micropterigidae** is a primitive family that specializes on liverworts, although some (e.g. *Epimartyria pardella*) eat mosses. The **Mnesarchaeidae** seem to prefer the periphyton living on the moss leaves and stems. The **Hepialidae** seem to ignore liverworts and feed mostly on mosses, but they are less likely to be specialists. Some include both bryophytes and tracheophytes or fungi in their diets. Bryophyte feeders seem to prefer bogs. *Heloxycanus* prefers cushion plants – mosses or otherwise. Many of the bryophyte dwellers spin a web on the bryophytes for feeding or pupation.

In the **Palaeosetidae**, only one species is known as a moss dweller and moss feeder. The **Psychidae** construct "bags" and cases that sometimes include bryophytes. The **Tineidae** make stone cases and these may include small moss fragments. The **Gelechiidae** hide, while feeding in such places as interiors of tracheophyte leaves, under bark or bryophytes, or in silken tubes of their own making, and some eat mosses. In the **Oecophoridae**, mosses are eaten by at least a few members, typically epiphytes on trees.

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Sarah Lloyd has been very helpful in this project and introduced me to the moss-dwelling bagworms by sending me some of their pictures. Thank you to John Steel for his continued support and for sending me articles from the Otago Daily Times about Lepidoptera associated with mosses. David Glenny and Javier Martínez-Abaigar provided me with the paper on Micropterigidae that feed on *Conocephalum conicum*. David Glenny also helped me in identification of the liverwort used for the *Sabatinea heighwayi* cocoon and provided me with the *Riccardia* cocoon image. Yume Imada provided me with additional information on Japanese Micropterigidae and their diet. I

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CHAPTER 12-14

TERRESTRIAL INSECTS:

HOLOMETABOLA – LEPIDOPTERA:

TORTRICOIDEA – PAPILIONOIDEA

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CHAPTER 12-14

TERRESTRIAL INSECTS:

HOLOMETABOLA – LEPIDOPTERA:

TORTRICOIDEA – PAPILIONOIDEA



Figure 1. Larva of *Lepidoptera* (Crambidae?) on the moss *Syntrichia*. Photo courtesy of Wynne Miles.

TORTRICOIDEA

Tortricidae – Tortrix Moths, Leaf-roller Moths

This family has larvae that live among bryophytes on tree trunks. A male *Pammene albuginana* (Figure 2) was reared from mosses collected from decaying beechwood in Ireland (Bond & O'Connor 2012). Buchanan White (1971) reported *Eana penziana* (Figure 3) from among mosses near Perth, Australia, where it spins its feeding web (Buchanan White 1971). It is also known from Europe and the Near East where it apparently feeds on tracheophyte roots (Wall 2016).



Figure 2. *Pammene albuginana* adult, a species that can survive on mosses in its larval stage. Photo by Patrick Clement, with permission.



Figure 3. *Eana penziana* adult. Larvae of this species spin feeding webs on mosses in Australia. Photo by Kurt Kulac, through Creative Commons.

Another sometimes bryophyte user is *Cnephasia pasiuana* (Figure 4) – a cereal leafroller in Europe. The young, 1 mm long larvae of this species crawl about on the bark for about 2 days, then hide in bark crevices or among mosses (Ulenberg 2015). They then weave a small white cocoon (**hibernaculum**). They spend the summer there and continue there into a winter dormancy.



Figure 4. *Cnephasia pasiuana* adult, a species whose larvae hide in bark crevices and among mosses. Photo by James K. Lindsey, with permission.

Celypha aurofasciana (Figure 5) lives in galleries on trunk-dwelling mosses and liverworts, but is also suspected of eating rotting wood in the UK (Meyrick 1895; Cryer 2016).



Figure 5. *Celypha aurofasciana* adult; larvae make galleries on mosses and liverworts on tree trunks. Photo by Phil Boggis, with permission.

Mosses may contribute to providing suitable breeding grounds for *Merophyas* sp., in Danseys Pass, New Zealand (Patrick 1982). These moths fly from March to May, but the females have short wings. Two females were found on mosses in wet locations, suggesting that the mosses may be suitable egg-laying sites, or that both the moths and bryophytes like the same habitats.

PYRALOIDEA

Crambidae – Grass Moth; Sod Worms

Members of this family are often included in the **Pyralidae**. I have separated them here because the crambids seem to have a relationship with bryophytes that is seldom seen in the remaining **Pyralidae**.

Members of this family construct silken tunnels on their food plants (grasses and mosses) and reside there in relative safety as they feed (Shield 1856). The subfamily **Scopariinae** is listed in The Peterson Field Guide to Moths of Northeastern North America (Beadle & Leckie 2012) as the moss-eating Crambidae. These include *Scoparia* and *Eudonia*. Munroe (1972) has found species of *Eudonia* (e.g. Figure 8-Figure 12), *Scoparia* (e.g. Figure 25-Figure 28), and *Cosipara* (Figure 6) adults among the mosses in forests of Vancouver, Canada.



Figure 6. *Cosipara* adult, a genus whose adults frequent forest mosses in Vancouver, Canada. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

I was introduced to this family when Will Haines (pers. comm. 17 February 2012) sent me a picture of *Eudonia* (Figure 7) from Hawaii. Over 60 species of this genus occur in Hawaii, many of which feed on mosses. This one came along with some mossy rocks that Haines collected for his terrarium. Loren Russell (pers. comm.) likewise suggested that this genus feeds on mosses in the forests of Vancouver. This suggestions is based on reports of the genus in the area (Munroe 1972) and Russell's own observations of adults in the genus in mossy habitats there.



Figure 7. *Eudonia* sp. caterpillar eating moss in Hawaii. Photo courtesy of Will Haines, with permission.

Eudonia meristis (Figure 8), an endemic in Hawaii, feeds on mosses (Wikipedia 2015a). In Europe, northwest Africa, and Asia, larvae such as *Eudonia lacustrata* (Figure 9-Figure 10) feed on mosses, usually on walls or tree trunks (Doremi 2016b). In eastern North America, *Eudonia strigalis* (Figure 11) larvae are moss eaters (Beadle & Leckie 2012).



Figure 8. *Eudonia meristis* adult, a Hawaiian species whose larvae feed on mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 9. *Eudonia lacustrata* larva on moss, where it feeds on walls and trees. Photo © Bob Heckford, with permission.



Figure 10. *Eudonia lacustrata* adult, a species whose larvae feed on mosses. Photo by James K. Lindsey, with permission.



Figure 11. *Eudonia strigalis* adult, a moth species whose larvae feed on mosses in eastern North America. Photo by Elizabeth, through Creative Commons.

Hoare (2011) suggested that *Eudonia steropaea* (Figure 12) feeds on the moss *Campylopus* (Figure 13) in New Zealand. To these *Eudonia* species, Patrick *et al.* (2011) added larvae of *Eudonia aspidota* (Figure 14), *E. dinodes* (Figure 15), and *E. minualis* (Figure 16) as having moss hosts in New Zealand; *Eudonia philerga* (Figure 17) lives in and presumably eats moss on wood. These researchers even added a new species of *Eudonia* feeding on mosses on coastal rocks.



Figure 12. *Eudonia steropaea* adult, a species whose larvae most likely feed on the moss *Campylopus*. Photo by Donald Hobern, through Creative Commons.



Figure 13. *Campylopus introflexus*, home and likely food for *Eudonia steropaea*. Photo by J. C. Schou, through Creative Commons.



Figure 14. *Eudonia aspidota* adult, a species whose larvae live on mosses in New Zealand. Photo by Jon Sullivan, through Creative Commons.



Figure 15. *Eudonia dinodes* adult, a species whose larvae feed on mosses in New Zealand. Photo by Steve Kerr, through Creative Commons.



Figure 16. *Eudonia minualis* adult, a species that lives among and eats mosses in New Zealand. Photo by Phil Bendle, through Creative Commons.



Figure 17. *Eudonia philerga* adult, a species whose larvae eat mosses on logs in New Zealand. Photo by Donald Hobern, through Creative Commons.

Shield (1856) described *Eudonia murana* (Figure 18-Figure 19) as a species that occupies mosses on walls in the British Isles, spinning their webs among these plants.



Figure 18. *Eudonia murana* larva on moss. Photo © Bob Heckford, with permission.



Figure 19. *Eudonia murana* adult, a species whose larvae live among mosses on walls in the British Isles. Photo by Chris Johnson, with permission.

Heckford (2009) found one larva of *Eudonia pallida* (Figure 20-Figure 22) on the moss *Calliergonella cuspidata* (Figure 23) in Cornwall, England. It had spun a small silken ball covered in frass (insect feces). In captivity, the larva constructed a silken gallery along the moss stems and was reluctant to leave it. Wegner and Kayser (2006) reported four larvae of the species with similar silken tunnels on the moss *Pleurozium schreberi* (Figure 24). These were enclosed in a strong cocoon made of moss fragments; their frass was usually attached. These larvae laid eggs on the mosses in the lab.



Figure 20. *Eudonia pallida* early instar larva on moss. Photo by Heckford, with permission.



Figure 21. *Eudonia pallida* last instar larva on moss. Photo by Bob Heckford, with permission.



Figure 22. *Eudonia pallida* larva in cocoon on moss. Photo by Bob Heckford, with permission.



Figure 23. *Calliergonella cuspidata*, home for *Eudonia pallida* larvae. Photo by David T. Holyoak, with permission.



Figure 24. *Pleurozium schreberi*, home for *Eudonia pallida* larvae. Photo by Malcolm Storey, Discover Life, through Creative Commons.

Included among the moss eaters in eastern North America are larvae of *Scoparia biplagiata* (Figure 25) and *S. basalis* (Figure 26) (Beadle & Leckie 2012).



Figure 25. *Scoparia biplagiata* adult, a species of larval moss eaters in eastern North America. Photo by Andy Reago and Chrissy McClarren, through Creative Commons.



Figure 26. *Scoparia basalis* adult, a species whose larvae eat mosses in eastern North America. Photo by Andy Reago and Chrissy McClarren, through Creative Commons.

Stainton (1871) likewise considered *Scoparia* larvae to be moss eaters, citing a number of species that live among mosses in Europe. Larvae of *Scoparia basistrigalis* (Figure 27) feed on moss (Heckford & Sterling 2005). Heckford (2011) made it clear that not all members of *Scoparia* are moss eaters. Rather, based on experiments by Thurnall (1907, 1908) we know that at least *S. pyralella* (= *S. dubitalis*; Figure 28) feeds on roots of *Rumex acetosella* (Figure 29), and possibly other roots.



Figure 27. *Scoparia basistrigalis* adult, a moth whose larvae are parasitized by *Braconidae* and that feeds on mosses. Photo by J. C. Schou through Biopix.com, with permission.



Figure 28. *Scoparia pyralella* adult, a species of *Scoparia* whose larvae do not feed on mosses. Photo by Hectonichus, through Creative Commons.



Figure 29. *Rumex acetosella*, host for *Scoparia pyralella* larvae in Europe. Photo by Forest and Kim Starr, through Creative Commons.

Paroplitis wesmaeli is a European species of **Braconidae**, a parasitic wasp that has larval **Lepidoptera** as hosts (Yu *et al.* 2012). Two of the **Lepidoptera** host larvae, *Scoparia basistrigalis* (**Crambidae**; Figure 27) and *Bryotropha umbrosella* (**Gelechiidae**; see Figure 30), feed on mosses (Heckford & Sterling 2005; Hantmoth 2012), the latter while living in a silken tube.



Figure 30. *Bryotropha boreella* larva on moss *Rhytidiadelphus squarrosus*. Photo © Bob Heckford, with permission.

In New Zealand, *Scoparia minusculalis* (Figure 31) uses mosses as host plants (Patrick *et al.* 2011). But mosses are not the only food for the Crambidae. Cowley (1988) found that in Waikato hill country (New Zealand) the **Scopariinae** larvae were abundant in mossy regions but consumed most of the pasture grasses. When they laid their eggs, they chose both grasses and moss stems, laying to depths of 10 mm just below the ground level. The larvae that hatched constructed silk **hibernacula** (cocoons). To these they attached fine soil particles and mosses. If mosses were prolific, the larvae constructed their retreats at the bases of moss plants. The large larvae cut whole blades of grass or stems of mosses and dragged them into their burrows for food. These mosses and grasses were clipped near the burrow so that eventually the burrows were surrounded by an area that was entirely clipped. This clearing resulted in weed invasion, hence affecting the vegetation. Cowley found that all the Waikato hill country species of the **Scopariinae** were able to survive on mosses alone in the lab.



Figure 31. *Scoparia minusculalis* adult with epiphylls on a leaf. Photo by Maurice, through Creative Commons.

Heckford (2009) provides us with a rare view of the details of moss use by the **Lepidoptera**. When *Scoparia ambigualis* (Figure 32-Figure 33) larvae were reared in the lab with only the moss *Polytrichum commune* (Figure 34) for food and home, these first instar larvae spun fine silken strands in the leaf axils. Heckford interpreted these silken nets as cushions because the larvae curled up on them when they were not feeding. These are not very hairy larvae, but nevertheless, Heckford suggested that this net cushion may permit the larvae to get support for their bodies without crushing their hairs.



Figure 32. *Scoparia ambigualis* larva on moss. Note the spun cushion under it and the frass around it. Photo © Bob Heckford, with permission.



Figure 33. *Scoparia ambigualis* adult, a species whose larvae spin "cushions" in the leaf axils of *Polytrichum commune*. Photo by James K. Lindsey, with permission.



Figure 34. *Polytrichum commune*, home and food for *Scoparia ambigualis* larvae. Photo by Michael Lüth, with permission.

These *Scoparia ambigualis* (Figure 32-Figure 33) larvae ate only moss leaves in this lab observation (Heckford 2009). Their feces (**frass**) were pale greenish or yellowish for young larvae. In later instars these became reddish brown. Then Heckford added the mosses *Rhytidiadelphus loreus* (Figure 35) and *Dicranum scoparium* (Figure 36), as well as fragments of fern fronds of *Pteridium aquilinum* (Figure 37), to the choices for the larvae. Larvae occur on all three of these species in Devon, England. The larvae fed on all the mosses, but none ate the fern fragments.



Figure 35. *Rhytidiadelphus squarrosus*, a food choice of *Scoparia ambigualis* larvae. Photo by Michael Lüth, with permission.



Figure 36. *Dicranum scoparium*, one of the food choices of *Scoparia ambigualis* larvae. Photo by Michael Lüth, with permission.



Figure 37. *Pteridium aquilinum*, a food choice that was refused by *Scoparia ambigualis* larvae. Photo by Sanja, through Creative Commons.

Patrick *et al.* (2011) reports *Gadira acerella* (Figure 38) and *Glaucoccharis elaina* (Figure 39) in moss on rocks in New Zealand, whereas *Helastia corcularia* (Geometridae; Figure 40-Figure 41) lives on moss and herbs there – an unusual non-specialist strategy. Gaskin (1971) also reported *Glaucoccharis elaina* on mosses, including *Funaria* (Figure 42). Hudson (1928) reared *G. microdora* (Figure 43) and *G. metallifera* (Figure 44-Figure 45) on bryophytes.

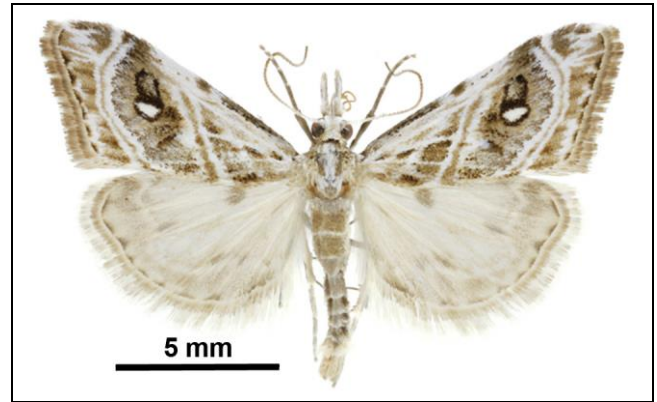


Figure 38. *Gadira acerella* adult. Larvae of this species live among mosses on rocks in New Zealand. Photo from Landcare Research, Manaaki Whenua, with online permission.

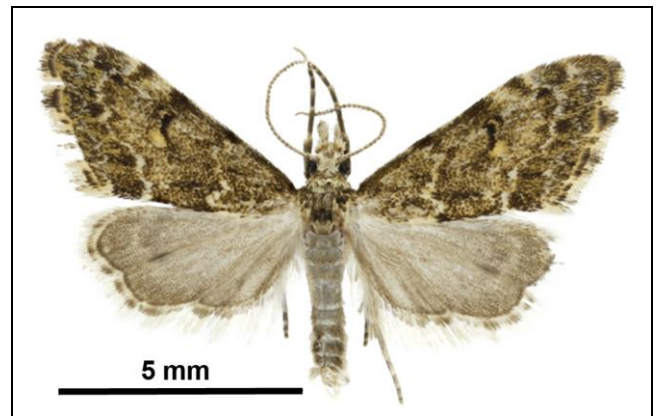


Figure 39. *Glaucoccharis elaina* adult. Larvae of this species live among mosses on rocks in New Zealand. Photo from Landcare Research, Manaaki Whenua, with online permission.



Figure 40. *Helastia corcularia* female adult, a species whose larvae eat both mosses and herbs. Photo by Phil Bendle, with permission through John Grehan.



Figure 41. *Helastia corcularia* male adult, a species whose larvae eat both mosses and herbs. Photo by Phil Bendle, with permission through John Grehan.



Figure 42. *Funaria hygrometrica* leaves, food for larvae of *Helastia corcularia*. Photo through Creative Commons.

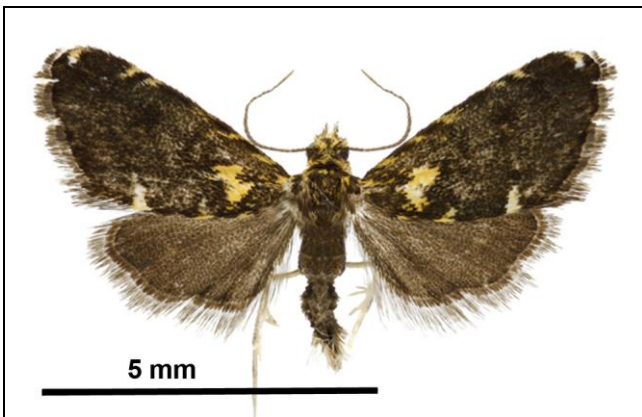


Figure 43. *Glaucoccharis microdora* adult male, a species that has been reared on bryophytes. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

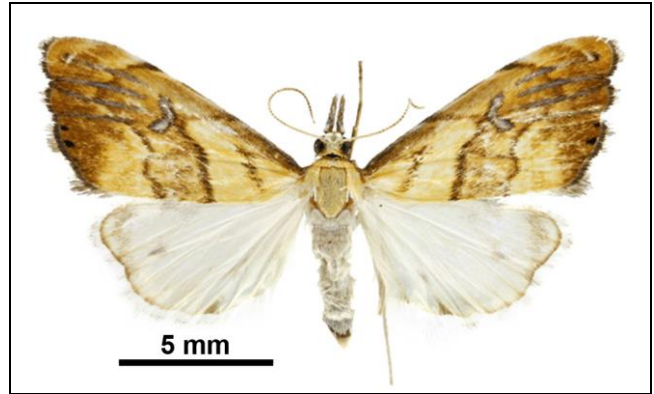


Figure 44. *Glaucoccharis metallifera* adult female, a species that has been reared on bryophytes. Photo from Landcare Research, NZ, with permission for non-commercial educational use.

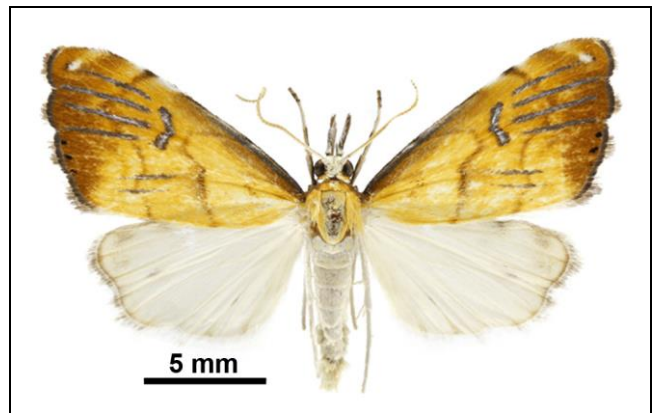


Figure 45. *Glaucoccharis metallifera* adult male, a species that has been reared on bryophytes. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

Beever and Dugdale (1994) observed severe damage to a colony of the moss *Dawsonia superba* (Figure 46) on a stream bank on the southern slopes of Mt Ruapehu, North Island, NZ. This damage was later determined to be the work of the moth larva *Glaucoccharis epiphaea* (Figure 47). Its feeding resulted in chewing off terminal portions of many leaves. They left the shoots with heavy encrustations of refuge tunnels made with silk, leaf fragments, and frass from the larvae. Leaves were severely chewed, with only 1-5 mm of green lamina remaining and the shoot apex completely destroyed. Beever (Beever & Dugdale 1994) also reared *G. bipunctella* (Figure 48) on liverwort cushions from a forest remnant.



Figure 46. *Dawsonia superba*, home for larvae of *Glucocharis epiphaea* (Figure 47). Photo by Phil Bendle, with permission from John Grehan.

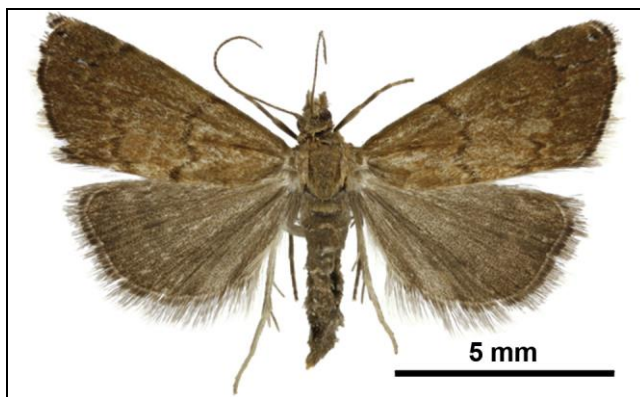


Figure 47. *Glucocharis epiphaea* adult female, a species whose larvae consume *Dawsonia superba* in New Zealand. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

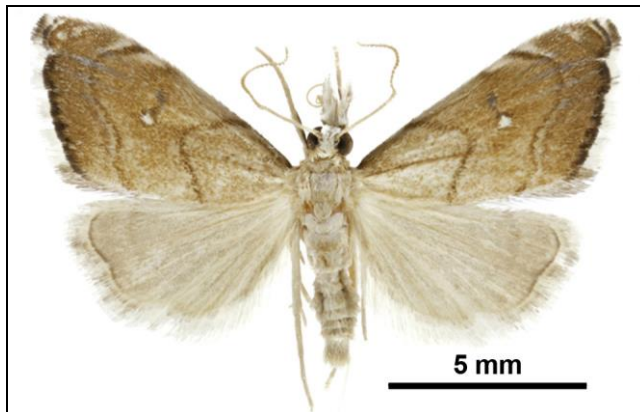


Figure 48. *Glucocharis bipunctella* adult male. Larvae of this species develop successfully on liverworts. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

Beever and Dugdale (1994) followed these observations by collecting larvae of *Glucocharis epiphaea* (Figure 47) in September and rearing them to adults on shoots of *Polytrichadelphus magellanicus* (Figure 49). *Glucocharis epiphaea* is an endemic that lives in the montane rainforests and alpine seepage areas in New Zealand.



Figure 49. *Polytrichadelphus magellanicus*, food for *Glucocharis epiphaea*, with capsules. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Members of the **Acentropinae** make cases or tunnels (Yen 2016). Many are aquatic and feed on aquatic plants, including mosses. However terrestrial larvae live in portable cases or make tunnels under mosses or lichens. The pupa of the *Paracymoriza nigra* (Figure 50) group rests in a chamber-like cocoon under mosses. Larvae of *Nymphicula morimotoi* (Figure 51) in the Philippines occur along streams on stones and rocks with rich growths of liverworts in the **Jungermanniaceae** (Yoshiyasu 1997). Females of *Nymphicula morimotoi* in the laboratory laid eggs one by one between the leaves of the liverwort. The hatchlings spin fine soil particles around themselves to construct small cases.



Figure 50. *Paracymoriza nigra* adult, a species that pupates in a cocoon under mosses. Photo through Creative Commons.



Figure 51. *Nymphicula queenslandica* adult. *Nymphicula morimotoi* larvae in the Philippines live among liverworts in the **Jungermanniaceae** on rocks along streams. Photo from Photography Group, BIO-CSIRO, through Creative Commons.

In Australia, *Pyrausta cingulata* (syn=*Ennychia cingulalis*; Figure 52-Figure 53) lives among mosses and spins its web in them (Buchanan White 1971). This behavior was known more than a century ago in Europe, where its retreat is among mosses and dead leaves (Heyden 1861). It can be located by the large heaps of frass nearby.



Figure 52. *Pyrausta cingulata* larva, a species that lives among mosses and spins its web there. Photo by Bob Heckford, with permission.



Figure 53. *Pyrausta cingulata* adult, a species that lives among mosses and spins its web there. Photo by Tiroler Landesmuseum, through Creative Commons.

Crambus tristellus (see Figure 54) occurs in damp locations along ditches where it makes silken galleries on mosses (Shield 1856). Other former members of *Crambus* (Figure 54) that dwell among mosses have been reclassified into a variety of genera. Buckler (1901) reported that members of *Crambus* feed among stems and roots of grasses or on moss (Stainton 1852), but these bryophages may now belong to other genera.



Figure 54. *Crambus pascuella* male adult. *Crambus tristellus* makes silken galleries on mosses in damp locations. Photo by Jérôme Albre, with permission.

Catoptria falsella (syn=*Crambus falsellus*; Figure 55) is a wall dweller (Doremi 2016a). The larva builds a silk tube that helps to hide it while it is feeding, typically on mosses, and especially on the moss *Tortula muralis* (Figure 56). This is the ultimate site for its pupation. Shield (1856) found larvae of *Catoptria falsella* in the unique habitat of mosses on thatch of a barn. This species primarily hides among mosses on walls, stones, and rocks in the daytime, feeding at night on mosses, including *Tortula muralis*, *Syntrichia ruralis* (Figure 57), *Barbula* (Figure 58), and *Brachythecium rutabulum* (Figure 59) (Wikipedia 2014). South (1890) reported *Catoptria verellus* (syn=*Crambus verellus*; Figure 60) among mosses on tree trunks, particularly older plum, apple, and poplar trees. The species also occurs in fir woods with moss-covered ground.



Figure 55. *Catoptria falsella* adults – wall dwellers, showing two color phases. Larvae typically feed on mosses, including *Tortula muralis*. Photos by Donald Hobern, through Creative Commons.



Figure 56. *Tortula muralis* with capsules on wall, food for *Catoptria falsella*. Photo by Mike, through Creative Commons.



Figure 57. *Syntrichia ruralis*, food for the nighttime feeder *Catoptria falsella*. Photo by Hermann Schachner, through Creative Commons.



Figure 58. *Barbula unguiculata*. Some members of this genus provide food for the nighttime feeder, *Catoptria falsella*. Photo by James K. Lindsey, with permission.



Figure 59. *Brachythecium rutabulum*, nighttime food for *Catoptria falsella*, with capsules. Photo by J. C. Schou <www.biopix.com>, with permission.



Figure 60. *Catoptria verellus* adult, a species whose larvae live on moss-covered tree trunks and moss-covered ground. Photo by Donald Hobern, with permission.

Chrysoteuchia culmella (= *Crambus hortuellus*; Figure 61) larvae build silken galleries on the ground under mosses (Shield 1856). Where it is damp along ditches, one can also find larvae of *Agriphila straminella* (syn=*Crambus culmellus*; Figure 62) with their silken galleries. The larvae mature there and spend their pupation there.



Figure 61. *Chrysoteuchia culmella* adult. Their larvae build their silken galleries under ground mosses. Photo through Wikimedia Commons.



Figure 62. *Agriphila straminella* adult; the larvae occur along damp ditches, including among mosses. Photo by André Karwath, through Creative Commons.

Huggins (2011) listed *Oxyelophila callista* (Figure 63) as a species of moss shredders, but these are aquatic mosses.



Figure 63. *Oxyelophila callista* adult; larvae are shredders of aquatic mosses. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Some evidence that **Crambidae** live among mosses is indirect (Russell 1979). Their head capsules have been found numerous times in mosses on logs and deciduous tree trunks. Webbing and fecal pellets occur among damaged mosses. Based on this evidence, it appears that *Hypnum circinale* (Figure 64) and *Tetraphis pellucida* (Figure 65) are most likely eaten by larvae of **Crambidae** (formerly placed in **Pyralidae**).



Figure 64. *Hypnum circinale*, food for larvae of the **Crambidae**, with capsules. Photo by Matt Goff, with permission.



Figure 65. *Tetraphis pellucida* with gemmae, a species most likely eaten by members of the **Crambidae**. Photo by Hermann Schachner, through Creative Commons.

Pyralidae – Snout Moths

There are few known bryophages remaining in this family in its more restricted definition. Fraenkel and Blewett (1947) suggested that some of this snubbery of the bryophytes may be due to the chemical composition. However, they failed to show that bryophytic linoleic acid was detrimental, and bryophyte arachidonic acid actually promotes growth of the larvae of *Ephestia kuehniella* (Figure 66-Figure 67).



Figure 66. *Ephestia kuehniella* larva, a species whose growth is promoted by arachidonic acid from bryophytes. Photo by Simon Hinkley and Ken Walker, Museum Victoria, through Creative Commons.



Figure 67. *Ephestia kuehniella* mating adults. Photo by Magne Flåten, through Creative Commons.

Synaphe punctalis (Figure 68) and *S. angustalis* (Figure 69) builds its scant webs among damp mosses on the ground (Meyrick 1895). In addition to these, in

Australia, *Phycis subornatella* lives among mosses and spins its web in it (Buchanan White 1971).



Figure 68. *Synaphe punctalis* adult, a species whose larvae build webs among damp ground mosses. Photo by Thorsten Denhard, through Creative Commons.



Figure 69. *Synaphe angustalis* adult, a species whose larvae build scant webs on damp mosses. Photo from ©entomart, through Creative Commons.

HESPERIOIDEA

Hesperiidae – Skippers

These lepidopteran differ from both moths and butterflies. They have short, fat bodies like moths, hooked antennae unlike the club antennae of butterflies or the feathery antennae of moths, and a unique rapid, skipping flight (Bartlett 2004; Wikipedia 2015c).

The skippers are generally not associated with mosses. However, *Polites mardon* (Figure 70-Figure 73) builds a larval shelter of silk with mosses, dry grass blades, litter, and dry frass serving to camouflage it (Henry & Beyer 2013). These are located at the bases of grasses near the soil surface.



Figure 70. *Polites mardon* larva, a species that incorporates pieces of mosses in its silk shelter. Photo by Jim P. Brock, with permission.



Figure 71. *Polites mardon* pupa, a species that incorporates pieces of mosses in its silk shelter. Photo by Jim P. Brock, with permission.



Figure 72. *Polites mardon* adult, a species whose larvae include mosses in their net. Photo by Lauren Sobkoviak, through Creative Commons.



Figure 73. *Polites mardon* adult, a species that incorporates pieces of mosses in its silk shelter. Photo by William Leonard, with permission.

PAPILIONOIDEA

Lycaenidae – Blues, Coppers, Hairstreaks, Harvesters (Butterflies)

Some Lepidoptera seem to have switched from feeding on leaves to feeding on the **epiphylls** (Figure 74) on the leaves (Callaghan 1992). It appears that in this case, the bryophytes, mostly the leafy liverworts in **Lejeuneaceae**, were an important food source. In a Nigerian cola forest, *Pentila picena cydaria* (Figure 75) lays its eggs singly on live trees. Its substrate includes not only the woody stems, but also green lichens and mosses. These eggs are initially white, but within a day they become dark brown, making them less conspicuous.



Figure 74. **Lejeuneaceae** epiphylls on leaf, food for several **Lepidoptera**, including *Pentila piceana cydaria*. Photo by Claudine Ah-Peng, with permission.



Figure 75. *Pentila picena* adult, a species whose larvae feed on epiphylls, including bryophytes. Adults include mosses among their oviposition sites. Photo by Sáfíán Szabolcs, with permission.

Nymphalidae – Brush-footed Butterflies

Singer and Mallet (1986) expressed excitement at finding *Euptychia insolata* (Figure 76) alighting on "green" tree trunks in Costa Rica. As they continued observations, they found six green spherical eggs, then observed the female ovipositing on the epiphytic moss *Neckeropsis undulata* (Figure 77). This species landed on tree trunks with green bryophytes, searching for oviposition sites. The larvae of this butterfly are well camouflaged on the moss. They are "moss-shaped" and moss-colored. This appears to be the first record for butterfly larvae that feed on a moss (Singer *et al.* 1983; Singer & Mallet 1986), but they were unable to determine if they were restricted to this moss species. Singer and Mallet (1986) were able to raise 5 adults from 6 eggs by using *Neckeropsis undulata* as the only food source. The larvae of this species are "moss-shaped" and have cryptic coloration, rendering them safe on this moss.



Figure 76. *Euptychia insolata* adult, a butterfly that oviposits on epiphytic mosses on tree trunks and its larvae eat there. Photo by Will & Gill Carter, with permission.



Figure 77. *Neckeropsis undulata*, oviposition site for *Euptychia insolata*. Photo by Bobby Hattaway, from <www.discoverlife.org>, through Creative Commons.

Hamm (2015) expressed surprise that members of *Euptychia* have switched from feeding on grasses to feeding on low-nutrient plants like *Selaginella* (a fern ally; Figure 78) and mosses (Scriber & Slansky 1981). On the other hand, Egorov (2007) concluded that the epiphytic mosses had sufficient nitrogen due to contributions from epiphytic *Cyanobacteria* (Figure 79) and the slow growth of the mosses. Furthermore, in experiments with *E. westwoodi* (Figure 80), Hamm (2015) found that the larvae would not eat grasses (*Lasiacis ruscifolia*, a preferred food of close relatives) when those were the only choice, losing weight and ultimately dying. Those fed with *Selaginella* ate and developed normally.



Figure 78. *Selaginella*, a fern ally that resembles a moss, has low nutrients, and serves as food for some species of *Euptychia*. Photo by Tim Waters, through Creative Commons.

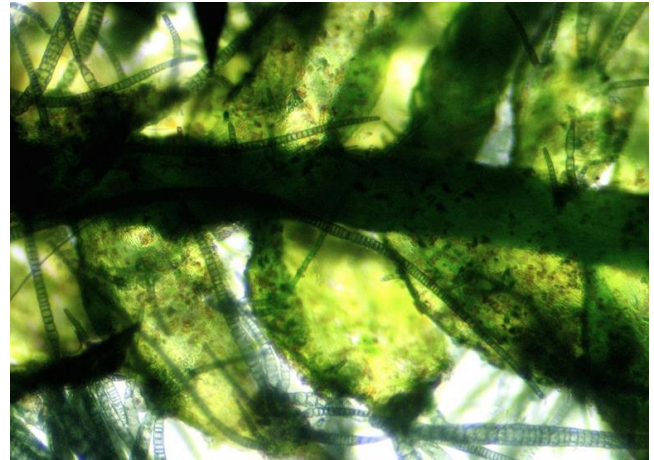


Figure 79. *Cyanobacteria* on a moss, a source of nitrogen for feeders on epiphytic bryophytes. Photo by Nat Tarbox, through Creative Commons.



Figure 80. *Euptychia westwoodi* adult, a species that will not eat grasses as larvae. Photo by Daniel H. Janzen, through Creative Commons.

The genus *Euptychia* occurs elsewhere in South America. Pulido *et al.* (2011) describe it as living in the mountain foothills and montane forests of the Andes in Colombia and Peru. Neild *et al.* (2014) described a new species from the Amazon Basin and the Guianas, describing the genus as occurring throughout the Neotropical region. This is a small butterfly and seems to generally have singular hosts among fern allies and mosses. Singer and Mallet (1986) predicted that we will eventually find that many South American *Euptychiines* feed on "lower" plants.

But not all members of *Euptychia* are bryophages. Beccaloni *et al.* (2008) reported that *Euptychia hilara* feeds on a member of *Poaceae* (grasses).

Bryophytes are often among a group of convenient locations for pupation. This is the case for the White Mountain Arctic butterfly (*Oeneis melissa semidea*; Figure 81) (Lucking 2000). Its larvae are night-active feeders, spending their day between or under rocks (Scudder 1874, 1889; Gradish & Otis 2015). Pupation, however, uses safe sites under rocks, moss, or soil. Male adults perch in areas with considerable Bigelow's sedge, the probable substrate for oviposition and food plant for the larvae (Scudder 1891, 1901).



Figure 81. *Oeneis melissa semidea* (White Mountain Arctic) adult, a species whose pupae often occur under mosses. Photo by Kent McFarland, through Creative Commons.

Some adult **Lepidoptera** provide very interesting mimics. The moth in Figure 82 resembles a leaf with epiphyllous liverworts (Figure 74). Is there some advantage to adding the liverworts? The leaf itself is brown, suggesting it may be high in tannins and not very palatable. Do the liverworts further discourage carnivory? Might the Lejeuneaceae they seem to mimic have secondary compounds that discourage "herbivory" (in this case on a fake)? Or do they just blend with leaves, hence avoiding larger carnivores such as birds?



Figure 82. Moth mimicking a leaf with epiphyllous bryophytes, especially liverworts, in Malaysia. Photo courtesy of Tamás Pócs.

The bog fritillary, *Boloria eunomia* (Figure 83-Figure 87), is of special concern in Wisconsin, USA (WDNR 2009). Its habitat is in classical acid bogs (Wikipedia 2011), a habitat that is diminishing. Schtickzelle and Baguette (2004) warn that glacial relict species such as this one are increasingly more vulnerable as their fragmented habitat becomes more and more rare. Typically, the *Sphagnum* (Figure 88) mosses provide the right conditions for the host plants. Natives of Scotland have been concerned about the conversion of the classic bog at Aucheninnes Moss to a landfill (Buglife 2011). This is the

location of the small pearl-bordered fritillary *Boloria selene* (Figure 89-Figure 92), a species of conservation concern, and the only site in Scotland for the sorrel pigmy moth *Enteucha acetosae* (Figure 93). A third species there, *Coenonympha tullia* (Figure 94-Figure 97), is listed as vulnerable in Europe. These moss-dominated bog habitats house many insects that are in danger of disappearing as these bogs disappear.



Figure 83. *Boloria eunomia* first instar caterpillar, a bog species. Photo by Gilles San Martin, through Creative Commons.



Figure 84. *Boloria eunomia* last instar, a bog species. Photo by James K. Lindsey, with permission.



Figure 85. *Boloria eunomia* adult, a bog dweller. Photo by Gilles San Martin, through Creative Commons.



Figure 86. *Boloria eunomia*, a bog dweller. Photo by Gilles San Martin, through Creative Commons.



Figure 89. *Boloria selene tollandensis* 5th instar larva, a bog dweller. Photo by Todd Stout, with permission.



Figure 87. *Boloria eunomia* egg, a bog species. Photo by Gilles San Martin, through Creative Commons.



Figure 90. *Boloria selene tollandensis* pupa, a bog species. Photo by Todd Stout, with permission.

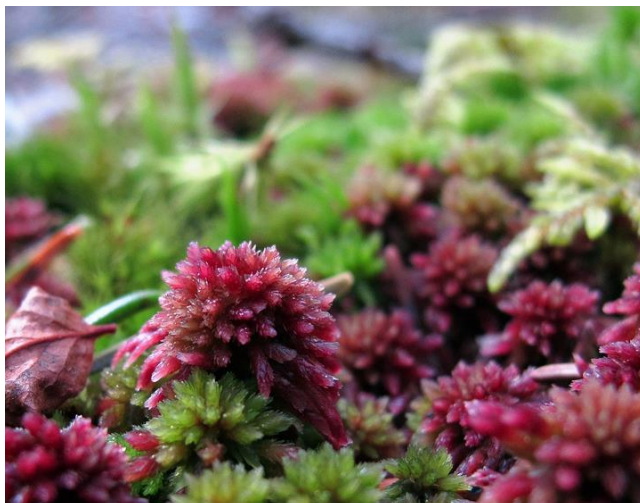


Figure 88. *Sphagnum capillifolium*, one of the bog mosses that provide suitable homes for *Boloria eunomia*. Photo by Michael Lüth, with permission.



Figure 91. *Boloria selene* adult, a bog dweller. Photo by Kristian Peters, through Creative Commons.



Figure 92. *Boloria selene* adult, a bog dweller. Photo by James K. Lindsey, with permission.



Figure 95. *Coenonympha tullia* larva on moss. Its colors permit it to blend with mosses in bogs. Photo by Wolfgang Wagner, with permission.



Figure 93. *Enteucha acetosae* adult, a rare bog dweller. Photo by Patrick Clement, with permission.



Figure 94. *Coenonympha tullia* egg, a vulnerable bog species. Photo by Wolfgang Wagner, with permission.



Figure 96. *Coenonympha tullia* pupa, a bog species. Photo by Wolfgang Wagner, with permission.



Figure 97. *Coenonympha tullia* adult, a bog species. Photo by Ryan Hodnett, through Creative Commons.

Some members of this family are so well adapted to living among mosses that their cryptic form and coloration has earned them the name of moss caterpillars. At least some of these unusual caterpillars are in the Western Hemisphere genus *Adelpha* (Figure 98-Figure 103). The earliest record of these seems to be that of Moss (1933) for *Adelpha melona leucocoma* larvae that resemble a moss. In Costa Rica, *Adelpha serpa celerio* resembles mosses on a twig (DeVries 1987). Wilmott (2003) cited several species in *Adelpha* that mimicked mosses, including *Adelpha leucophthalma leucophthalma* larvae that resemble moss-covered twigs. There seem to be multiple forms of these mimics, and those forms may contribute to their occurrences in different habitats, potentially leading to separation as species.



Figure 98. *Adelpha serpa celerio*, moss-mimicking caterpillar in Panama, blending with its habitat. Photo by Arthur Anker, with permission



Figure 99. *Adelpha serpa celerio*, showing the byrophyte-like appendages of this moss-mimicking caterpillar in Panama. Photo by Arthur Anker, with permission.



Figure 100. *Adelpha serpa celerio* spinning its web on a leaf. Photo by Arthur Anker, with permission.



Figure 101. *Adelpha* (?) larva from Brazil, showing head and appendages. Photo by Troy Bartlett, through Creative Commons.



Figure 102. *Adelpha* (?) larva looking like moss on a twig. Photo by Troy Bartlett, through Creative Commons.



Figure 103. *Adelpha fessonia* adult, a member of the moss caterpillar genus showing the differences in coloration from its cryptic larva. Photo by Thomas Bresson, through Creative Commons.

Rionidae – Tropical Butterflies

This small family of butterflies does not seem to have a common name.

The species *Sarota gyas* (Figure 104) in the tropics can be found on leaves of tracheophytes, but Mota *et al.* (2014) pointed out that these are not the real hosts. Instead, the larvae are there to feed on the **epiphylls** (Figure 74) – the non-nitrogen-fixing epiphylls (DeVries 1988). In one case, larvae on a member of the Urticaceae fed on leafy liverwort epiphylls in the **Lejeuneaceae** (Figure 74). Apparently the host tree is unimportant for either oviposition or larval feeding. These larvae have long setae that provide defense and they are camouflaged among the epiphylls.



Figure 104. *Sarota gyas* adult, a species whose larvae live on leaves of tracheophytes where they feed on epiphylls (Figure 74). Photo by Harold Greeney, through Creative Commons.

Summary

The **Tortricidae** include a few bryophyte associates, particularly those on tree trunks. The **Crambidae**, on the other hand, construct silken tunnels on mosses and grasses where they feed in safety. The subfamily **Scopariinae** is known as the moss-eating **Crambidae**. This family has been separated from the **Pyralidae** and few bryophyte associates remain in the **Pyralidae**. The **Hesperiidae** are skippers and seem to have only one member (*Polites mardon*) that associates with mosses. The **Lycaenidae** feed on the **epiphylls** on leaves, particularly the leafy liverworts in the **Lejeuneaceae**. In the **Nymphalidae**, *Euptychia insolata* adults are cryptically colored to be able to alight on moss-covered tree trunks without being obvious. These are butterflies and among the ones that feed on mosses. They may use the mosses as a source of nitrogen derived from their epiphytic **Cyanobacteria**. *Adelpha*, in the **Nymphalidae** also exhibits moss mimicry. Members of this family are common bog dwellers. The **Rionidae** has one member, *Sarota gyas*, that feeds on epiphylls such as members of the **Lejeuneaceae**, in particular to obtain nitrogen from the associated nitrogen fixers.

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CHAPTER 12-15

TERRESTRIAL INSECTS:

HOLOMETABOLA – LEPIDOPTERA:

GEOMETROIDEA – NOCTUOIDEA

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CHAPTER 12-15

TERRESTRIAL INSECTS:

HOLOMETABOLA – LEPIDOPTERA:

GEOMETROIDEA – NOCTUOIDEA



Figure 1. **Geometridae** larva eating *Hypopterygium tamarisci*. Photo by Adaises Maciel da Silva, with permission.

GEOMETROIDEA

Geometridae – Geometrid Moths (Inch Worms)

The **Geometridae** get their name from their larvae, popularly known as inch worms (Figure 2). The method of movement has suggested that the larvae are measuring the earth. This family has cryptic coloration as larvae (Figure 2) (Bodner *et al.* 2010). In the montane rainforest of southern Ecuador, the brown, green, and gray tones help them to blend with the montane rainforest. For example, *Phyllodonta semicava* (see Figure 3) and *Cargolia arana* (Figure 4-Figure 5) resemble the mossy bark where they live.



Figure 2. **Geometridae** larva "inching" along the stem. Photo by Jérôme Albre, with permission.



Figure 3. *Phyllodonta* sp. adult; some species resemble the mossy bark where they rest. Photo by Daniel H. Janzen, through Creative Commons.



Figure 4. *Cargolia arana* larva, resembling mossy banks where it lives. Photo by Wilmer Simbaña and Luis Salgaje, through Creative Commons.



Figure 5. *Cargolia arana* adult with cryptic coloration. Photo by James Sullivan, with online permission.

In tropical montane rainforests of Brazil, larvae in the **Geometridae** are the culprits that feed on the mosses *Hypopterygium tamarisci* (Figure 7-Figure 14) and *Lopidium concinnum* (Figure 15), especially at the beginning of the rainy season (September to December)

(Maciel-Silva & dos Santos 2011). Using an index of damage (ID) in 2007 and 2008, Maciel-Silva and dos Santos found that *H. tamarisci* had higher damage (68%, 35%) than *L. concinnum* (38%, 23%) in these two years (Figure 6), but they were unable to separate that of the geometrid from that of a cohabiting snail. Furthermore, these rates were lower than those for tracheophytes. They found no correlation of herbivory with phenols, proteins, or the ratio between these (Figure 6).

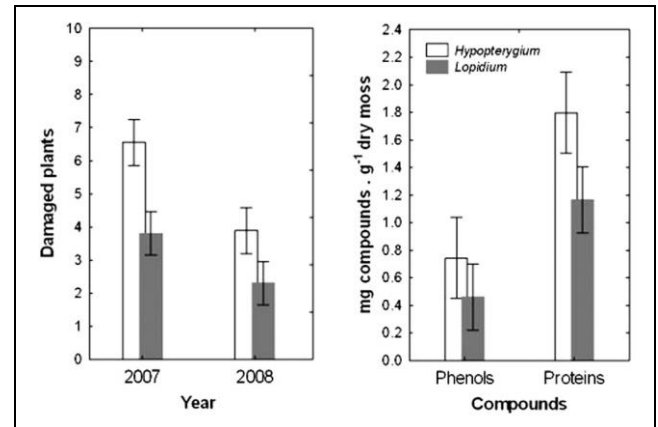


Figure 6. **Charopidae** (snail) and **Geometridae** damage to mosses in 10 colonies of plants. Modified from Adaisies Maciel-Silva and Nivea Dias dos Santos.



Figure 7. Field damage to *Hypopterygium tamarisci* by larvae of the **Geometridae**. Photo by Adaisies Maciel-Silva and Nivea Dias dos Santos, with permission.



Figure 8. Field damage to *Hypopterygium tamarisci* by larvae of the **Geometridae**. Photo courtesy of Adaisies Maciel-Silva and Nivea Dias dos Santos, with permission.



Figure 9. Damage to leaves (circled) of *Hypopterygium tamarisci* by a *Geometridae* larva in the laboratory over about 50 days. Photo courtesy of Adais Maciel da Silva.



Figure 10. *Geometridae* on its host plant, *Hypopterygium tamarisci*. Photo courtesy of Adais Maciel da Silva.



Figure 11. *Geometridae* on the host plant *Hypopterygium tamarisci*. Photo courtesy of Adais Maciel da Silva.

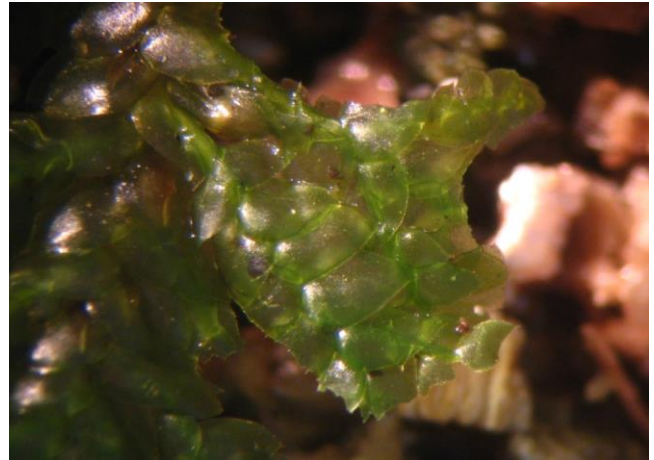


Figure 12. *Hypopterygium tamarisci* herbivory by *Geometridae* larvae. Photo courtesy of Adais Maciel da Silva.



Figure 13. *Hypopterygium tamarisci* herbivory by *Geometridae*. Photo courtesy of Adais Maciel da Silva.



Figure 14. Larva of *Geometridae* feeding on *Hypopterygium tamarisci*. Photo by Adais Maciel-Silva and Nivea Dias dos Santos, with permission.



Figure 15. *Lopidium concinnum*, food for some larvae of *Geometridae*. Photo by Leon Perrie, through Creative Commons.

Orthonama obstipata (= *Camptogramma fluviata*; Figure 16) is not a moss feeder as far as I can tell, but it does "retire" among mosses or just below the soil surface (Hellins 1871). One must wonder if the mosses are an important component of its niche. It constructs a cocoon that is weak, thin, and made of silk. Mosses may help to buffer the temperature and maintain moisture.



Figure 16. *Orthonama obstipata* adult, a species that "retires" among mosses, or in the soil just below them. Photo by Ben Sale, through Creative Commons.

Helastia mutabilis (Figure 17) larvae feed on mosses in eastern Otago, New Zealand (Patrick 2016). The larva of *Helastia mutabilis* feeds on the moss *Racomitrium* (Figure 18) in the local area of Otago, thus far the only known host plant for it.



Figure 17. *Helastia mutabilis* adult, a species whose larvae feed on mosses in New Zealand. Photo by Donald Hobern, through Creative Commons.



Figure 18. *Racomitrium lanuginosum*. *Helastia mutabilis* larvae feed on members of this genus. Photo by Juan Larrain, through Creative Commons.

Perizoma taeniatum (= *Martania taeniata*; Figure 19) is one of the macro-moths that most likely feeds on mosses as larvae (Pescott *et al.* 2015). Pescott and coworkers expressed concern that air pollution is harming the lichens and bryophytes and may lead to the demise of those that feed on them.



Figure 19. *Perizoma taeniatum* adult, a species whose larvae apparently feed on mosses and may be harmed by loss of mosses and lichens due to air pollution. Photo by M. Virtala, through Creative Commons.

Eupithecia austeraria (Figure 20) pupae occur among mosses on stumps, close to the moisture of the rotting wood (Shield 1856). *Eupithecia irriguata* (Figure 21) spends its pupal winters under bark and mosses (Dietz 1871). Krampl (1994) reported *Eupithecia thalictрата* (Figure 22) pupation in cocoons, usually in dry mosses near the base of its host plants. The pupae overwinter and adults emerge that spring.



Figure 20. *Eupithecia austeraria* adult, a species that pupates among mosses on stumps. Photo from Wikiwand.



Figure 21. *Eupithecia irriguata* adult, a species that overwinters as a pupa under bark and mosses. Photo by Marko Mutanen, through Creative Commons.



Figure 22. *Eupithecia thalictрата* adult, a species that pupates in dry mosses. Photo by Püngeler, through Public Domain.

Scotorythra paludicola (Figure 23) larvae don't eat mosses – they eat leaves and phyllodes of *Acacia koa* (Haines *et al.* 2013) and other members of the Fabaceae (Barton & Haines 2013). But the adults do use the mosses. The females lay their eggs in bark crevices and in mosses on the trunks of host trees, providing them with cover during development while keeping them close to their host leaves.



Figure 23. *Scotorythra paludicola* larva, a species that begins its life among mosses on *Acacia koa* where females lay eggs on tree trunks. The larvae then move to the leaves and phyllodes to feed. Photo by Forest Starr and Kim Starr, through Creative Commons.

Hyposidra talaca (Figure 24-Figure 25) lives in the tea plantations of northeastern India (Sinu *et al.* 2013). The species is a pest there, and the tree bark and its moss cover offer protection for the eggs of this species. This is one of the moths that oviposits in different places from the ones where it feeds (Wiklund 1977; Tammaru *et al.* 1995). Similarly, the Bruce spanworm (*Operophtera bruceata*; Figure 26-Figure 27) infests tree leaves, but the eggs are often laid among mosses growing at the bases of these trees (Ives 1984).



Figure 24. *Hyposidra talaca* larva, a pest in tea plantations. The female deposits eggs where they are hidden by mosses. Photo by Vaikoover, through Creative Commons.



Figure 25. *Hyposidra talaca* adult, a pest in tea plantations. It deposits eggs where they are hidden by mosses. Photo by Sterling Sheehy, through Creative Commons.



Figure 26. *Operophtera bruceata* larva (Bruce spanworm) that begins its life among mosses at the base of host trees. Photo by E. Bradford Walker, through Creative Commons.



Figure 27. *Operophtera bruceata* adult. Females lay their eggs among mosses at the base of trees. Photo by Cody Hough, through Creative Commons.

Not all bryophyte associates are drab browns and grays. *Milionia isodoxa*, although not a bryophyte dweller, does make use of them and is quite colorful. The adults of *Milionia isodoxa* (Figure 28) in Papua New Guinea illustrate the method that seems typical for obtaining water among many **Lepidoptera** (Wylie 1982). These moths probe and feed at moist sand and mud and in soil of puddle margins. Occasionally they obtain their water from mosses on rocks or on stream debris, but they do not drink from the free water itself.



Figure 28. *Milionia isodoxa* adult, a species that drinks from the moist mosses on rocks or along streams. Photo by David Polluck, through Creative Commons.

Camouflage is important, and even adults may rest where they are not easily seen. In New Zealand, *Declana griseata* (Figure 29) larvae feed on mistletoe that grows as a parasite in the trees, but as adults these moths rest on the mossy trunks of trees in the vicinity, blending with the color patterns there (Patrick & Dugdale 1997).

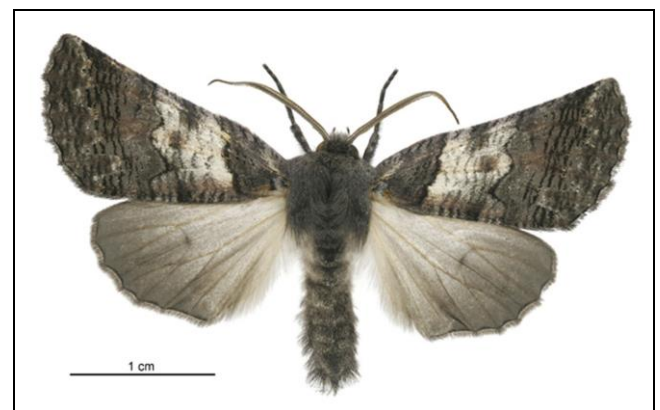


Figure 29. *Declana griseata* male adult, a species that rests on mossy tree trunks. Photo by Landcare Research, Manaaki Whenua, with permission.

Shaking a carefully removed clump of epiphytic moss may reveal the cocoon of *Odontopera bidentata* (Figure 30) attached to the tree trunk and looking like "dark whitey-brown paper with a few pieces of moss attached to it" (Shield 1856). The larvae are good mimics of lichens on a twig (Figure 31).



Figure 30. *Odontopera bidentata* adult showing its cryptic coloration for resting on bark. Photo by Donald Hobern, through Creative Commons.



Figure 31. *Odontopera bidentata* larva, a species that builds a cocoon on tree trunks, attaching mosses to it. This one is a lichen mimic. Photo by Kimmo Silvonen, with permission.

Hydriomena impluviata (syn=*Ypsipetes impluviaria*; Figure 32) pupates in mosses and Shield (1856) describes the method to look for them. He warns that one must remove the moss carefully from its bark substrate, starting at the moss tips and holding it on both sides. A sample the size of one's hand should be removed, then shaken to dislodge the black pupae. The moss should be kept intact as a sheet. Unfortunately, this method is quite destructive of the mosses.



Figure 32. *Hydriomena impluviata* adult, a species that pupates among mosses. Photo by Fvlamoen, through Creative Commons.

Erannis jacobsoni (Figure 33) larvae defoliate the trees in the spruce-fir forests of Russia (Тырова & Юрченко 1996). Outbreaks of this species are primarily in the "green-moss" types of these forests, suggesting that the mosses may be important in their life cycle, perhaps as a place for laying eggs. For example, Kinghorn (1952) found that the western hemlock looper lays eggs among mosses and that oviposition increases when the density of the mosses is greater. On the trees, having mosses grow to higher positions increases the correlation between egg density and height on tree. Kinghorn suggested that moss density might be the strongest single factor influencing the place where eggs were deposited.



Figure 33. *Erannis jacobsoni* larva, a species that defoliates trees in spruce-fir forests with abundant moss ground cover. Photo by Vladimir Petko, through Creative Commons.

The western hemlock looper, *Lambdina fiscellaria lugubrosa* (Figure 34), along the western coast of North America lays most of its eggs in mosses on tree trunks, branches, and logs (Hopping 1934; Carolin *et al.* 1864; Shore 1990). But in the forests of the interior, their preferred oviposition sites are on the pendant lichen *Alectoria* spp. (Figure 35) (Thomson 1958). *Lambdina fiscellaria fiscellaria* (Figure 36) usually lays its eggs singly, but sometimes these are in groups of 2 or 3 (Carroll 1956). These are typically placed on mosses and lichens on the tree trunk or under old bark scales, but also on mosses covering stumps and logs.



Figure 34. *Lambdina fiscellaria lugubrosa* (western hemlock looper) larva, a species that often lays its eggs in mosses. Photo by Jerald E. Dewey, through Creative Commons.



Figure 35. *Alectoria sarmentosa*, one of the preferred oviposition sites for *Lambdina fiscellaria lugubrosa* (Figure 34). Photo by Jason Hollinger, through Creative Commons.



Figure 36. *Lambdina fiscellaria fiscellaria* larva. Photo from Pennsylvania Department of Conservation and Natural Resources, through Creative Commons.

Shepherd and Gray (1972) bemoaned the difficulty of counting the eggs (Figure 37) of the hemlock looper (*Lambdina fiscellaria lugubrosa*; Figure 34) that were attached to mosses. Finding it both tedious and inaccurate, they devised a more consistent method for this process. They treated moss samples with 0.5% NaOH for 1 minute to release the eggs. These were then washed and filtered out of the moss sample. A solution of 15% NaCl helps to separate other debris from the sample by flotation. Using this method, they were able to obtain density estimates with two standard errors.



Figure 37. *Lambdina fiscellaria* eggs on fir. Photo from Natural Resources Canada, Canadian Forest Service, with online permission.

Otvos and Bryant (1972) likewise tested methods for assessing the eggs present on mosses and bark. They tried a range of bleach solutions and found that a 2% bleach solution bath for 45 minutes would release eggs of *Lambdina fiscellaria* (Figure 38) eggs without deleterious effects.



Figure 38. *Lambdina fiscellaria* adult, the hemlock looper. Photo by D. Gordon E. Robertson, through Creative Commons.

Dobesberger (1989) developed a management plan for *Lambdina fiscellaria fiscellaria* (Figure 36). Dobesberger determined that only six midcrown branches were adequate to obtain an average sample number. More eggs were present on the midcrown area of the balsam fir, *Abies balsamea* (Figure 39), than on other substrates including ground mosses – mostly *Hylocomium splendens* (Figure 40), *Pleurozium schreberi* (Figure 41), and *Ptilium crista-castrensis* (Figure 42), as well as loose bark of paper birch and lichens in the crown (mostly *Usnea longissima*; Figure 43).



Figure 39. *Abies balsamea*, most common egg-laying site for *Lambdina fiscellaria fiscellaria* (Figure 36). Photo by DVS, through Creative Commons.



Figure 42. *Ptilium crista-castrensis*, lesser egg-laying site for *Lambdina fiscellaria fiscellaria* (Figure 36). Photo by Li Zhang, with permission.



Figure 40. *Hylocomium splendens*, lesser egg-laying site for *Lambdina fiscellaria fiscellaria* (Figure 36). Photo by Andrew Spink, with permission.



Figure 41. *Pleurozium schreberi* occasional egg-laying site for *Lambdina fiscellaria fiscellaria* (Figure 36). Photo by Michael Lüth, with permission.



Figure 43. *Usnea* sp., one of the substrates for egg laying of *Lambdina fiscellaria fiscellaria*. Photo by T.cegy, through Creative Commons.

Eggs of *Lambdina fiscellaria lugubrosa* (Figure 34) in coastal forests of British Columbia, Canada, could be sampled at 6-7 m intervals from the ground level to the top of tree trunks by sampling the mosses (Richmond 1947). When defoliation averaged 82%, the egg count was 226 healthy eggs per 30 cm square of moss from ground level

to the top of the tree at 27 m elevation. But at 427 m, the mean defoliation dropped to 10% and the egg count to 0.3 eggs per 30 cm square of moss.

But why are the entomologists so interested in counting eggs of this species on mosses? Feeding on the leaves by the hemlock looper can devastate a hemlock forest in only one year, fir trees in 2-3 (USDA 2016). Hébert *et al.* (2003) found that the outbreaks of *Lambdina fiscellaria* (Figure 38) have a sudden rapid increase and patchy distribution across wide areas. This means that predicting where control is needed can be difficult. To be prepared, it is necessary to conduct egg surveys, a tedious and expensive process. But Hébert and coworkers found a simpler means. They used white polyurethane foam substrates with the Luminoc insect trap and a portable light trap. These oviposition traps were highly efficient for sampling eggs and the results were highly correlated with those of extracting eggs from mosses on 1-m branches.

Otvos and Bryant (1972) pointed out the importance of assessing *Lambdina fiscellaria* eggs (Figure 37), present September to June, as a means to help them prepare for potentially devastating years. The larvae that cause the damage are present for only two weeks before the damage becomes serious. By counting eggs, managers can assess and prepare for the upcoming year. These larvae are able to cause great damage not by fully consuming leaves, but by nibbling the ends of leaves, causing rapid and permanent desiccation (USDA 2016).

But all is not well for the eggs of the eastern hemlock looper (*Lambdina fiscellaria fiscellaria*; Figure 36). A pest on the balsam fir, *Abies balsamea* (Figure 39), the eggs (Figure 37) of this species are subject to parasitism (Otvos 1977). Otvos experimented with these in the lab using eggs collected on the peat moss *Sphagnum* spp. (Figure 44), the lichen (*Usnea* sp.; Figure 43) and on birch bark (*Betula* spp.; Figure 45). Otvos found that the percentage of mortality for overwintering eggs is inversely related to the difference between the mean winter temperature and normal winter temperature. Mortality from parasites was about the same for eggs collected in autumn and spring.



Figure 44. *Sphagnum magellanicum* and *Sphagnum fimbriatum*, egg laying sites for *Lambdina fiscellaria fiscellaria*. Photo from NY Botanical Garden, through Public Domain.



Figure 45. Birch (*Betula*) bark where *Lambdina fiscellaria fiscellaria* deposits eggs. Photo by Sue Sweeney, through Creative Commons.

The hemlock looper also uses mosses for pupation. *Lambdina fiscellaria somniaria* (Figure 46-Figure 48) uses both mosses and bark crevices on the lower branches and tree trunks as well as debris on the ground near the host trees, providing them with protection during this stage (Willhite 2013). In Alaska, when it is time for pupation, the full-fed larvae of *Lambdina fiscellaria* extend a silken thread and descend from the conifer needles to the ground where they pupate under mosses or bark scales or in crevices of rotting tree stumps (Torgersen & Baker). In 14-20 days the adult emerges.



Figure 46. *Lambdina fiscellaria somniaria* (hemlock looper) larva, a species that uses mosses for pupation. Photo from USFS, through Public Domain.



Figure 47. *Lambdina fiscellaria somniaria* larva in moss. Photo from USFS, through Public Domain.



Figure 48. *Lambdina fiscellaria somniaria* pupa in moss. Photo from USFS, through Public Domain.

LASIOCAMPOIDEA

Lasiocampidae – Snout Moths

Norman (1871) noted that *Macrothylacia rubi* (as *Lasiocampa rubi*; Figure 49-Figure 50) larvae swarm on mosses in autumn in Morayshire, Scotland. These larvae are known to the ophthalmologists because their hairs cause conjunctivitis of the eye.



Figure 49. *Macrothylacia rubi* female adult. In Scotland, larvae of this species swarm on mosses in autumn. Photo by Jérôme Albre, with permission.



Figure 50. *Macrothylacia rubi* female adult. Larvae of this species swarm on mosses in autumn in Scotland. Photo by Jérôme Albre, with permission.

Some of the interactions get complicated. *Bracca* sp. occurs on the ground where moss and leaf litter are common in their habitat between tree buttresses (Brown 2006). What makes this interesting is that the *Bracca* sp. mimics the coral snake (*Hemibungarus calligaster*) in the Philippines. These two species share this habitat.

NOCTUOIDEA

Arctiidae – Tiger Moths etc.

You may be familiar with this family through the woolly bear caterpillar. Few members of the family seem to be bryophyte dwellers. Nevertheless, I have already noted that the subfamily **Lithosiinae** eat bryophyte capsules (Liu 1989 in Fang & Zhu 2012). Yuanfu (1989) concluded that the large number of species and individuals in this family that occur in the tropical mountain rainforest of Hainan Island can "be explained" by the large number of mosses and lichens here.

The larvae of *Cybosia mesomella* (Figure 51-Figure 52) (sometimes placed in **Erebidae**) consume liverwort leaves, particularly the genus *Jungermannia* (Figure 53), as well as lichens (Coutin 2004). Some of the larvae of the lichen moths (**Lithosiinae**) (e.g. *Hypoprepia miniata*; Figure 54-Figure 55) feed on mosses as well as algae and lichens (Rawlins 1984; Anonymous 2011). Members of this subfamily normally feed on cryptogams such as algae, lichens, and bryophytes, eating only the photosynthetic partner in the lichens (Simonson 2016).



Figure 51. *Cybosia mesomella* larva, a species that eats the leafy liverwort *Jungermannia*. Photo by Wolfgang Wagner, with permission.



Figure 52. *Cybosia mesomella* adult, a species that eats leafy liverworts as larvae. Photo by Stanislav Krejčík, through Creative Commons.



Figure 53. *Jungermannia leiantha* with perianths, a genus that is a food source for *Cybosia mesomella*. Photo by Hermann Schachner, through Creative Commons.



Figure 54. *Hypoprepia miniata* larva, a species that feeds on both mosses and lichens. Its coloration hides it well among mosses. Photo by M. J. Hatfield, through Creative Commons.



Figure 55. *Hypoprepia miniata* adult. Photo by Tom Peterson, Fermilab, through Public Domain.

In northern Europe *Nudaria mundana* (Figure 56) larvae feed on both lichens and liverworts growing on rocks (Forster & Wohlfahrt 1960).



Figure 56. *Nudaria mundana* adult; larvae feed on lichens and liverworts on rocks. Photo by James K. Lindsey, with permission.

Erebidae

Many of the bryophyte-feeding species have been removed from **Arctiidae** and placed in **Erebidae**, whereas other systematists keep them in **Arctiidae**. I have chosen to list them under **Erebidae** because the majority of bryophyte feeders are grouped here. My usual source for nomenclature, Encyclopedia Online, is inconsistent in its placement of them.

Atolmis rubricollis (Figure 57-Figure 59) is one of these species. Its larvae feed on mosses and lichens growing on the trunks of trees (epiphytes) (Shield 1856; Dincă 2005). Hence, it is not surprising that the pupae occur under moss, but on decaying trees. *Atolmis rubricollis* is a tiny, inconspicuous moth that makes its winter cocoon in mosses and litter (Coutin 2004).



Figure 57. *Atolmis rubricollis* larva, a stage that eats mosses and makes cocoons there on trees. Photo by Harald Süpfle, through Creative Commons.



Figure 58. *Atolmis rubricollis* pupa on moss where it spends its winter. Photo by Harald Süpfle, through Creative Commons.



Figure 59. *Atolmis rubricollis* adult, emergent from a pupa that overwinters in mosses and litter. Photo by Sanja565658, through Creative Commons.

Larvae of both *Miltochrista miniata* (Figure 60-Figure 62) and *Lithosia quadra* (Figure 63-Figure 64) are bryophyte and lichen feeders in Romania (Dincă 2005). Likewise, *Dysauxes ancilla* (Figure 65-Figure 67) and the genus *Eilema* include bryophytes in their larval diet there, including *E. lurideola* (Figure 68-Figure 70), *E. complana* (Figure 71-Figure 72), *E. pseudocomplana* (Figure 73), and *Eilema sororcula* (Figure 74-Figure 76). In addition to these, Wagner (2016b) adds *E. morosina* (Figure 77-Figure 80) as a species that includes mosses in its diet in Europe.



Figure 60. *Miltochrista miniata* eggs on rotting wood, a species whose larvae include mosses among their food. Photo by Wolfgang Wagner, with permission.



Figure 61. *Miltochrista miniata* larva on moss, one of its food sources. Photo by Wolfgang Wagner, with permission.



Figure 62. *Miltochrista miniata* adult, a species whose larvae feed on bryophytes. Photo by Stanislav Krejčík, through Creative Commons.



Figure 63. *Lithosia quadra* larva, a species that includes mosses and lichens in its diet. Photo by Wolfgang Wagner, with permission.



Figure 64. *Lithosia quadra* adult, a species whose larvae feed on bryophytes. Photo by František Šaržík, through Creative Commons.



Figure 65. *Dysauxes ancilla* larva, a species that includes mosses in its diet. Photo by Wolfgang Wagner, with permission.



Figure 66. *Dysauxes ancilla* habitat. Photo by Wolfgang Wagner, with permission.

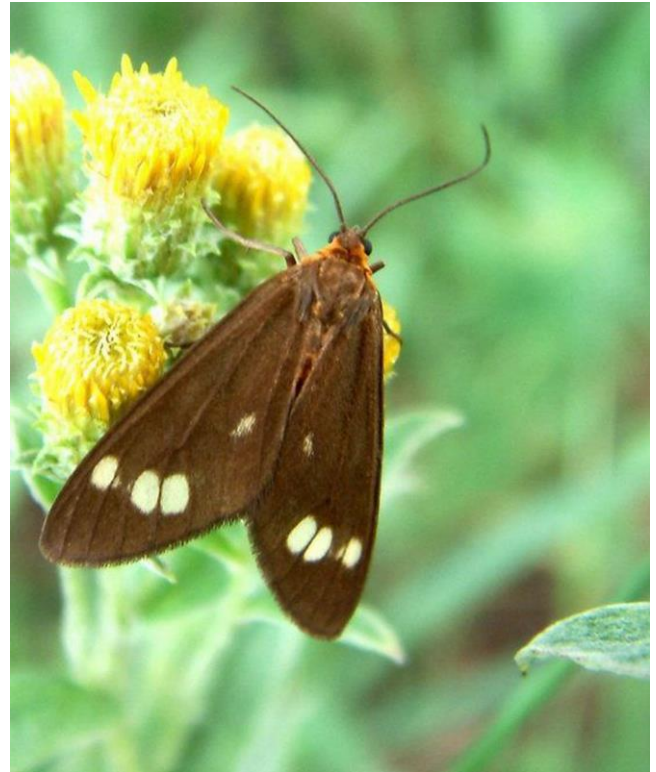


Figure 67. *Dysauxes ancilla* adult, a species whose larvae include mosses in their diet. Photo by Ondřej Zicha, through Creative Commons.



Figure 68. *Eilema lurideola* larva, a moss and lichen feeder. Photo by Wolfgang Wagner, with permission.



Figure 69. *Eilema lurideola* pupa, a species that includes bryophytes in its larval diet. Photo by Wolfgang Wagner, with permission.



Figure 70. *Eilema lurideola*, a species whose larvae feed on a variety of plants, including mosses. Photo by Kurt Kulac, through Creative Commons.



Figure 71. *Eilema complana* larva on moss, one of its food items. Photo by Tristan Bantok, with permission.



Figure 72. *Eilema complana* adult, a species with a broad larval diet that includes mosses. Photo by Ondřej Zicha, through Creative Commons.



Figure 73. *Eilema pseudocomplana* adult, a species whose larvae include mosses in the diet. Photo by Matthew Gandy, with permission.



Figure 74. *Eilema sororcula* larva, a species with a broad diet that includes mosses and lichens. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 75. *Eilema sororcula* larval head, a species having a broad diet that includes mosses and lichens. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 76. *Eilema sororcula* adult, a species whose larvae include mosses in their diet. Photo by Miroslav Fiala, through Creative Commons.



Figure 77. *Eilema morosina* larva, a moss eater. Photo by Wolfgang Wagner, with permission.



Figure 78. *Eilema morosina* larval habitat. Photo by Wolfgang Wagner, with permission.



Figure 79. *Eilema morosina* pupa. Photo by Wolfgang Wagner, with permission.



Figure 80. *Eilema morosina* adult, a species whose broad larval diet includes mosses. Photo by Wolfgang Wagner, with permission.

Hypercompe scribonia (syn. = *Ecpantheria deflorata*; Figure 81-Figure 82) actually eats the thallose liverwort, *Conocephalum conicum* in western Indiana, USA (Figure 83) (Spencer *et al.* 1984). It normally feeds on two species of *Plantago* (Figure 84), a seed plant, and Spencer and coworkers suggest that the surface is similar to that of the liverwort and the two plants grow intermixed, possibly causing the shift despite major differences in chemistry. They noted this liverwort feeding behavior in the autumn, which suggests the possibility that the chemical shift may be a means of preparing for winter. Nevertheless, they raised several larvae to adults in the lab, using *C. conicum* as the only food source.



Figure 81. *Hypercompe scribonia* larva, a herbivore on *Conocephalum conicum*. Photo by Micha L. Rieser, through Creative Commons.



Figure 82. *Hypercompe scribonia* adult, a species whose larvae consume the liverwort *Conocephalum conicum*. Photo by R. A. Nonenmacher, through Creative Commons.



Figure 83. *Conocephalum conicum*, a food source for *Hypercompe scribonia*. Photo by Hermann Schachner, through Creative Commons.



Figure 84. *Plantago major*, a genus that is normal food for *Hypercompe scribonia*. Photo by Olivier Pichard, through Creative Commons.

The secondary compounds of *Conocephalum conicum* (Figure 83) are well known. This liverwort is rich in mono- and sesquiterpenoids (Asakawa *et al.* 1976; Markham & Porter 1978; Spencer 1979). We also know that some terpenoids from liverworts inhibit Lepidoptera feeding (Wada & Munakata 1971). *Plantago* (Figure 84), on the other hand, is rich in iridoid glycosides (Jensen *et al.* 1975). It is possible that whatever permits the larvae to feed on the toxic glycosides also permits them to feed on the terpenoids in liverworts.

The **Lithosiini** have been known from several studies as bryophyte feeders (Forbes 1960; Holloway 1988; Aba 2013). Moreno *et al.* (2014) summarized feeding in the family by stating that the members of the tribe **Arctiini** feed on a wide range of plant species whereas the **Lithosiini** specialize on lichens, algae, and bryophytes (Wagner 2009).

Several species of Tribe **Lithosiini** resemble **Microlepidoptera** as adults (Coutin 2004). Furthermore, the larvae consume liverworts. Larvae of *Thumatha senex* (Figure 85) likewise consume liverwort leaves, particularly the genus *Jungermannia* (Figure 53), as well as lichens. Manley (2009) treated *Thumatha senex* as a nighttime cryptogam feeder that includes mosses in its diet (Macek *et al.* 2007; Manley 2009).



Figure 85. *Thumatha senex* adult, a liverwort and lichen consumer. Photo by James K. Lindsey, with permission

Lymantriidae – Tussock Moths

Lymantria dispar (Figure 86-Figure 87), the gypsy moth, spins threads over its retreat in a crack in the bark (Rennie 1857). Occasionally they may use a curtain of moss such as *Hypnum* (Figure 88) growing there instead of spinning these threads.

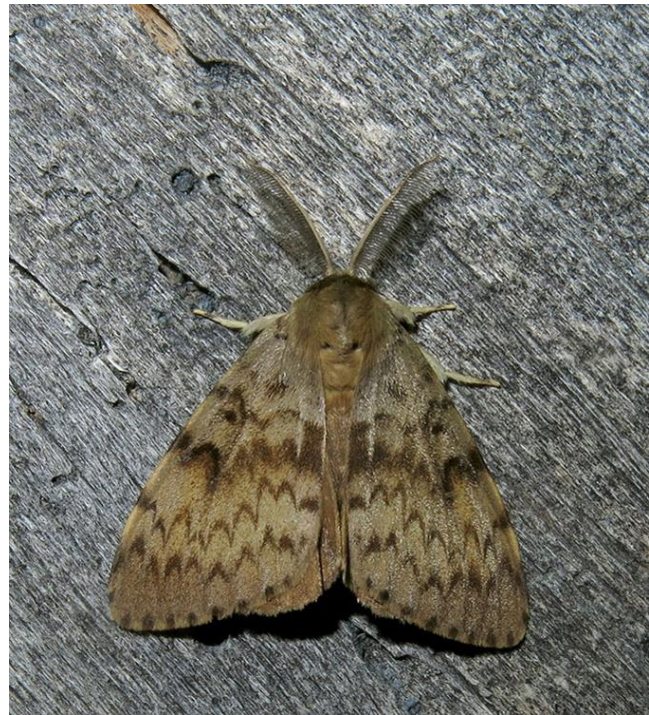


Figure 86. *Lymantria dispar* (gypsy moth) male adult. Larvae of this species sometimes use mosses instead of spinning threads over their retreat on bark. Photo by Jérôme Albre, with permission.



Figure 87. **Lymantridae** larva. *Lymantria dispar* sometimes uses mosses instead of spinning a cocoon. Photo by Jérôme Albre, with permission.



Figure 89. *Bryum argenteum*, a moss avoided by *Trichoplusia ni* in feeding trials. Photo by Michael Becker, through Creative Commons.



Figure 88. *Hypnum cupressiforme* with young sporophytes on bark. *Hypnum* is sometimes used to cover larvae of *Lymantria dispar*. Photo by Dick Haaksma, with permission.



Figure 90. *Climacium americanum*, a moss avoided by *Trichoplusia ni* in feeding trials. Photo by Li Zhang, with permission.

Noctuidae – Owlet Moths

Haines and Renwick (2009) summed up the paucity of bryophagous insects. They considered that three deterrents were responsible for their limited consumption: chemical defenses, low digestibility, and low nutrient content. They examined this phenomenon by testing pre and post-ingestive defenses of four species of mosses [*Bryum argenteum* (Figure 89), *Climacium americanum* (Figure 90), *Leucobryum glaucum* (Figure 91), *Sphagnum warnstorffii* (Figure 92)]. Even when they had no other choice, larvae of *Trichoplusia ni* (cabbage looper; Figure 93-Figure 94) ate considerably more lettuce or wheat germ than they did any of the moss species. Post ingestive responses could only be evaluated in *C. americanum* because the larvae ate too little of the other species for evaluation. Digestibility, assimilation, and overall utilization efficiency did not differ between lettuce and *C. americanum*. In disk choice experiments, ethanol extracts of *Leucobryum glaucum* were deterrent, explaining why this was the least consumed moss in the experiment and providing evidence of pre-ingestive mechanisms. The hypotheses of poor nutrient content and low digestibility were not supported in these experiments.



Figure 91. *Leucobryum glaucum*, a moss avoided by *Trichoplusia ni* in feeding trials. Photo by James K. Lindsey, with permission.



Figure 92. *Sphagnum warnstorffii*, a moss avoided by *Trichoplusia ni* in feeding trials. Photo by Michael Lüth, with permission.



Figure 93. *Trichoplusia ni* larva, a species that avoids eating bryophytes. Photo by M. J. Hatfield, through Creative Commons.



Figure 94. *Trichoplusia ni* adult, a species whose larvae do not choose mosses even with no other choice. Photo by Barry Stewart, with permission.

Several species in Romania feed on mosses (Dincă 2005). These include *Parascotia fuliginaria* (Figure 95), *Calymma communimacula* (Figure 96), *Cryphia receptricula* (Figure 97), and *Cryphia raptricula* (Figure 98). Wagner (2016a) also includes *Cryphia muralis* (Figure 99) and *C. algae* (Figure 100-Figure 102) among the moss feeders in Europe.



Figure 95. *Parascotia fuliginaria* adult, a species whose larvae include mosses in their diet. Photo by Biopix, through Creative Commons.



Figure 96. *Calymma communimacula* adult, a species whose larvae include mosses in their diet. Photo by Dumitru, through Creative Commons.



Figure 97. *Cryphia receptricula* adult, a species whose larvae feed on mosses. Photo by Peter Huemer, through Creative Commons.



Figure 98. *Cryphia raptricula* adult, a species whose larvae eat mosses. Photo by Biopix, through Creative Commons.



Figure 99. *Cryphia muralis* larva, a species that includes mosses and lichens in its diet. Photo by Wolfgang Wagner, with permission.



Figure 100. *Cryphia algae* larva, a species that eats mosses, algae, and lichens. Photo by Wolfgang Wagner, need permission.



Figure 101. *Cryphia algae* larval habitat. Photo by Wolfgang Wagner, with permission.



Figure 102. *Cryphia algae* adult, a species whose larvae include mosses in their diet. Photo by Jérôme Albre, with permission.

Kimmo Silvonen (pers. comm. 1 March 2016) told me about *Caradrina montana* (Figure 103) in Europe. He found this larva on a rocky hill on a moss. It accepted the moss as food during rearing, but it may be a polyphagous species that eats a variety of plants. Among these, it feeds on alfalfa leaves in northwestern North America (McLeod 2005).



Figure 103. *Caradrina montana* larva, a species that can be reared on moss. Photo courtesy of Kimmo Silvonen.

The feeding of *Agrotis* sp. (Figure 104) on moss capsules (Figure 105-Figure 106) of *Haplocladium microphyllum* (Figure 107) is well documented. Fang and Zhu (2012) experimented to see what else they would eat and found they would feed to various degrees on capsules of *Ditrichum pallidum* (Figure 108), *Funaria hygrometrica* (Figure 109), *Physcomitrium sphaericum* (Figure 110), *Pogonatum inflexum* (Figure 111), and *Trematodon longicollis* (Figure 112). The latter two species were only sparsely grazed and caused a high mortality rate. Fang and Zhu suggested that the lipid content may be important in their selection.



Figure 104. *Agrotis puta* adult male, member of a genus in which larvae of at least some species feed on moss capsules. Photo by Jérôme Albre, with permission.



Figure 105. *Agrotis* eating capsules of *Haplocladium microphyllum*. Photo by Rui-Liang Zhu, with permission.



Figure 106. *Haplocladium microphyllum* capsules missing due to feeding by *Agrotis*. Photo by Rui-Liang Zhu, with permission.



Figure 107. *Haplocladium microphyllum* with capsules. Species of *Agrotis* feed on these capsules. Photo by Scott Zona, through Creative Commons.



Figure 108. *Ditrichum pallidum* with capsules that serve as food for *Agrotis*. Photo by Bob Klips, with permission.



Figure 109. *Funaria hygrometrica* with capsules that serve as food for *Agrotis*. Photo by Li Zhang, with permission.



Figure 110. *Agrotis* sp. eating a capsule of *Physcomitrium sphaericum*. Photo by Rui-Liang Zhu, with permission.



Figure 111. *Pogonatum inflexum* with capsules that serve as food for *Agrotis*. Photo through Creative Commons.



Figure 112. *Trematodon longicollis* capsules that serve as food for *Agrotis*. Photo by Bobby Hattaway, through Creative Commons.

Agrotis sp. avoids the capsules of *Pogonatum inflexum* (Table 1; Fang & Zhu 2012). On the other hand, when only *Haplocladium microphyllum* was available as food, a late-instar larva consumed 190 capsules (Figure 113). Similar herbivory occurred on *Physcomitrium sphaericum* and *Funaria hygrometrica* (Figure 113) Fang and Zhu compared the phenolic content (Figure 114) and nutrient content (Figure 115) among several mosses. They found that These capsules contained significantly more lipids than the tracheophyte leaves from the same environment (Figure 115).

Table 1. 24-hour consumption of moss capsules in three samples of 30 capsules each by an individual *Agrotis* sp. in early, mid, and late instar stages. Based on Fang & Zhu 2012.

	instars		
	early	mid	late
<i>Haplocladium microphyllum</i>	30	– 30	– 30
<i>Funaria hygrometrica</i>	30	– 30	– 30
<i>Physcomitrium sphaericum</i>	30	– 30	– 30
<i>Trematodon longicollis</i>	30	– 30	– 28
<i>Ditrichum pallidum</i>	30	– 2	– 3
<i>Pogonatum inflexum</i>	5	– 4	– 7

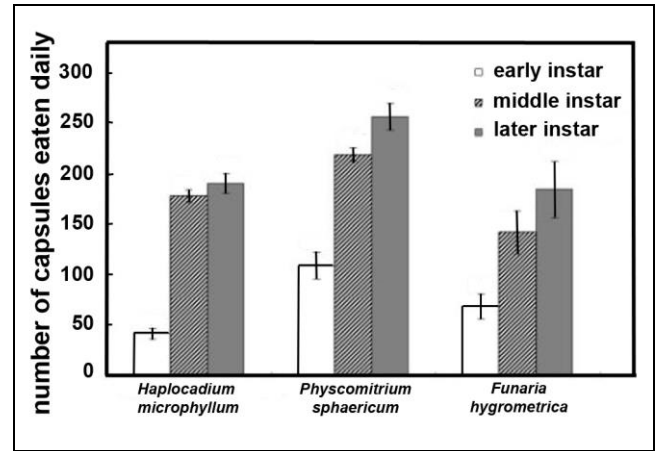


Figure 113. Number of moss capsules consumed in 24 hours by individuals of *Agrotis* sp. Based on Fang & Zhu 2012.

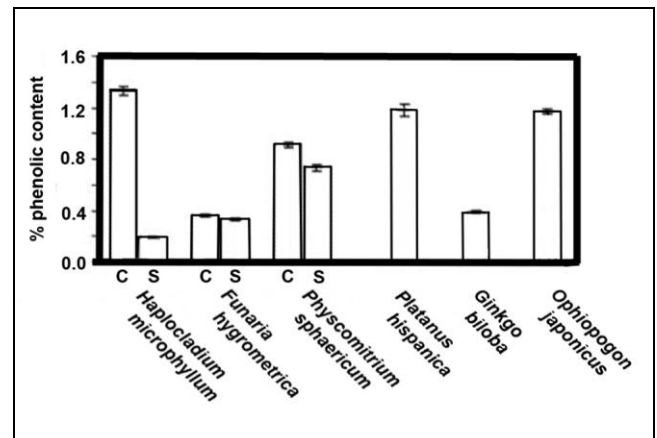


Figure 114. Phenolic content of capsules of three mosses compared to that of three tracheophytes. Based on Fang & Zhu 2012.

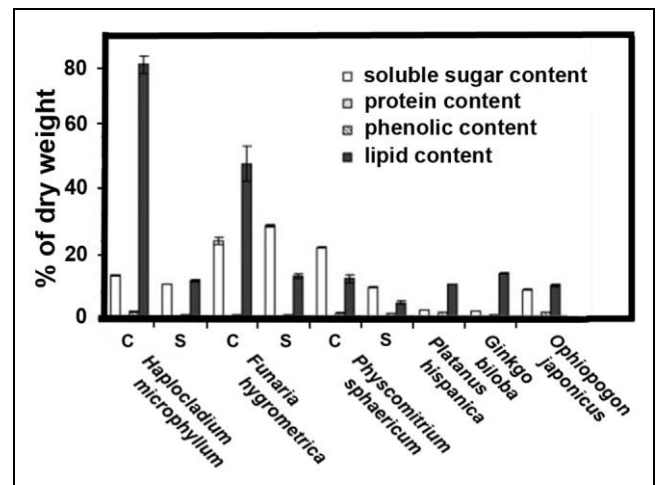


Figure 115. Percentage nutrient content of moss capsules (C) and setae (S) by weight, compared to that of three tracheophytes. Leaves of *Ophiopogon japonicus* (flowering plant) were fresh; the other two seed plant leaves were fallen. Redrawn from Fang & Zhu 2012.

In Europe under mosses on the spreading beech roots, one can find the brown pupae (Figure 116) of *Herminia grisealis* (Noctuidae; Figure 117-Figure 119) (Shield 1856).



Figure 116. *Herminia grisealis* pupa; these can be found under mosses on beech roots. Photo by Wolfgang Wagner, with permission.



Figure 117. *Herminia grisealis* larva, a species that pupates under mosses. Photo by Wolfgang Wagner, with permission.



Figure 118. *Herminia grisealis* adult, gray color variant, a species that pupates under mosses among beech roots. Photo by ©entomart, through Creative Commons.



Figure 119. *Herminia grisealis* brown color variant, a species that pupates under mosses among beech roots. Photo by Donald Hobern, through Creative Commons.

Larvae of the green mahoe moth (*Feredayia graminosa*; Figure 120-Figure 123) in New Zealand feeds on mahoe (*Melicytus ramiflorus*; Figure 124), a woody member of the violet family (Harris 2015). But when it becomes an adult, it rests on tree trunks, where its 18 mm length makes it very obvious on white bark. Fortunately for these moths, they are able to seek out epiphytic mosses on these trees, resting on them during the day undetected because their cryptic coloration hides them from the casual view of avian predators. They feed at night when their predators are sleeping. The males smell like vanilla and use their enlarged hind wings to fan this odor over females during mating.



Figure 120. *Feredayia graminosa* adult on moss, showing its ability to blend with mosses. Photo by Donald Hobern, through Creative Commons.



Figure 121. *Feredayia graminosa* adult looking like a patch of moss on bark. Photo by Jon Sullivan, with permission.



Figure 122. *Feredayia graminosa* blending with mosses and lichens on bark as it rests during the day. Photo by Pete McGregor, with permission.

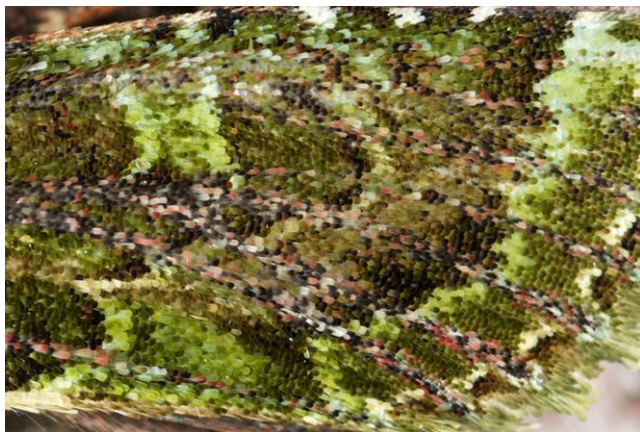


Figure 123. *Feredayia graminosa* wing scales showing cryptic coloration that blends with lichens and mosses on bark. Photo by Jon Sullivan, with permission.



Figure 124. *Melicytus ramiflorus*, food plant of *Feredayia graminosa*. Photo by Jon Sullivan, through Creative Commons.

Rennie (1857) discovered interesting behavior of a species of the moth in the genus *Bryophila* (Figure 125–Figure 126). This caterpillar is small and feeds on minute mosses and lichens on old walls. It builds its cocoons from moss branchlets cut into suitable lengths, including a portion of earth with these detached pieces (Figure 126). In making its cocoon, it arranges the earth on the inside and moss on the outside to make a vault. If this species is

deprived of soil in the lab, but provided with moss, it will build a hollow ball by interweaving the moss.

Shield (1856) reported that larvae of *Bryophila domestica* (= *Cryphia domestica*; Figure 125) include bits of mosses in their webbing (Figure 126). They bite their way out of these cocoons when the weather is warm, returning to them and resealing them when it is again too cold. The included mosses and other bits help to conceal them while they are in hiding. Shield observed them biting off bits of moss and weaving them between the threads of silk, completely hiding the larva inside.



Figure 125. *Bryophila domestica* adult, a species whose larvae include mosses in their webbing. Photo by Ian Kimber, with permission.

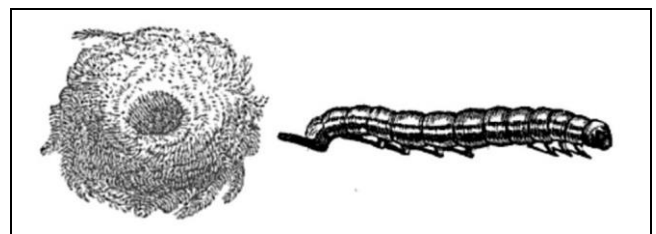


Figure 126. *Bryophila domestica* (maybe) nest with mosses and caterpillar. Image by James Rennie (book from 1800's), through public domain.

Acronicta myricae (see Figure 127) is also among the moths that spin silken cocoons, in this case covered with mosses (Buckler 1871).



Figure 127. *Acronicta euphorbiae* larva; *Acronicta myricae* builds its cocoons on mosses. Photo by Harald Süpfle, through Creative Commons.

We don't always know the role of the mosses, and they may only be indicators of a suitable environment. For example, in areas with boreal forest, *Xestia rhaetica* (Figure 128) is distributed in the old, moist spruce forests where mosses form a thick layer (Mönkkönen & Mutanen 2003). But what is the role of these mosses, if any?



Figure 128. *Xestia rhaetica* adult, an occupant of old, moist spruce forests with a thick layer of mosses. Photo by Dumi, through Creative Commons.

Now there appears to be a new noctuid added to the bryophages. Timea Deakova has sent me images that appear to be those of *Noctua pronuba* (Figure 129-Figure 130). A hoard of these hungry larvae devoured a large portion of her experiments on nitrogen. Could it be the nitrogen in the experiment or do these larvae just like mosses?



Figure 129. *Noctua pronuba* larva eating *Bryum capillare* and surrounded by frass. Photo courtesy of Timea Deakova.



Figure 130. *Noctua pronuba* larva on *Polytrichum juniperinum*. Photo courtesy of Timea Deakova.

Summary

In the **Geometridae**, larvae are often colored to blend with their surroundings (including bryophytes), having patterns of brown, green, and gray. Some of these larvae can do considerable damage to the bryophytes, particularly mosses, through herbivory. Some overwinter among mosses as pupae. Others lay eggs on mosses, close to the tree leaves that are eaten by the larvae. And some use the water associated with the bryophytes. The hemlock looper often lays eggs among mosses, then becomes a nuisance when its larvae migrate to conifer leaves and consume the leaf tips, killing the leaves.

One member of the **Lasiocampidae** swarm on mosses in autumn – for whatever reason. Few of the **Arctiidae** are bryophyte associates, but some members of the subfamily **Lithosiinae** eat bryophyte capsules. Other members feed on liverwort leaves or moss leaves. The **Erebidae**, sometimes included in the **Arctiidae**, includes most of the bryophyte dwellers that were once **Arctiidae**. **Lymantridae** sometimes use mosses in place of making a web to hide themselves.

Some **Noctuidae** find bryophytes distasteful; in *Climacium americanum*, digestibility, assimilation, and overall use efficiency did not differ from that of lettuce, but there was far more consumption of lettuce. However, some species do feed on mosses. And a species of *Agrotis* feeds on moss capsules, but avoids those of *Pogonatum inflexum*. In fact, the other moss capsules contained more lipids than the local tracheophytes. Some species also use mosses for pupation sites. And some adults have coloration that permits them to rest on tree-trunk bryophytes without being seen easily. Some species incorporate bryophytes in their cocoons.

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CHAPTER 12-16

TERRESTRIAL INSECTS:

HOLOMETABOLA – MECOPTERA

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CHAPTER 12-16

TERRESTRIAL INSECTS:

HOLOMETABOLA – MECOPTERA



Figure 1. *Boreus hyemalis*, female, among *Polytrichum piliferum*, Thetford Warren Lodge, Norfolk, UK. Photo by Brian Eversham, with permission.

MECOPTERA – SCORPIONFLIES

The **Mecoptera** comprise a small order of about 550 known species (Wikipedia 2016), 9 families, and 32 genera (Byers & Thornhill 1983). They were more abundant in the Permian, Mesozoic, and Tertiary periods, with 348 species in 87 genera and 34 families known. They are known as scorpionflies because of the position of the

Scorpionfly larvae (Figure 2) are among those that live in mosses (as well as damp soil) (Miall 1902). It is interesting that many of the relatively few **bryophagous** animals (including arthropods) often show unusually high levels of winter activity. Larvae of snow scorpionflies (**Mecoptera: Boreidae**) are active **ONLY** in the winter in temperate regions, hopping about and even mating on the snow (Figure 3). Some insects, including gall aphids, move from a summer angiosperm host to a winter moss host. Could these snow scorpionflies and gall aphids, and probably other insects, be sequestering compounds from mosses that allow them to remain active at sub-freezing temperatures? Aside from chemistry, the correlation

between bryophagy and cold weather could be explained by the simple fact that mosses remain green throughout the winter, and therefore might become a more attractive host plant during this period. Or do the winter-active fauna simply have the right enzymes or gut pH to permit them to gain nutrients from mosses and survive by being active at a time of year when predators are limited in their activity?



Figure 2. *Panorpa* sp. larva, genus that lives among bryophytes. Photo by Pierre-Marc Brousseau, with permission.



Figure 3. *Boreus westwoodi* mating on snow. Photo by hrasiranta, with online permission.

Choristidae

Tillyard (1926) was among the early reporters on the relationship of the **Mecoptera** with bryophytes. He considered the Australian *Choristes* to be both a bryophyte resident and a **bryophage** (eats bryophytes). However, this genus name has been pre-empted by other phyla (the genus *Choristes* is a sea snail in the Gastropoda) and was changed to *Chorista* (Figure 4) in the **Mecoptera** (see <<http://direct.biostor.org/reference/80557.text>>).



Figure 4. *Chorista australis* adult, a bryophyte dweller and bryophage. Photo by John Tann, through Creative Commons.

Chorista is a small genus of only two apparent species. Its family, the **Choristidae**, lives among mosses as larvae (Wikipedia 2015). The larvae are unusual among holometabolous insects in having **compound eyes** with ommatidia, a trait shared by the scorpionflies *Neopanorpa* (Figure 93) and *Panorpa* (Figure 94), both in the **Panorpidae** and also bryophyte dwellers (Ramel 2016). Compound eyes are best at detecting motion. Could it be that living among bryophytes selects for these compound eyes in an environment where there is limited light and many of the inhabitants tend to blend in until they move?

The food of *Chorista* (Figure 4) seems to be contested, or perhaps just wide ranging. Tillyard (1926) considered them to eat mosses. On the other hand, in the lab both larvae and adults fed on dead insects, fresh fruit, strained carrots, and beef (Bush 1967; Byers & Thornhill 1983).

Members of *Chorista* (Figure 4) oviposit loose clusters of eggs, using pre-existing cavities in moist soil (Miyake 1912; Tillyard 1926; Byers 1963; Riek 1970). We need to look for the eggs among or under the bryophytes as well. If the larvae feed on bryophytes, surely the eggs must be near the host plants.

Boreidae

The family **Boreidae** has only three genera (Cannings & Scudder 2005). *Boreus* (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27) has 14 known species in Eurasia and 12 in North America; only two of these are in the eastern USA. *Hesperoboreus* (Figure 89) has only two species, confined to western North America from Washington to California. *Caurinus* (Figure 28-Figure 30, Figure 38-Figure 39) has two species, one occurring only in Oregon and Washington, USA, and another in Alaska. Both larvae and adults of the **Boreidae** feed exclusively on bryophytes (Russell 1979a, b). Because of their small size and clandestine habitat, it is likely that more species await our discovery.

The **Boreidae** are small (2-5 mm), dark-colored mecopterans and are most easily seen when they are on the snow (Figure 5) (Byers 2002). They resemble fleas, but use their legs to propel them. When they land, they tuck their legs against their bodies (Figure 6) and resemble a bit of dirt on the surface of the snow. The dark body color (Figure 5-Figure 13) may help them to maintain sufficient temperature when they are bouncing around on snow (Cannings & Scudder 2005).



Figure 5. *Boreus brumalis* on snow. Photo by J. Mihuc, through Creative Commons.



Figure 6. *Boreus brumalis* adult, showing the legs tucked against the body as they are when the adults land after a hop. Photo by Tom Murray, through Creative Commons.

The **Boreidae** are boreal, with the adults appearing in winter or at high elevations. They are sufficiently different from other **Mecoptera** that some systematists consider them to be a separate order, the **Neomecoptera** (Cannings & Scudder 2005). The larvae lack both abdominal prolegs and conspicuous dorsal setae. They have lateral eyes and usually have three **ommatidia** (units of the compound eye) per eye.

Several researchers have provided lists of moss species from which boreids have been collected or on which they have been reared (e.g. Svensson 1972; Cooper 1974; Penny 1977). Both larvae and adults in the **Boreidae** feed on mosses (Svensson 1972; Cooper 1974; Penny 1977; Byers & Thornhill 1983). But Brauer (1863 in Carpenter 1931) found that they also feed on other small animals that live among the moss rhizoids. And Penny (2006) stated that they feed on leaves of mosses, club mosses (*Selaginella*?), and liverworts as adults, but feed on the rhizoids of these same plants as larvae. They seem to require little food (Withycombe 1926), but need "a great deal of moisture" (Penny 2006). Penny (1977) concluded that **Boreidae** prefer mosses that form low, compact cushions with their rhizoids tightly matted. The loose mats, which had fewer **Boreidae**, may have more predator **Carabidae** beetles. Or they may lose moisture too quickly.

In contrast to *Chorista* (Figure 4), the **Boreidae** oviposit single eggs or small clusters in the soil surrounding moss rhizoids (Cooper 1974; Penny 1977; Byers & Thornhill 1983). Some deposit eggs among epiphytic bryophytes (Russell 1979a; Byers & Thornhill 1983).

As one might guess for a boreal species that hops about on the snow, temperature is an important parameter in the niche of **Boreidae** (Byers & Thornhill 1983), even more important than light (Cooper 1974). Nevertheless, the minimum temperature for adult activity is close to 0°C (Sauer 1966; Svensson 1966; Penny 1977; Byers & Thornhill 1983). When their mossy habitat becomes dry,

the boreid larvae may go as much as 20 cm down into the soil below the mosses to attain suitable humidity (Strübing 1950).

Scorpionfly larvae [*Boreus* (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27), *Caurinus* (Figure 28-Figure 30, Figure 38-Figure 39)] feed on moss cushions on trees in damp woodlands (Penny 1977; Russell 1979a, b; Shorthouse 1979), making mosses their principal food. Adults of the family **Boreidae** are well known for their moss diet (Cooper 1974; Penny 1977).

Boreus

Although *Boreus* (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27) seems always to be associated with mosses, its distribution is clearly not limited by its host mosses, but rather by some other parameter of its environment that is more restrictive (Cooper 1974). I suggest that limitation is moisture, combined with bryophytes that are suitable food. Both larvae and adults of *Boreus* eat mosses (Withycombe 1922; Fraser 1943; Strübing 1950; Svensson, 1966; Hågvar 2010).

Boreus brumalis (Figure 7, Figure 13) includes the mosses *Dicranella heteromalla* (Figure 8-Figure 9) and *Atrichum angustatum* (Figure 10-Figure 11) in its diet in Illinois, USA (Webb et al. 1975) and New England, USA (Maier 1984).

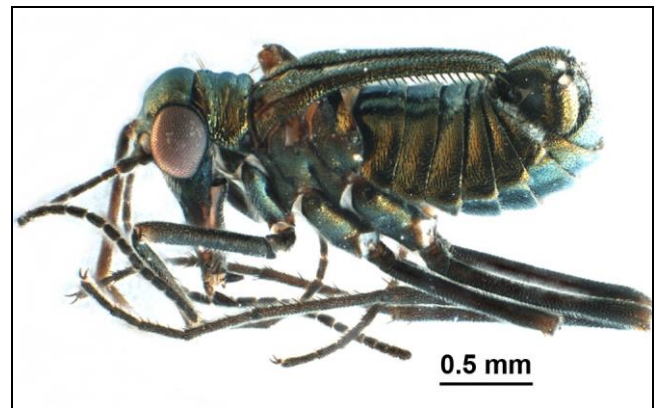


Figure 7. *Boreus brumalis* male showing modified wings that are used to clasp the female. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 8. *Dicranella heteromalla* on soil bank – food for *Boreus brumalis*. Photo by Janice Glime.



Figure 9. *Dicranella heteromalla* with capsules – food and home for *Boreus brumalis*. Photo by Michael Lüth, with permission.



Figure 10. *Atrichum angustatum*, home and food for *Boreus brumalis*. Photo by Michael Lüth, with permission.



Figure 11. *Atrichum angustatum*, home and food for *Boreus brumalis*. Photo by Michael Lüth, with permission.

Desiccation can be a problem, and the moss habitat would seem to be ideal for these organisms. It typically stays moist longer than other kinds of plants, it provides cover against not only desiccation but also many kinds of predators, and it is a food source. Furthermore, being flightless, it is an advantage to have your food and cover in the same place.

This genus has a somewhat different mating behavior from that of other **Mecoptera** (Byers 2002). The male has slender, hardened wings that he uses to grasp the female (Figure 7). He manipulates her to a position above his back (Figure 12) with the lower part of her ovipositor inserted into his ninth (genital) segment (Figure 12) (Cockle 1908).



Figure 12. Mating pair of the snow scorpionfly, *Boreus westwoodi*. Note the female is on top of the male, held by two wings of male. Photo by Barbara Thaler-Knoflach, with permission.

Boreus brumalis (Figure 7, Figure 13) feeds primarily on bryophytes (Gerson 1982). Shorthouse (1979) determined that both larvae and adults of *Boreus brumalis* (Figure 13) in Ontario, Canada, eat the bryophytes in the winter under the snow.



Figure 13. *Boreus brumalis* female adult on snow. Photo by Tom Murray, through Creative Commons.

Boreus hyemalis (Figure 1, Figure 14), an inhabitant of heaths and moors, is well known for its habitation of mosses (Plant 1994; Winnall 2009). Nevertheless, because of this seclusion, it is often overlooked (Whitehead 2010). This insect is flightless (Hågvar 2010) and can be seen moving about on the snow in exposed locations. Carpenter

(1931) reported that adults could be seen in spring and early summer among moss rhizoids and under stones, but that their activity is confined to winter. On sunny winter days they hop on the snow, as far as 15 cm in a single leap.



Figure 14. *Boreus hyemalis* in moss at Ellerburn Beck, UK. Photo by Roger S. Key, with permission.

Bingham (2012) found that the typical habitat for *Boreus hyemalis* (Figure 1, Figure 14) in Wyre Forest (UK) seemed to be oak woodlands or other open woodlands with sparse ground flora to compete with the mosses, mostly *Polytrichastrum formosum* (Figure 15) and *Dicranum scoparium* (Figure 16). He also perceived a possible connection between acid woodland and the presence of *B. hyemalis*.



Figure 15. *Polytrichastrum formosum*, home of *Boreus hyemalis*. Photo by David T. Holyoak, with permission.



Figure 16. *Dicranum scoparium*, home for *Boreus hyemalis*. Photos from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Boreus hyemalis (Figure 1, Figure 14) lays its eggs among mosses and the larvae make tunnels between the moss and the substrate – soil, logs, walls (Russell 1979a). Although many entomologists have reported this species from the mosses, only Fraser (1959) has identified the moss used for oviposition as *Polytrichum commune* (Figure 17). Most likely other species of bryophytes are also used. Carpenter (1931) observed that the larvae eat both moss "roots" and liverworts.



Figure 17. *Polytrichum commune*, home and oviposition site for *Boreus hyemalis*. Photo by Michael Lüth, with permission.

Boreus in Norway takes advantage of mosses to provide protective space. This is a safe space in which they lay their eggs (Hågvar 2001). And it appears that mosses might be a site of copulation (Figure 12), an event rarely observed on the snow (Figure 3). The chambered air spaces most likely also provide space for this winter-active scorpionfly to move about in safety. Adults of *B. elegans* (Figure 18) and *B. californicus* (Figure 19-Figure 20) feed on *Racomitrium heterostichum* (Figure 21); larvae and pupae of *B. elegans* can be found under *Brachythecium* (Figure 22) and other mosses (Russell 1979a). Russell (1979a) has found *B. elegans* on mosses on a north-facing roadcut, in mosses near a hillside spring, and among mosses on logs in a coastal forest in the Pacific coastal states, USA. Both larvae and pupae were present under a mat of *Brachythecium* sp. and other mosses.



Figure 20. *Boreus californicus* on one of the compact mosses it calls home. Photo by Baldo Villegas <www.discoverlife.com>, through Creative Commons.



Figure 18. *Boreus elegans* adult, a species that feeds on *Racomitrium heterostichum*. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 21. *Racomitrium heterostichum*, food for *Boreus californicus* and *B. elegans*. Photo by Michael Lüth, with permission.



Figure 19. *Boreus californicus* male, a species that lives in compact mosses such as *Grimmia*. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 22. *Brachythecium rutabulum*, home for *Boreus elegans*. Photo by Michael Lüth, with permission.

Boreus californicus (Figure 19-Figure 20) occurs primarily east of Cascade Mountain (Russell 1979a). In western Oregon, it seems to occur in more open, rocky sites than *B. elegans* (Figure 18), but in some sites both species occur. Larvae of *B. californicus* also occur in soil under mosses in crevices of jointed basalt and under moss among grasses in deep sandy loam on a stream bank. In California, Penny (2006) found *B. californicus* on the tightly compacted *Grimmia* (Figure 23).



Figure 23. *Grimmia longirostris*, exhibiting the compact cushion character of many **Grimmiales**. Photo by Hermann Schachner, through Creative Commons.

Boreus reductus (Figure 24) is likewise east of the Cascades, but in semi-arid regions of the Northwest (Russell 1979a, b). Although the larvae usually inhabit mosses (Russell 1979a, b), they can also occur in mats of *Selaginella* (Figure 25-Figure 26), a moss look-alike that is related to club mosses (tracheophytes) (Penny 1977).

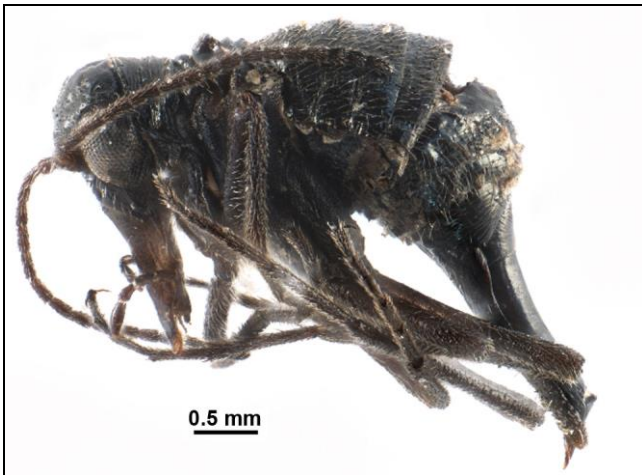


Figure 24. *Boreus reductus* female, a species east of the Cascades that eats mosses and *Selaginella*. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 25. *Selaginella wallacei* in its epiphytic habitat where one might find *Caurinus dectes*. Photo by Paul Slichter, with permission.



Figure 26. *Selaginella wallacei*, home for *Caurinus dectes*. Photo by Paul Slichter, with permission.

In Fennoscandia, *Boreus westwoodi* (Figure 3, Figure 12, Figure 27) and *B. hyemalis* (Figure 14) larvae develop in the soil that occurs among the mosses (Hågvar 2010). The adults hatch in autumn before the new snow becomes established. Each adult migrates in its own separate and fixed direction by continuous jumping, achieving 1.2 m per minute (Hågvar 2001). The adults spend most of winter below the snow, among the mosses. On warmer days when the temperature is just above freezing, they climb tree trunks to reach the snow surface where they hop about. Jumping about on sunny, cloudless days may be risky because the temperature is likely to drop rapidly as the sun sets.



Figure 27. *Boreus westwoodi* adult female on one of the mosses where it lives. Photo by Petr Kočárek, with permission.

These adults lay eggs throughout the winter (Hågvar 2001) and *Boreus hyemalis* (Figure 14) is able to produce a maximum of 320 eggs per female (Steiner 1937). They oviposit in mosses in the **subnivean** (beneath snow) air spaces (Hågvar 2001), laying 1-2 eggs at a time (Withycombe 1922; Strübing 1950; Svensson 1966; Cooper 1974). Larvae develop there, feeding on the mosses, and continue to feed on them as adults.

Caurinus

I was delighted when, in January of 2008, David Wagner sent me a note about his former student who had studied a small boreid, *Caurinus dectes* (Figure 28-Figure 30) (Russell 1979a, b, 1982). Unlike *Boreus* (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27), this insect feeds primarily on liverworts! Wagner helped me contact his former student, Loren Russell, who has been very helpful in providing me with further information. Russell learned how to find his study insect by a change in the branching pattern of the leafy liverwort, *Scapania bolanderi* (Figure 31), the preferred food of the boreid (David Wagner, pers. comm. January 2008). It chewed the tender tips, which caused the liverwort to branch, causing a fluffy appearance that is in evidence even from a distance! The larvae feed on the liverwort in mines or galleries constructed there (Penny 2012).



Figure 28. *Caurinus dectes* female, a liverwort dweller. Photo courtesy of Loren Russell.



Figure 29. *Caurinus dectes* male. Photo courtesy of Loren Russell.



Figure 30. *Caurinus dectes* larva on a species of the leafy liverwort *Scapania*. Photo courtesy of Loren Russell.



Figure 31. *Scapania bolanderi*, a common home for *Caurinus dectes*. Photo by Matt Goff, with permission.

Fabian *et al.* (2015) took advantage of this knowledge of food choice to locate larvae of *Caurinus dectes* (Figure 28-Figure 30) for their study on larval morphology. Penny (2012) used heat to cause adults of this species to drop from the epiphytic liverworts (*Porella navicularis*; Figure 32) on vine maple (*Acer circinatum*). Penny noted that the most common mosses associated with these vine maple stems are *Rhytidiadelphus loreus* (Figure 33), *Metaneckera menziesii* (Figure 34-Figure 35), and *Neckera douglasii* (Figure 36-Figure 37). Nevertheless, its favorite food is *Porella navicularis*. Penny contends that *C. dectes* breeds in these epiphytes.



Figure 32. *Porella navicularis*, an epiphytic liverwort where one can find *Caurinus dectes* larvae feeding on the liverwort. Photo by John Davis, with permission.



Figure 33. *Rhytidiadelphus loreus*, potential home for *Caurinus dectes*. Photo by Martin Hutten, with permission.



Figure 34. *Metaneckera menziesii*, potential home for *Caurinus dectes*. Photo by Dale Vitt, with permission.



Figure 35. *Metaneckera menziesii*, potential home for *Caurinus dectes*. Photo by Michael Lüth, with permission.



Figure 36. *Neckera douglasii*, one of the epiphytic mosses in areas where one can find *Caurinus dectes*. Photo by Kirill Ignatyev, through Creative Commons.



Figure 37. *Neckera douglasii*, potential home for *Caurinus dectes*, but refused as a food source. Photo by Dale Vitt, with permission.

Caurinus dectes (Figure 28-Figure 30) survives in a warmer climate than other members of the **Boreidae**. Its distribution is in Washington and Oregon, USA (Russell 1979a, b; Rood *et al.* 2015). It occurs in moist forests where mosses are abundant both on trees and on the ground. Knowing where to look often adds new species. In 2013, Sikes and Stockbridge described a new species, *Caurinus tlagu* (Figure 38) from Prince of Wales Island, Alaska, USA. Its habitat is different from the primary forested habitat of *C. dectes* (Figure 28-Figure 30), but *C. dectes*, like *C. tlagu*, also occurs in open rocky sites with the moss *Rhytidiadelphus loreus* (Figure 33). This moss species provides 20% of the cover at the Alaskan alpine tundra site where *C. tlagu* occurs.



Figure 38. *Caurinus tlagu*, a moss dweller in Alaska, USA. Photo by Derek Sikes, through Creative Commons.

Byers and Thornhill (1983) conjectured that *Caurinus* (Figure 28-Figure 30) probably pupates in damp mosses without making a cell (Russell 1979a). Russell (1982) pointed out that its larvae, unlike other **Mecoptera**, make a silk-lined cell or cocoon where pupation occurs. Pupation occurs in July to August in northwestern USA. The life cycle is **univoltine** (one generation per year), but two generations may overlap for a period.

Penny (2006) pointed out that in *Caurinus dectes* (Figure 28-Figure 30), the larvae (Figure 30) are almost legless. Furthermore, the adults lack hind wings (Figure 28-Figure 29). Hence, this small (1.4-1.9 mm) insect is not going to travel very far to escape unfavorable conditions of weather or other environmental change. It lives in moist forests where both epiphytic and terrestrial bryophytes are abundant. The adults feed on the epiphytic leafy liverwort *Porella navicularis* (Figure 32), but also occur on mosses (Russell 1979a). When females lay their eggs, the eggs are coated with black cement and they are attached to the bryophytes (Figure 39) (Russell 1982).



Figure 39. *Caurinus dectes* eggs on a leafy liverwort. Photo courtesy of Loren Russell.

Because other boreids are known to feed on mosses, Russell (1979a, b) provided his *Caurinus* (Figure 28-Figure 30) with several epiphytic moss choices: *Antitrichia curtispindula* (Figure 40-Figure 41), *Isoetecium spiculiferum* (Figure 43), *Metaneckera menziesii* (Figure 34-Figure 35), and *Rhytidiadelphus loreus* (Figure 33), all common on the trees in forests where *C. dectes* occurs. Although most of the larvae survived for three weeks, there was no evidence of feeding. He broadened their choices, providing *Rhizomnium glabrescens* (Figure 44), the foliose lichen *Peltigera canina*, the common mushroom *Agaricus campestris*, apple slices, and springtails. Again, nothing was eaten. Finally, when the leafy liverwort *Porella navicularis* (Figure 32) was presented, the boreids had dinner.



Figure 40. *Antitrichia curtispindula* growing epiphytically and providing a potential home, but not food, for *Caurinus dectes*. Photo by Michael Lüth, with permission.



Figure 41. *Antitrichia curtispindula* with snow, a potential refuge for *Caurinus dectes* under snow, but not eaten by them. Photo by Michael Lüth, with permission.



Figure 42. *Antitrichia curtispindula*, a species in the range of *Caurinus dectes*, but not eaten even when there is no other food choice. Photo by James K. Lindsey, with permission.



Figure 43. *Isoetecium spiculiferum*, potential home of *Caurinus dectes*, but not eaten by them. Photo by Ben Carter, through Creative Commons.

The boreid *Caurinus dectes* (Figure 28-Figure 30) apparently feeds only on leafy liverworts and completes its life cycle on *Scapania* (Figure 45), and several other liverwort epiphytes (Loren Russell, pers. comm. Jan. 2008). Among 11 liverwort taxa tested, the adults accepted about two-thirds of the species. *Scapania* serves as both

food and home for depositing eggs. Russell studied three other local species of boreids, but these three are all moss specialists, never feeding on liverworts.



Figure 44. *Rhizomnium glabrescens*, a moss not eaten by *Caurinus dectes* even when there is no other food choice. Photo by Paul Slichter, with permission.



Figure 45. *Scapania bolanderi*, food of *Caurinus dectes*. Matt Goff, with permission.

Russell (1979a) learned that *Caurinus dectes* (Figure 28-Figure 30) is an excellent liverwort taxonomist. In its various habitats, it recognized certain species to eat or to avoid, both as larvae and adults. On deciduous trees and shrubs, it readily accepted (as host and food) *Porella navicularis* (Figure 32) and *Frullania tamarsci* (Figure 46) (less so, and only if primary hosts were not available), but would not accept *Radula bolanderi* (Figure 47) or *Metzgeria conjugata* (Figure 48). On decaying logs and stumps with bark, it recognized a new array of species, accepting *Scapania bolanderi* (Figure 31) and *Bazzania tricenata* (Figure 49) and less preferentially (when given no choice) *Ptilidium californicum* (Figure 50), *Bazzania ambigua*, and *Lophocolea cuspidata*. Here *Lepidozia*

reptans (Figure 51) was not accepted, even under starvation conditions. On older logs and stumps that had lost their bark, it found *Calypogeia fissa* (Figure 52), *C. muelleriana* (Figure 53), *Kantius trichomanis*, *Scapania bolanderi*, *S. umbrosa* (Figure 54-Figure 55), and *Lophocolea heterophylla* (Figure 56) to be highly acceptable, whereas *Geocalyx graveolens* (Figure 57), *Lophozia incisa* (Figure 58), *Cephalozia bicuspidata* (Figure 59) (larvae only), *C. lunulifolia* (Figure 60) (adults only), *Calypogeia fissa*, *Jamesoniella autumnalis* (Figure 61), *Jungermannia atrovirens* (Figure 62), and *Riccardia latifrons* (Figure 63) were only secondary hosts, used when preferred choices were unavailable. *Cephalozia bicuspidata* (adults only), *C. lunulifolia* (larvae only), *Blepharostoma trichophyllum* (Figure 64), *Chiloscyphus pallescens* (Figure 65), and *Lepidozia reptans* were not accepted. Although refusing some members, *Caurinus deces* is apparently mostly a *Jungermanniales* specialist.



Figure 48. *Metzgeria conjugata*, a species that is not accepted as food by *Caurinus deces*. Photo by Michael Lüth, with permission.



Figure 46. *Frullania tamarisci*, an epiphytic liverwort that is eaten by *Caurinus deces* when the primary food (*Porella navicularis*) is not available. Photo by Bernd Haynold, through Creative Commons.

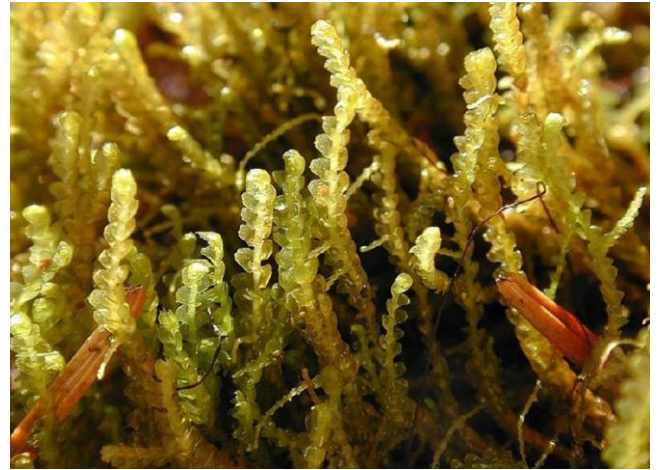


Figure 49. *Bazzania tricrenata*, food for *Caurinus deces* on logs. Photo by Michael Lüth, with permission.



Figure 47. *Radula bolanderi* growing epiphytically, a species that *Caurinus deces* would not eat.. Photo by Ken-ichi Ueda, through Creative Commons.



Figure 50. *Ptilidium californicum*, a secondary choice for food by *Caurinus deces* on logs. Photo by Scot Loring, through Creative Commons.



Figure 51. *Lepidozia reptans*, a food choice refused by *Caurinus decies* on logs, even when no other choice was available. Photo by David T. Holyoak, with permission.



Figure 54. *Scapania umbrosa* on an old log where it is an acceptable food for *Caurinus decies*. Photo by Hermann Schachner, through Creative Commons.



Figure 52. *Calypogeia fissa*, an acceptable food for *Caurinus decies* on older logs. Photo by Bernd Haynold, through Creative Commons.



Figure 55. *Scapania umbrosa*, an acceptable food for *Caurinus decies* on older logs. Photo by Hermann Schachner, through Creative Commons.



Figure 53. *Calypogeia muelleriana*, an acceptable food for *Caurinus decies* on older logs. Photo by Hermann Schachner, through Creative Commons.



Figure 56. *Lophocolea heterophylla* on a log that has lost its bark where it is an acceptable food for *Caurinus decies*. Photo by Sture Hermansson, with online permission.



Figure 57. *Geocalyx graveolens*, a species on old logs that *Caurinus dectes* larvae eat when their primary host liverworts are not available. Photo by Michael Lüth, with permission.



Figure 58. *Lophozia incisa* with perianth, a species on older logs and that *Caurinus dectes* larvae eat when their primary host liverworts are not available. Photo by J. C. Schou, with permission.



Figure 59. *Cephalozia bicuspidata*, a species on older logs and that *Caurinus dectes* larvae (but not adults) eat when their primary host liverworts are not available. Photo by Christian Peters, with permission.



Figure 60. *Cephalozia lunulifolia*, a species on older logs and that *Caurinus dectes* adults (but not larvae) eat when their primary host liverworts are not available. Photo by Michael Lüth, with permission.



Figure 61. *Jamesoniella autumnalis*, a species on older logs and that *Caurinus dectes* eats when its primary host liverworts are not available. Photo by Michael Lüth, with permission.



Figure 62. *Jungermannia atrovirens*, a species on older logs and that *Caurinus dectes* eats when its primary host liverworts are not available. Photo by Hermann Schachner, through Creative Commons.



Figure 63. *Riccardia latifrons*, a species on older logs and that *Caurinus decetes* eats when its primary host liverworts are not available. Photo by Julita Klusa <daba.dziedava.lv>, with online permission.



Figure 64. *Blepharostoma trichophyllum*, although common on logs where *Caurinus decetes* lives, is an unacceptable food. Photo by Hermann Schachner, through public domain.



Figure 65. *Chiloscyphus pallescens*, although common on logs where *Caurinus decetes* lives, is an unacceptable food. Photo by Michael Lüth, with permission.

On compacted soil, highly accepted food species for *Caurinus decetes* (Figure 28-Figure 30) included *Gyrothya underwoodiana* (Figure 66), *Nardia scalaris* (Figure 67),

Diplophyllum albicans (Figure 68), and *D. obtusifolium* (Figure 69), with secondary hosts of *Gyrothya underwoodiana* (adults only), *Jungermannia rubra* (Figure 70), and *Blasia pusilla* (Figure 71) (Russell 1979a). They did not accept *Pellia neesiana* (Figure 72), *Athalamia hyalina* (Figure 73), *Conocephalum conicum* (Figure 74), or *Anthoceros punctatus* (Figure 75), all thallose species. On boulders and outcrops they preferred *Plagiochila porelloides* (Figure 76), with *Porella cordaeana* (Figure 77) and *Scapania americana* (Figure 78) serving as alternatives when their preferred foods were unavailable. Even forest litter provided a suitable host in the form of *Plagiochila porelloides*.



Figure 66. *Gyrothya underwoodiana*, a highly accepted food for larvae and secondary food for adults of *Caurinus decetes* on compacted soil. Photo by Tab Tannery, through Creative Commons.



Figure 67. *Nardia scalaris*, a highly accepted food for *Caurinus decetes* on compacted soil. Photo by Hermann Schachner, through Creative Commons.



Figure 68. *Diplophyllum albicans*, a highly accepted food for *Caurinus dectes* on compacted soil. Photo by Hermann Schachner, through Creative Commons.



Figure 71. *Blasia pusilla*, a secondary food for *Caurinus dectes* on compacted soil. Photo by Tim Faasen, with permission.

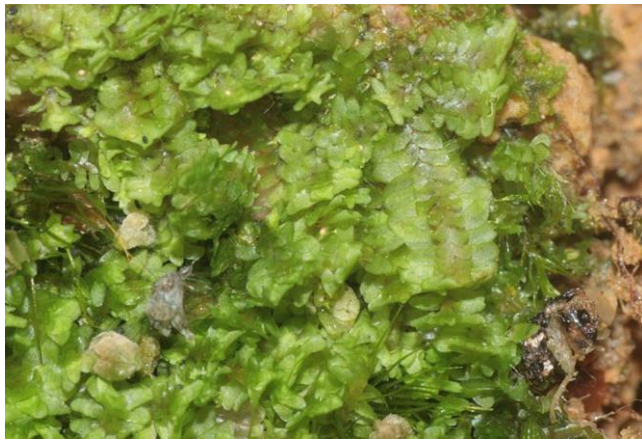


Figure 69. *Diplophyllum obtusifolium*, a highly accepted food for *Caurinus dectes* on compacted soil. Photo by Hermann Schachner, through Creative Commons.



Figure 72. *Pellia neesiana*, a potential food on highly compacted soil, but that is refused by *Caurinus dectes*. Photo by Bernd Haynold, through Creative Commons.



Figure 70. *Jungermannia rubra*, a secondary food for *Caurinus dectes* on compacted soil. Photo by Ken-Ichi Ueda, through Creative Commons.



Figure 73. *Athalamia hyalina*, a potential food on highly compacted soil, but that is refused by *Caurinus dectes*. Photo by Jason Hollinger, through Creative Commons.



Figure 74. *Conocephalum conicum*, a potential food on highly compacted soil, but that is refused by *Caurinus dectes*. Photo by Hermann Schachner, through Creative Commons.



Figure 77. *Porella cordaeana*, a secondary food for *Caurinus dectes* on rocks where the preferred foods are unavailable. Photo by Michael Lüth, with permission.



Figure 75. *Anthoceros punctatus*, a potential food on highly compacted soil and seepages, but that is refused by *Caurinus dectes*. Photo by Proyecto Musgo, through Creative Commons.



Figure 78. *Scapania americana*, a secondary food for *Caurinus dectes* on rocks where the preferred foods are unavailable. Photo by Chris Wagner, with permission.

Russell (1979a, b) was not able to locate any highly acceptable hosts for *Caurinus dectes* among liverworts from streams and seepages, but *Chiloscyphus polyanthos* (Figure 79), *Riccardia multifida* (Figure 80), and *Blasia pusilla* (Figure 71) served as "emergency" foods when others were not available. *Scapania undulata* (Figure 81) and *Anthoceros punctatus* (Figure 75) were rejected.



Figure 76. *Plagiochila porelloides*, a preferred food for *Caurinus dectes* on boulders. Photo by Bernd Haywold, through Creative Commons.



Figure 79. *Chiloscyphus polyanthos*, an emergency food for *Caurinus dectes* from streams and seepages. Photo by Kristian Peters, with permission.



Figure 80. *Riccardia multifida*, an emergency food for *Caurinus polyanthos* from streams and seepages. Photo by Hermann Schachner, through Creative Commons.



Figure 81. *Scapania undulata*, a rejected food for *Caurinus polyanthos* from streams and seepages. Note that some species of *Scapania* are eaten. Photo by Hermann Schachner, through Creative Commons.

One of the most interesting observations by Russell (1979a, b) was that although these boreids had accepted

Porella navicularis (Figure 32) as food, and readily tasted *Porella roellii* (Figure 82), they soon showed a distinct distaste for *P. roellii*. Evidence included regurgitation, signs of distress, and repeated grooming of their mouthparts. This behavior commenced within 30 seconds of tasting the *P. roellii*. Once eating this species, they subsequently would no longer eat *P. navicularis*, a previously staple food source for them in the lab. *Porella roellii* is known for its "violent, burning taste" which is evidenced after a few seconds of delay.

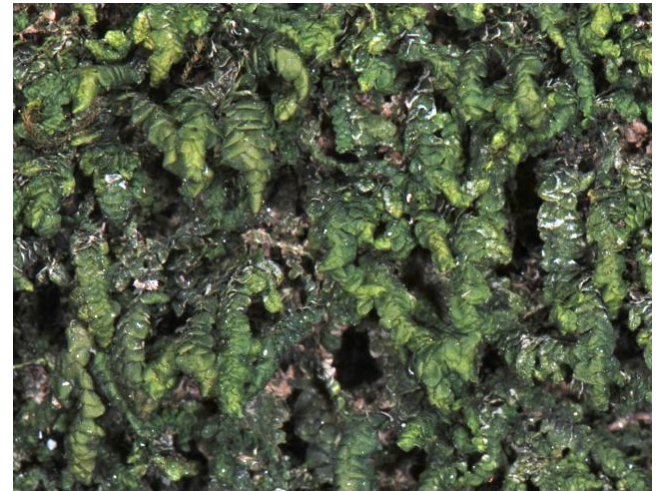


Figure 82. *Porella roellii*, a leafy liverwort that appears to be repugnant to *Caurinus dectes*. Photo by Paul Wilson, with permission.

Russell (1979a, b) rejected the hypothesis that liverworts provided better nutrient quality than the less preferred mosses. In fact, the liverworts seemed to have less nitrogen, an essential component of protein, and rarely exceeded the content of mosses for any of the nutrients tested (Table 1). The switch in some cases from larval to adult preferences is interesting. Also of interest is that this insect specializes on Jungermanniales, with 18 species accepted in laboratory tests.

Table 1. Macronutrient concentrations in the gametophytes of some bryophytes collected in *Caurinus dectes* habitat at Marys Peak, Oregon, USA. From Russell 1979a.

		P	N	Na	K	Ca	Mg
Mosses							
<i>Dicranum fuscescens</i>	Figure 83	.142	.932	.038	.546	.418	.145
<i>Rhizomnium glabrescens</i>	Figure 44	.251	2.083	.043	1.125	.972	.261
<i>Eurhynchium oreganum</i>	Figure 84-Figure 85	.146	.829	.056	.741	.518	.190
<i>Isoetecium spiculiferum</i>	Figure 43	.142	.949	.034	.512	.516	.177
<i>Antitrichia curtipendula</i>	Figure 40-Figure 41	.151	.686	.028	.631	.430	.170
<i>Rhytidiadelphus loreus</i>	Figure 33	.164	.727	.072	.770	.440	.171
mean		.166	1.034	.045	.721	.551	.186
Liverworts							
<i>Scapania bolanderi</i>	Figure 31	.072	.748	.035	.659	.275	.111
<i>Porella navicularis</i>	Figure 32	.155	.890	.026	1.040	.426	.156
<i>Frullania tamarisci</i>	Figure 46	.107	.874	.030	.904	.515	.134
ssp. <i>nisquallensis</i>							
mean		.111	.834	.030	.868	.405	.134



Figure 83. *Dicranum fuscescens*, a food species for adults of *Hesperoboreus brevicaudus*. Photo by Michael Lüth, with permission.



Figure 84. *Eurhynchium oreganum* habitat in area where *Caurinus dectes* lives. Photo by Matt Goff, with permission.



Figure 85. *Eurhynchium oreganum* in habitat where *Caurinus dectes* lives. Photo by Matt Goff, with permission.

Hesperoboreus

In Oregon, USA, *Hesperoboreus brevicaudus* (see Figure 89) larvae are inhabitants of epiphytic mosses, whereas adults may also occur among thick, matted mosses on rocks (Russell 1979a, b). Penny (2006) reported them from vertical moss banks and epiphytic mosses in

California, USA. In the lab, adults feed on *Polytrichum* (Figure 1, Figure 17) leaf lamellae (Figure 86), *Rhizomnium glabrescens* (Figure 44), and *Dicranum fuscescens* (Figure 83) (Russell 1979a). Larvae feed extensively on *Funaria hygrometrica* (Figure 87), *Rhytidiadelphus loreus* (Figure 33), *Antitrichia curtipendula* (Figure 40-Figure 41), and *Plagiothecium undulatum* (Figure 88) in the lab.

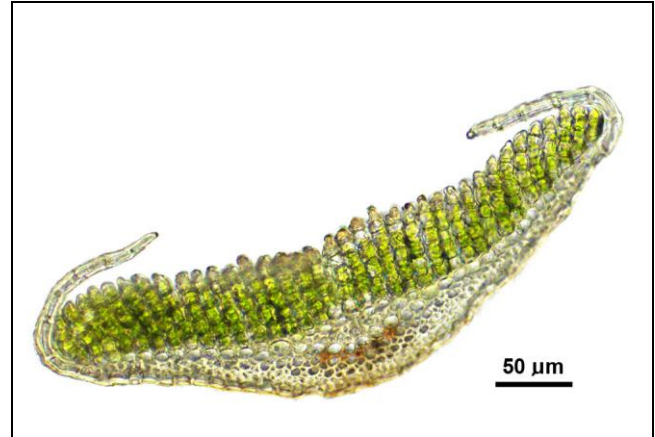


Figure 86. *Polytrichum juniperinum* leaf cs, showing lamellae that are eaten by adults of *Hesperoboreus brevicaudus*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 87. *Funaria hygrometrica*, food of *Hesperoboreus brevicaudus*. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.



Figure 88. *Plagiothecium undulatum*, food of *Hesperoboreus brevicaudus*. Photo by Walter Obermayer, with permission.

These mossy habitats, especially among epiphytic mosses, dry out in seasons with little rainfall (Gerson 1982). To accommodate for this unwelcome dryness, the larvae of *Hesperoboreus notoperates* (Figure 89) make hardened cells, using salivary secretions, among the moss rhizoids (Cooper 1974). These cells apparently conserve water until moisture returns. After sufficient rainfall, the larvae break out of the cells and begin feeding again.



Figure 89. *Hesperoboreus notoperates*, a species that prefers compact cushion mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Cooper (1974) noted parasites, especially on *Hesperoboreus notoperates* (Figure 89) in Southern California. Living in such confined quarters may be dangerous for the young boreids because it most likely makes transfer of the parasites from one to another easy. Nevertheless, tight cushions of *Grimmiales* (Figure 23) and *Isobryales* (Figure 90) (Cooper 1974) seem preferable to open mats (Penny 1977), perhaps for greater conservation of moisture.



Figure 90. *Fontinalis antipyretica*, a member of *Isobryales*. Photo by Tab Tannery, through Creative Commons.

Nannochoristidae

Nannochorista (Figure 91) has carnivorous aquatic larvae that feed on larvae of *Chironomidae* (midges) (Tillyard 1917; Byers & Thornhill 1983; Byers 1989; Palmer 2009). The adult diet is unknown. But during

pupation, *Nannochorista* sometimes uses damp mosses as a substrate, avoiding the need to make a special cell for that purpose (Pilgrim 1972; Byers & Thornhill 1983). Those larvae that migrate to soil or bark for pupation create a cell by excavating the soil or wet wood. They pupate above the water, but within 10-20 cm of it (Pilgrim 1972). *Nannochorista philpotti* (Figure 91) is a predatory species that sometimes spends part of its life among bryophytes.



Figure 91. *Nannochorista philpotti* adult, a predatory species that sometimes spends part of its life among bryophytes. Photo by Steve Kerr, with permission.

Panorpidae

It is the **Panorpidae** that have earned the name of scorpionflies for the order **Mecoptera** (Wikipedia 2016). The genitalia of the males are enlarged and curved upward, arching over the back, much like the stinger of a scorpion (Figure 92).



Figure 92. *Panorpa nuptialis* male adult. Note the resemblance to a scorpion. Photo by Karen Perez, through Creative Commons.

The larvae of **Panorpidae** are unusual among holometabolous insects in having compound eyes with ommatidia, a trait shown by *Neopanorpa* (Figure 93) and *Panorpa* (Figure 94) (Ramel 2016). As Farkač *et al.* (2005) have reminded us, *Panorpa hybrida* (Figure 94) is an endangered species in the Czech Republic. And this species lives mostly among mosses.



Figure 93. *Neopanorpa* sp. adult, a species whose larval eyes are compound. Photo by E. S. Ross <www.discoverlife.com>, with online permission.



Figure 94. *Panorpa hybrida* adult, a moss dwelling species in Europe. Photo by Ivelina Assyova, with permission.

But the members of the genus *Panorpa* (Figure 94) are not all associated with bryophytes. Some are carnivores, eating freshly killed katydids, grasshoppers, and caterpillars in the lab (Cai & Hua 2009).

Panorpa (Figure 94) has three types of mating (Ramel 2016). In all cases, the male emits a **pheromone** that attracts females, and unfortunately, also other males. In one strategy, the male offers the female a gift, food of course (Figure 95), that she devours during copulation (perhaps helping to prevent her from eating her mate as is known in other carnivores such as the preying mantis). In fact, Cockle (1908) observed the female of *Boreus californicus* (Figure 19-Figure 20) drag the male around on his back until he died. The second strategy is similar – the male finds a dead arthropod, which he partially consumes (Ramel 2016). Then the male stands beside it and emits the pheromone attractant or secretes a salivary mass on a nearby leaf or other substrate, again resting beside it and secreting a pheromone. Copulation occurs while the female feeds, either on the arthropod or the salivary mass. In the third strategy, the male offers nothing – no food and no pheromones. Rather, he rushes at the female and attempts to mate with her, a strategy known as **forced copulation**, and often he succeeds. This latter strategy is most used by those males who lose to other males in their

attempt to gain food for a gift. Not surprisingly, females prefer the males with gifts, and those that do receive gifts lay more eggs than females that have had forced copulation.



Figure 95. Male *Panorpa communis* with prey item (*Diogma glabrata glabrata*) such as that offered to females before mating. Photo by Richard Bartz, through Creative Commons.

Kullmann and Sauer (2005) investigated other species of *Panorpa* and learned that other strategies are present as well. They found that the males of both *Panorpa similis* and *Panorpa connexa* carry out their copulations with one salivary mass as a nuptial gift or have copulations without any nuptial gift, but always without the use of force.

Earlier researchers reported that *Panorpa* oviposits loose clusters of eggs, using pre-existing cavities in moist soil (Miyake 1912; Tillyard 1926; Byers 1963; Riek 1970; Byers & Thornhill 1983). But *Panorpa communis* (Figure 95-Figure 96), the common scorpionfly that was named by Linnaeus, oviposits beneath mosses (Malyshev 1968). Byers (1963) found that in *P. nuptialis* (Figure 92, Figure 97) size increase is rapid in the young larvae, but the prepupal stage is prolonged. Adults emerge from pupae in about 20 days.



Figure 96. *Panorpa communis* male adult, a species that oviposits under mosses. Photo by Gail Hampshire, through Creative Commons.



Figure 97. *Panorpa nuptialis* adult. Photo by Robby Deans, through Creative Commons.

Apteropanorpidae

This tiny family has only one genus (*Apteropanorpa*; Figure 99) with four species known as Tasmanian snow scorpionflies (Palmer *et al.* 2007; Wikipedia 2011). The larvae live among mosses in Tasmania and southern Australia (Byers & Yeates 1999; Wikipedia 2011). Adults are wingless predators, but likewise live among mosses (Kaltenbach 1978; Byers & Yeates 1999).

Like the **Boreidae**, the **Apteropanorpidae** are active in the cold of winter (Byers & Thornhill 1983). Both larvae and adults live among mosses (Kaltenbach 1978; Ferrington 2008) where conditions remain moist most of the time (Russell 1979a). Although Ferrington (2008) considered this family to be aquatic, Palmer (2009) argues that they are not, stating "There is no evidence suggesting that adults of any species of *Apteropanorpa* predictably occupy riparian or aquatic vegetation." Further, Evans (1942) collected two **Mecoptera** larvae from mosses at 600-900 m on Mt. Wellington and these have now been determined to be *Apteropanorpa* (Palmer 2009). Balian *et al.* (2008) noted the ability of mosses to retain a film of water that permits limnoterrestrial invertebrates to live there. But Palmer cautions that larval stages of this genus are poorly known and mosses may not be their only habitat.

But danger lurks among the bryophytes. Like several other mecopteran families, this one is plagued by parasitism. Adults of *Apteropanorpa tasmanica* (Figure 99-Figure 99) are parasitized by larvae of the mites *Leptus agrotis* and *Willungella rufusanus* (Seeman & Palmer 2011).



Figure 98. *Apteropanorpa tasmanica*, a species whose larvae live among mosses. Photo © Simon Grove, Tasmanian Museum and Art Gallery, with permission.



Figure 99. *Apteropanorpa tasmanica*, a species whose larvae live among mosses. Photo © Simon Grove, Tasmanian Museum and Art Gallery, with permission.

Meropeidae

This tiny family has only two members, one in eastern USA – *Merope tuber* (Figure 100-Figure 101) and one in Australia – *Austromerope poultoni* (Byers 1973, 1988; Kaltenbach 1978). It appears to be an ancient family that was once more widespread.

Merope tuber (Figure 100-Figure 101) adults live among aquatic or riparian vegetation or bryophytes (Ferrington 2008). Presumably the bryophytes provide sufficient moisture for these terrestrial living sites.



Figure 100. *Merope tuber* adult, a species that includes bryophytes among its substrates. Photo by Tom Murray, through Creative Commons.



Figure 101. *Merope tuber* adult male showing claspers. Photo by R. Machado, R. Kawada, and J. Rafael, through Creative Commons.

Merope tuber is a poorly known species (Dunford *et al.* 2007). Its larvae have never been described and its habits are largely unknown. We do know that the adults are nocturnal, and flight traps have revealed that the species is more common than we had imagined (Byers 2005). Its range is from southeastern Canada to Florida and west to Kansas, Minnesota, and eastern Iowa Byers (1973, 1993; Dunford *et al.* 2007). The Appalachian Mountain range and eastern mesic forests provide it with suitable habitat (Dunford *et al.* 2007). Its presence in the more western and southern parts of its range suggest that these disjunct locations may be relict habitats where it found refuge during glacial advances (Byers 1969, 1993; Schiefer & Dunford 2005). The two species are able to survive in these two distant geographic locations on opposite sides of the Earth along streams in ravines (Killington 1933; Byers 1988) that provide temperatures that vary little from 20°C (Means 1985).

Bittacidae

The **Bittacidae** are not true bryophyte associates, but they do occasionally feed on mosses (Setty 1931). More commonly they are **saprophagous** and feed on things like dead earthworms or dead insects (Setty 1931, 1940; Byers & Thornhill 1983). Like the **Nannochoristidae**, *Harpobittacus australis* (Figure 102) uses pheromones for attracting attraction (Crossley & Waterhouse 1969). Most of the bittacids hang on vegetation by their legs to drop their eggs to the ground (Ramel 2016). Hence, any association of eggs with bryophytes is probably coincidental.



Figure 102. *Harpobittacus australis* adult, a species that uses pheromones to attract his mate. Photo by John Tann, through Creative Commons.

Currie (1932) relates fascinating observations of the larval behavior of *Harpobittacus tillyardi* in the lab. In preparation for molting, the larvae move to a higher location on a soil mound or on a liverwort leaf. When the larvae molt, they move their body fluids forward, causing the anterior to swell. Eventually the head capsule splits and the larva crawls out, then eats its former skin. After a 10-minute rest, the larvae moved the posterior end up above the head capsule. They then proceeded to expell sand and soil from the anus and to cover the larval skin with it as they moved the anus backward. After about 20 minutes, this process was repeated. This covering rendered the larvae nearly invisible on its substrate. During feeding, which was almost entirely on dead matter, the larva occasionally took a bit of liverwort in the lab. Maintenance of moisture was important, and larvae would expel fluids from the mouth to spread over the body to keep it moist. If it ran out of this fluid, it would die in the dryness.

Summary

The **Mecoptera** include the snow scorpionflies, and these typically feed on mosses or algae associated with them. **Chorista** (**Choristidae**) is among the bryophages. The **Boreidae** has three genera, all of which feed almost exclusively on bryophytes as both larvae and adults. In addition to food, the mosses may be important as a moist refuge. Many lay their eggs on mosses under the snow. For *Boreus*, mosses seem to be important, whereas for *Caurinus*, liverworts are important. *Hesperoboreus brevicaudus* species occur among epiphytic mosses as larvae but migrate to mosses on rocks as adults.

In the **Nannochoristidae**, has aquatic larvae that are carnivorous, but the larvae may move to damp mosses for pupation. The **Panorpidae** have compound eyes, unusual in this order, that may help them to detect motion in their dark bryophyte habitat. However, not all **Panorpidae** are bryophyte associates. Both larvae and adults of **Apteropanorpidae** live among mosses and are winter-active. *Merope* (**Meropeidae**) adults can live among aquatic vegetation or among bryophytes. The **Bittacidae** only occasionally associate with bryophytes and feed on them.

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CHAPTER 12-17 TERRESTRIAL INSECTS: HOLOMETABOLA – DIPTERA BIOLOGY AND HABITATS

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CHAPTER 12-17

TERRESTRIAL INSECTS:

HOLOMETABOLA – DIPTERA OVERVIEW



Figure 1. Adult **Diptera** resting on mosses in a canyon in Ohio, USA. Insects this large are unlikely to move within the moss mat, but the mat can still be important in keeping them alive. Such rest stops may be for getting from one place to another, rehydrating the body, drinking, or ovipositing. Photo by Janice Glime.

Diptera Overview

Diptera derive their name from having only two wings (Figure 1). In place of the second pair of wings, they have a pair of **halteres** (Figure 2), structures that resemble a knob on a stalk, like the dumbbells of the same name. The halteres instead serve as a guidance system (Wikipedia 2016). They record both vertical and horizontal changes in direction, permitting the flies to maintain balance and stabilize the head and to perform their acrobatic maneuvers quickly.

Wagner (1980) concluded that in the Breitenbach of Germany, changes in fly populations are linked with changes in the bryophyte cover. When Andrew and Rodgerson (1999) developed a kerosene extraction technique for removing invertebrates from bryophytes, they found that **Acari**, **Collembola**, and **Diptera** were the most

abundant arthropods. This chapter will explore the many ways in which the **Diptera** are associated with bryophytes and often depend on them. Bryophytes play an important role in the life cycles of a number of dipteran taxonomic groups (Kinchin 1992).

The **Diptera** are part of the panorpidae complex (Britannica 2008). This group includes the **Mecoptera**, **Trichoptera**, **Lepidoptera**, **Siphonaptera**, and **Diptera**. It is a current belief that all these orders evolved from a moss-dwelling ancestor. They are all 4-winged insects (except the halteres of **Diptera**) that resemble crane flies, some making cases as larvae.

Most bryologists are probably unaware that some **Diptera** larvae behave as parasites in the thalli of liverworts. Pettet (1967) reported such an interaction in

thalli of *Riccia frostii*. The rosettes of thalli each had 5-25 small, yellow-orange larvae. The thallus loses its turgidity and becomes flabby. In the last larval stage, the upper surface of the thallus disintegrates. Pupation follows inside the thallus.

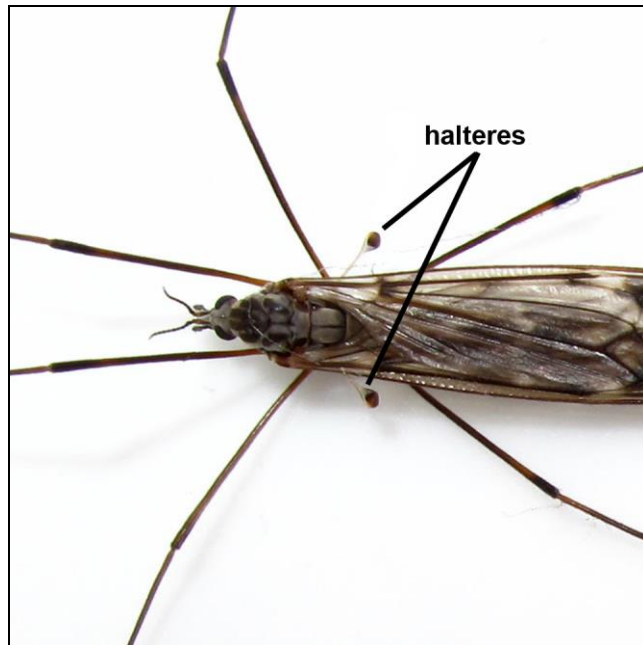


Figure 2. Cranefly (*Tipula* cf. *scripta*) halteres. Photo from BugBlog, through Creative Commons.

Role of Bryophytes

As with other insects, bryophytes provide a safe haven for small dipterans to hide from predators. They likewise provide a moist haven from the sun and drying winds. And they are a source for food. For some dipterans, the bryophytes themselves are eaten. For others, microorganisms, fungi, and other arthropods that live among the bryophytes provide food sources. Galas *et al* (1996) reported that in the cave water they tested the amount of energy released by the bryophyte microorganisms was greater than that for the litter species they tested.

Andrew *et al.* (2003) summed up the advantage of bryophytes – they are able to absorb water rapidly, reduce evaporation, and provide insulation against extreme environmental conditions of cold and wind (see also Gerson 1982; Smrz 1992). Several researchers suggest that by modifying the environment, bryophytes permit aggregations of **Diptera** to live where they would not otherwise be able to tolerate the dry conditions (Joosse & Verhoef 1974; Leinaas & Somme 1984; Usher & Booth 1984).

Clément and Touffet (1981) examined the role of bryophytes in the big picture of heathlands in Brittany. The larvae of *Tipula* (**Diptera**; Figure 3) were responsible for the death of many bryophytes following fire. Bryophytes were destroyed by the scraping of rabbits and roe-deer. Once bryophytes returned, led by *Funaria hygrometrica* (Figure 4) and *Ceratodon purpureus* (Figure 5) following fire, organic matter built up quickly, permitting the invertebrate fauna to flourish.



Figure 3. *Tipula abdominalis* larva, a genus responsible for destroying bryophytes in burned areas. Photo by Tom Murray, through Creative Commons.



Figure 4. *Funaria hygrometrica* with capsules, bryophytes that colonize after a fire, permitting invertebrates such as **Diptera** to begin colonization. Photo by Janice Glime.



Figure 5. *Ceratodon purpureus*, bryophytes that colonize after a fire, permitting invertebrates such as **Diptera** to begin colonization. Photo by Janice Glime.

Substrate type is important in the establishment and emergence of **Diptera** from lakes (Čmrlec *et al.* 2013). In lake outlets in Poland, mosses were the most preferred substrate for emergence, especially on tufa and pebbles. Mosses provide a place to climb to the surface without being carried away by the current, then extending above ground to give a solid surface from which to escape the aquatic realm. In particular, the **Athericidae** (Figure 6) select mosses for emergence, but then, they also select mosses for their pupation, making this a readily available emergence site (Thomas 1997). The **Chironomidae** (Figure 7-Figure 10) and **Dixidae** (Figure 11-Figure 12)

(Poepperl 1999) have no substrate preference, but **Empididae** (Figure 13-Figure 15) not only use the mosses for emergence, but also use them for food and shelter (Watson & Rose 1985; Nolte 1991; Ivković *et al.* 2007).



Figure 6. *Ibisia marginata*, a member of the family **Athericidae**, many of which select mosses for emergence. Photo by Hectonicus, through Creative Commons.



Figure 7. **Chironomidae** larva, a stage often found in aquatic mosses and also occurring in terrestrial ones. Photo by Jason Neuswanger, with permission.



Figure 8. **Chironomidae** pupa, a stage that is sometimes spent among mosses. Photo by Jason Neuswanger, with permission.



Figure 9. **Chironomidae** adults emerging from pupae in moss at Helfdi, Myvatn, Iceland. Photo by Janice Glime.



Figure 10. *Chironomus plumosus* (**Chironomidae**), one of the many midges that emerge in large numbers from mosses. Photo ©entomart, through Creative Commons.



Figure 11. **Dixidae** larva, a stage that sometimes occurs in mosses but has no preference for them. Photo by Aina Maerk Aspess, NTNU, through Creative Commons.



Figure 12. **Paradixa** pupa, a stage that sometimes occurs in mosses. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.



Figure 13. **Empididae** larva, a moss inhabitant and feeder. Photo through Manaaka Whenua, NZ, with online permission.

Like many other orders discussed earlier, the **Diptera** have their parasites. The crane fly **Limonia** (**Limoniidae**; Figure 16) is one of these (Wohltmann *et al.* 1994), as is **Paradixa** (**Dixidae**; Figure 17). Larvae of **Limonia** are subject to the parasitic mite, **Johnstoniana tuberculata** (Figure 18) (Wohltmann *et al.* 1994). It appears that the moss provides suitable conditions for both the crane fly and the parasite. This mite overwinters in its egg stage and the

larvae emerge in May-June – the same time their hosts become available.



Figure 14. **Empididae** pupa, a stage often found in mosses. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.



Figure 15. **Empis stercorea** adult, member of the **Empididae**, a family that often pupates in mosses and that also eats them as larvae. Photo from ©entomart, through Creative Commons.



Figure 16. **Limonia** (**Limoniidae**) larva, a genus that lives among mosses and has mite parasites. Photo from Manaaka Whenua, Landcare Research, NZ, with online permission.



Figure 17. *Paradixa* (Dixidae) larva with parasitic mites. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.



Figure 18. *Johnstoniana* sp., a parasitic mite such as those found on moss-dwelling **Diptera**. Photo by Walter Pfliegler, with permission.

Collection and Extraction Methods

Several methods of collection are usually necessary to assess the **Diptera** fauna. Most larvae are difficult to identify and often must be reared to adults for certain identification. This need can sometimes be eliminated by a thorough sampling of the adult fauna during their active seasons. The most common method I encountered for adult surveys was the use of the **Malaise traps** (e.g. Salmela 2001; Salmela & Ilmonen 2005; Figure 19). These are large, tent-like structures used for trapping flying insects, especially **Hymenoptera** and **Diptera**. Insects are directed to the top of a slanted pyramid where they encounter a vial of preservative. Other methods for flying insects include **window traps** (Figure 20) and **sweep netting** (Figure 21) (Salmela 2001).



Figure 19. Malaise trap for emergent and flying insects. Photo by Ceuthophilus, through Creative Commons.



Figure 20. Window-pane trap used to capture adult insects including **Diptera**. Photo from North Dakota State University, with online permission.



Figure 21. Sweep net used to catch adult insects, including **Diptera**. Picture from Peter Oboyski, with permission.

Window-pane traps (Figure 20) are made with clear plexiglass to serve as a barrier over a container of ethylene glycol (anti-freeze). The window is mounted on a wooden frame that is suspended between two pipes anchored in the ground. The frame height should be at the top of the

growing vegetation, or at least above the peak of the bryophyte clumps.

Ground dwelling **Diptera**, including larvae and pupae, are often sampled by **pan traps** (Figure 22) (Taillefer & Wheeler 2010) or **pitfall traps** (Figure 23-Figure 24) (Galbraith *et al.* 1993; Horsfield & MacGowan 1997; Miller *et al.* 2008). These are placed among the vegetation, and for our purposes this would be among mosses. The rim should be below the moss surface so that insects don't have to climb up to enter the trap. **Pan traps** (Figure 22) are simple small pans with soapy water in them (MacGowan 2015). One drop of detergent in the pan or bowl is sufficient to break the surface tension and cause the insects to drown. The pans can be in colors chosen to suit the insect group you are interested in, with meat red being a suitable color for catching **Diptera**. On the other hand, a neutral color may give a more representative sample, avoiding the bias of attracting a particular group. The traps should be checked at least once a day to prevent mold. When removing the insects, pour the soap-water solution through a fine aquarium mesh net. Then rinse the net with water into a jar of 95% ethanol. The water will dilute the solution to the approximately 70% ethanol needed for preservation.



Figure 22. Pan trap used for ground insects. These are usually positioned so the rim is at the same height as the tops of the ground vegetation such as mosses. Photo by Peter Oboyski, with permission.



Figure 23. Pitfall trap to capture ground-dwelling insects. Photo from Stephen F. Austin State University, through Creative Commons.



Figure 24. Barber pitfall trap. The cover helps keep out rain and debris. Photo by Mnolf, through Creative Commons.

A **pitfall trap** (Figure 23) is similar to a pan trap. It is used for small animals, including insects, especially for ecological studies. Two types of traps can be used: dry and wet. The **dry pitfall trap** is simply a container buried in the ground with its rim at the soil surface. The **wet pitfall trap** differs only in containing a preserving liquid such as 10% formaldehyde, methyl alcohol, ethanol, ethylene glycol (anti-freeze), trisodium phosphate, or picric acid. A drop of detergent will remove the surface tension, making it easier for insects to fall to the bottom and be preserved. Water (plus soap) can be used if traps are checked within a day. Both wet and dry traps usually have a raised cover to reduce entry of rainfall and debris. If the insect is one that can climb or fly out, then the wet trap is preferable.

Extracting invertebrates from bryophytes is always challenging, and sorting the **Diptera** from the bryophytes is no exception. This separation is further complicated by the small size of some of the members. Andrew and Rodgerson (1999) tested several methods for extracting the invertebrates. They used **Tullgren funnels** with sugar flotation and a new technique using **kerosene phase separation**. Bryophyte samples were placed in 95% ethanol when they were collected to preserve the insects, some of which would die in the changed conditions of their habitat and others would be eaten if their predators were not immobilized. In the kerosene method, the bryophyte samples are placed in two large test tubes and 95% ethanol added to make the tube ~3/4 full. Kerosene is added to within 1 cm of the top. The tubes are shaken vigorously to ensure thorough mixing of the kerosene and ethanol. After

10-15 minutes the tubes should be rolled to eliminate any trapped bubbles of kerosene, causing them to rise from the bottom and sides. Once the ethanol and kerosene separate (kerosene on top), the invertebrates settle onto the interface layer. When this separation is complete, the kerosene should be pipetted off to within 5 mm of the interface and discarded. Then the remaining interface plus kerosene is collected. A second ethanol wash should be used to dislodge kerosene from the sides of the tube and the new interface pipetted and collected. This whole procedure should then be repeated, a part of the technique that Andrew and Rodgers found increased the number of invertebrates collected by 16%. The collected interface material should then be examined in a Petri dish under the binocular microscope in a fume hood. Any invertebrates trapped in the kerosene should be pushed into the alcohol with a fine brush to remove the kerosene. This method retrieved significantly more invertebrates than the sugar extraction.

Identification of larvae often requires rearing to adulthood. Ferreira and Rafael (2006) developed a method for rearing immature horseflies by using bryophytes and sand. They considered this method advantageous for rearing species with long development periods.

Fly Dispersal of Spores

Revill *et al.* (1967) experimented with ability of **Diptera** to carry viable propagules, including moss spores. Using *Tipula triplex* (Tipulidae; Figure 25), *Chaoborus punctipennis* (Chaoboridae; Figure 26-Figure 27), *Chironomus* sp. (Chironomidae; Figure 10), and *Bittacomorpha clavipes* (Ptychopteridae; Figure 28), these researchers demonstrated that moss protonemata could be transported and subsequently germinate. Moss protonemata were among the least frequent, but at least five of them germinated in 51 cultured washings, demonstrating that diptera adults are possible dispersal vectors.



Figure 25. *Tipula triplex*, a crane fly that is able to disperse moss spores. Photo by Paul Rhine <www.discoverlife.org>, through Creative Commons.

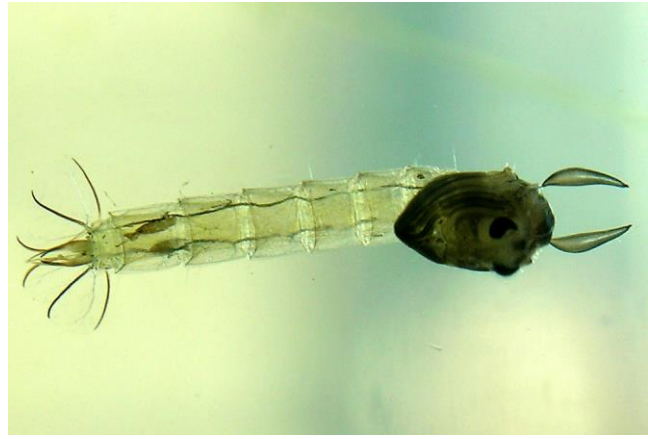


Figure 26. *Chaoborus* sp. pupa. Photo by Piet Spaans, through Creative Commons.



Figure 27. *Chaoborus punctipennis* adult, a species that is able to disperse moss spores. Photo by Tom Murray, through Creative Commons.



Figure 28. *Bittacomorpha clavipes* adult, a species that is able to serve as a vector for moss spores. Photo by Phil Myers, through Creative Commons.

Perhaps the best-known of the dipteran associations with bryophytes is that of flies that help in the dispersal of spores of the bryophyte family **Splachnaceae** (Bequaert 1921; Erlanson 1930; Walsh 1951; von der Dunk 1971; Koponen & Koponen 1978; Troilo & Cameron 1981; Marino 1988, 1991a, b; Koponen 1990; Eriksson 1992; Marino *et al.* 2009). This family of mosses lives exclusively on organic matter, including dung, bone, owl pellets, corpses, and enriched gravel (Koponen 1990). Among the frequent visitors to *Splachnum ampullaceum* (Figure 29) in the Great Lakes area is the muscid dipteran *Eudasyphora cyanicolor* (Figure 30) (Troilo & Cameron 1981).



Figure 29. *Splachnum ampullaceum* capsules showing expanded hypophysis that produces chemicals and a reddish color that attract flies. Photo by Michael Lüth, with permission.



Figure 30. *Eudasyphora cyanicolor*, one of the visitors to capsules of *Splachnum ampullaceum*. Photo by Tristram Brelstaff, through Creative Commons.

The **Splachnaceae** that attract flies are adapted for that attraction by their substrate, capsule shape, and chemical attractants that typically mimic the odor of dung (Koponen 1990; Koponen *et al.* 1990). These odors are produced only in the capsule and its **hypophysis** (enlarged portion at base of spore-bearing part of capsule). The odors are created by volatile compounds – octane derivatives and organic acids including acetic, propionic, and butyric acids.

It is of evolutionary significance that four families of flies are known to visit the aromatic **Splachnaceae** (Cameron & Wyatt 1986). About half the members of the **Splachnaceae** use wind dispersal, and insect dispersal arose more than once in the family, with dispersal mechanisms going back and forth between wind and insects (Goffinet *et al.* 2004; Marino *et al.* 2009). Evidence suggests that the moss capsule diversification may have followed the transition to **coprophily** (loving dung and dead animal matter) and **entomochory** (insect dispersal) (Marino *et al.* 2009).

There also appear to be differences in attraction ability. There are a number of cases in which the sporophyte colors and odors differ and the fly visitors differ accordingly (Marino *et al.* 2009). For example, *Splachnum ampullaceum* (Figure 30) associated with dung had more spores carried by the flies than did *S. luteum* (Figure 31-Figure 32) (Marino 1991b). There was also a greater proportion of flies associated with *S. ampullaceum* than with *S. luteum*.



Figure 31. *Splachnum luteum* capsules among peat mosses. Note the broad umbrella-like hypophysis. Photo by Dick Haaksma, with permission.



Figure 32. *Splachnum luteum* capsules. Photo courtesy of Bernard Goffinet.

Members of **Scatophagidae** – *Scatophaga furcata* (Figure 33), **Anthomyiidae** – *Delia platura* (Figure 34), **Phorida** (Figure 35), and **Muscidae** – *Myospila metidabunda* (Figure 36), *Eudasyphora cyanicolor* (Figure

30) are all known as North American and European visitors to the **Splachnaceae** that effect spore dispersal (Bequaert 1921; Cameron & Wyatt 1986; Koponen 1990). Cameron and Wyatt found the **Scatophagidae** to be both the most frequent and the most effective visitors to the capsules in Isle Royale National Park, Michigan, and Alaska, USA. They were able to demonstrate that wind is not an effective mechanism of dispersal for ***Splachnum rubrum*** (Figure 37-Figure 38) and that the visitation to dung by the **Scatophagidae** was an important component of the restriction of this moss species to dung.



Figure 33. *Scathophaga furcata* adult, a species that visits Northern Hemisphere **Splachnaceae** capsules. Photo by Aiwok, through Creative Commons.



Figure 34. *Delia platura*, a Northern Hemisphere visitor to **Splachnaceae** capsules. Photo by Janet Graham, through Wikimedia Commons.



Figure 35. *Phorbia longipilis*, a Northern Hemisphere visitor to **Splachnaceae** capsules. Photo by James K. Lindsey, with permission.



Figure 36. *Myospila mediatubunda* female, member of a genus in which some flies visit **Splachnaceae** capsules. Photo by James. K. Lindsey, with permission.

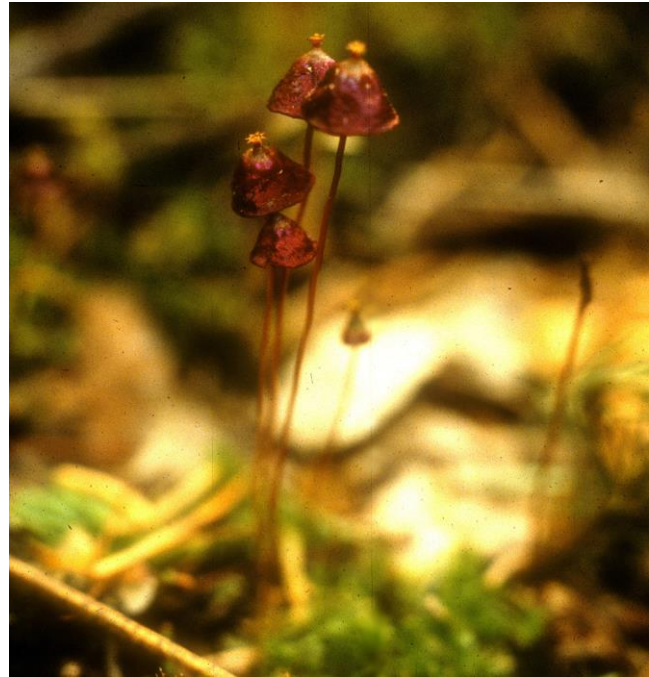


Figure 37. *Splachnum rubrum* capsules showing the umbrella-shaped hypothesis that is the color of red meat and slightly iridescent. Photo by Janice Glime.



Figure 38. *Splachnum rubrum* with fly. Photo courtesy of Bernard Goffinet.

The common **Splachnaceae** visitor *Eudasyphora cyanicolor* (Muscidae; Figure 30) prefers carrion, but

when it is not available, the adults choose dung and thus are able to interact with *Splachnum ampullaceum* (Figure 29) capsules (Troilo & Cameron 1981). Nevertheless, they leave the capsules when they discover no food is present. Troilo and Cameron found that the capsules of *S. ampullaceum* were more attractive to these flies than either carbohydrates or fly medium.

Tayloria dubyi (Splachnaceae; Figure 39) is unusual in that it lives exclusively on bird dung (Figure 40) in the sub-Antarctic Magallanes (Jofre *et al.* 2011). Furthermore, this dung is predominately, and perhaps only, that of the Upland Goose *Chloephaga picta* (Figure 41-Figure 42). Jofre and coworkers set up traps (Figure 43) above the capsules of the moss and above the adjacent *Sphagnum* (Figure 39) to see if this species also attracted flies. In traps above the *T. dubyi* capsules they captured 64 flies comprised of Muscidae – *Palpibracus chilensis*, Tachinidae – *Dasyuromyia* sp., and Sarcophagidae (Figure 44). No flies were captured above the adjoining *Sphagnum*.



Figure 39. *Tayloria dubyi* with capsules growing on Upland Goose dung amid *Sphagnum*. Photo by Jocelyn Jofre, through Creative Commons.



Figure 40. Goose dung, home for some *Splachnaceae*. Photo courtesy of Kim Barton.



Figure 41. Upland Goose (*Chloephaga picta*) male, the one that deposits dung that is colonized by *Tayloria dubyi*. Photo by Bernard Dupont, through Creative Commons.



Figure 42. Goose dung. Although this is not the Upland Goose, it illustrates the large size and nature of the dung of that species. Photo by Janice Glime.



Figure 43. *Splachnum luteum* with fly trap. Photo courtesy of Bernard Goffinet.



Figure 44. **Sarcophagidae** adult; some members of this family visit *Taylora dubyi* capsules. Photo by Toby Hudson, through Creative Commons.

Marino (1988) found that few **Splachnaceae** species ever co-existed on the same set of dung droppings. There seemed to be few mechanisms that would promote the co-existence of the mosses. Differences in timing of capsule maturation kept *Tetraplodon angustatus* (Figure 45) and *Tetraplodon mnioides* (Figure 46) from being on the same dung at the same time. Surprisingly, each species of **Splachnaceae** attracted 10-17 spore vector flies (Marino 1991b). The fly species attracted to each moss species had 77-99% different species composition from each other. Furthermore, the competition between species of **Splachnaceae** is strong. When grown together from spores there were fewer individuals of each species than when the species were grown separately (Marino 1991a). The competitive abilities between species grown in the lab related to differences in growth rates. Differences between lab and field growth suggest that habitat differences may keep species separate. Marino (1991b) demonstrated that in wet habitats *Splachnum* (Figure 29, Figure 31, Figure 37) is the primary **Splachnaceae** genus, whereas in dry habitats the dung mosses are primarily *Tetraplodon* (Figure 45-Figure 46).



Figure 45. *Tetraplodon angustatus* with capsules that attract flies. Photo by Des Callaghan, with permission.



Figure 46. *Tetraplodon mnioides* with mosquito on capsules. Photo courtesy of Lynden B. Gerdes.

Bequaert (1921) described details of the behavior of *Phorbia* (**Anthomyiidae**; Figure 35) flies visiting *Tetraplodon mnioides* (Figure 46). They landed on the upper end of the capsules and moved downward to reach the hypophysis, travelling from one capsule to another. They would pass the soft part of the proboscis over the upper part of the hypophysis, licking up its secretions. If they were disturbed, they flew away but returned quickly, apparently unwilling to pass up the treat. As these flies leave the capsules where they alight, they inevitably carry away some of the sticky spores on their hairs, legs, and other parts. The upper half of the hypophysis has exceptionally large, crowded stomata. Bequaert suggested that these stomata may exude the substance that seems so important to the visiting *Phorbia*.

In Chile, *Taylora mirabilis* (Figure 47-Figure 48) is endemic to temperate rainforests. Mighell (2011) used pitfall traps to trap flies over this species, then germinated the spores collected from these flies. Of the 218 flies collected (Figure 48), 63 were carrying spores of *T. mirabilis*. These included seven species from **Muscidae** (4 species of *Palpibracus*) and **Calliphoridae**. The dung represented multiple types, indicating that the mosses, and perhaps the flies were not specific in their dung substrate. Furthermore, the forest mammals providing the dung are introduced species, but the moss is endemic to Chile.



Figure 47. *Taylora mirabilis* with capsules, a **Splachnaceae** member that is endemic to Chile and for which flies aid in dispersal of spores. Photo from NYBG, through public domain.



Figure 48. *Tayloria mirabilis* capsules with fly, near Cape Horn, Chile. Photo by Adam Wilson, NYBG, through public domain.

The fascinating dispersal relationships are described in detail in Volume 1 in the chapter on Adaptive Strategies: Spore Dispersal.

Habitats

Wetlands

Peat mosses, as might be expected, have a significant fauna of flies, particularly larvae and pupae. Warner and Asada (2006) concluded that bryophytes contribute the most to species richness in bogs. This richness includes the animals that inhabit them. Holarctic peatlands typically have both diverse and abundant dipteran fauna (Roháček 1982; Blades & Marshall 1994; Taillefer & Wheeler 2010).

In reference to Canadian peatlands, Warner and Asada (2006) reported for mosquitoes (**Culicidae**; Figure 49-Figure 51) 10 species in bogs and 11 species in fens, for horse flies and deer flies (**Tabanidae**; Figure 52-Figure 56) 32 in bogs and 11 in fens, and for the no-see-ums (**Ceratopogonidae**; Figure 57-Figure 59) 3 in bogs. But none of these species seems to be restricted to bogs – *i.e.*, there are no true **bryobionts** among these **Diptera**.



Figure 49. *Anopheles* sp. larva, a member of **Culicidae** that is commonly found in wetlands. Photo by Steve Marshall, through Creative Commons.



Figure 50. *Culex* larvae getting oxygen while hanging from surface water. These larvae can occur in pools and in pitcher plants in wetlands, including bogs. Photo by James Gathany, through Creative Commons.



Figure 51. **Culicidae** adult, a well-known pest in wetlands. Photo by Mathias Krumbholz, through Creative Commons.



Figure 52. *Chrysops vittatus* larva. Deerflies in this genus inhabit wetlands, bogs, and forests. Photo by Sturgis McKeever, through Creative Commons.



Figure 53. *Tabanus americanus* pupa, a wetland inhabitant. Photo by Sturgis McKeever, through Creative Commons.



Figure 54. *Chrysops caecutiens* (Tabanidae) adult. Deerflies in this genus live in wetlands, bogs, and forests. Photo by Hectonichus, through Creative Commons.



Figure 55. Tabanidae female laying eggs, a site one might see in a wetland. Photo by Bernard Dupont, through Creative Commons.



Figure 56. *Tabanus imitans* eggs. Look for these in wetlands. Photo by Sturgis McKeever, through Creative Commons.



Figure 57. *Ceratopogonidae* larvae, a family that lives in wetlands and bogs. Photo by Landcare Research, Manaaka Whenua, with online permission.



Figure 58. *Ceratopogonidae* pupa, a family one can find in wetlands and bogs. Photo by Tom Murray, through Creative Commons.



Figure 59. *Ceratopogonidae* female, a family that lives in wetlands and bogs. Photo by Walter Pfliegler, with permission.

But these numbers seem modest compared to other studies. Salmela *et al.* (2007) reported 156 species of nematoceran **Diptera** in southern Finnish wetlands. Among their 8,606 specimens, they identified **Limoniidae** (80 species; Figure 16), **Psychodidae** (26; Figure 60-Figure 62), **Tipulidae** (20; Figure 3, Figure 25; Figure 80-Figure

82), **Pediciidae** (10; Figure 63-Figure 64), **Dixidae** (9; Figure 11-Figure 12; Figure 17), **Cylindrotomidae** (4; Figure 65-Figure 67), **Ptychopteridae** (4; Figure 68), **Thaumaleidae** (1; Figure 69-Figure 70), **Pleciidae** (1; Figure 71), and **Pachyneuridae** (1; Figure 72). One reason for the high diversity of **Diptera** is the high diversity of microhabitats in bogs and fens. But this also makes it difficult to assess the number of terrestrial species in these sites that live among mosses. In these studies, the microhabitat is often not described. Furthermore, the habitat changes with seasons (Blackstock *et al.* 1993). During the summer, the wetlands, both bogs and fens, become dry. Hence the life cycles of the invertebrates must be synchronized between their moisture needs and availability. And it means that the organisms moving about in the wet season are likely to be different from those that are active when it is dry.



Figure 60. *Clogmia albipunctata* larvae, representing the **Psychodidae** in wetlands. Photo by Ashley Bradford, through Creative Commons.



Figure 61. *Clogmia albipunctata* pupae, representing the **Psychodidae** of wetlands. Photo by Ashley Bradford, through Creative Commons.



Figure 62. **Psychodidae** adult, a family common in wetlands. Photo by Fritz Geller-Grimm, through Creative Commons.



Figure 63. *Pedicia albivitta* larva, representing a family that is common in Finnish Wetlands. Photo by Jason Neuswanger, with permission.



Figure 64. *Pedicia albivitta* adult, representing a family that is common in Finnish wetlands. Photo by M. J. Hatfield, through Creative Commons.



Figure 65. *Phalacrocer replicata* (**Cylindrotomidae**) pupa among mosses in a wetland. Photo by Janice Glime.

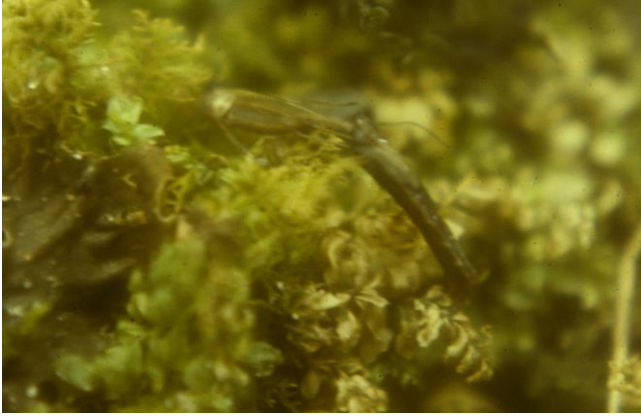


Figure 66. *Phalacrochera replicata* (Cylindrotomidae) adult emerging from its pupal enclosure among mosses. Photo by Janice Glime.



Figure 67. *Cylindrotoma distinctissima* adult female, a wetland inhabitant. Photo by James K. Lindsey, with permission.



Figure 68. Ptychopteridae larva, a wetland inhabitant. Photo by Jason Neuswanger, with permission.



Figure 69. Thaumaleidae larva, a wetland inhabitant. Photo from Landcare Research, Manaaka Whenua, with permission.



Figure 70. Thaumaleidae adult, an inhabitant of wetlands. Photo by Walter Pfliegler, with permission.



Figure 71. *Plecia nearctica* adult, representing a family that occurs in wetlands. Photo by Alexpb, through Creative Commons.



Figure 72. *Cramptonomyia spenceri* (Pachyneuridae) adult, representing a family from wetland habitats. Photo by Lynette Elliott, through Creative Commons.

In the examination of the effects of drainage ditches on peatlands, Taillefer and Wheeler (2010) likewise found much greater numbers in southern Quebec, Canada, peatlands. Their study focused on the predominately terrestrial peat remaining near drainage ditches. They examined the **Brachycera** at the Johnville Bog and Forest Park in Quebec. They found 1453 individuals of **Brachycera**, comprising 24 families and 166 species. Simpson's species diversity index indicated a higher diversity at 6 and 11 m than at 1 m from the ditch. Taillefer and Wheeler suggested that this difference may be due to the homogeneous moss cover and moister conditions at greater distance from the ditch. On the other hand, raw species richness was greater at 1 m and the numbers of specimens per sample were 177.5 at 1 m, decreasing to 92 at 11 m, based on pan trap sampling.

Blades and Marshall (1994) identified a range of 62-106 species of acalyptrate **Diptera** in four peatlands in southern Ontario, Canada. Diversity in individual localities ranged from 12 in an **oligotrophic** (low nutrient) fen to 69 in a rich fen. One reason for this high diversity is the wide range of habitats, including both aquatic and terrestrial.

Other select taxa groups studied in peatlands include **Chironomidae** (Figure 7-Figure 10) (Wrubleski 1987), biting flies (Lewis 1987), **Empididae** (Figure 13-Figure 15; Figure 73) (Barták & Roháček 1999), **Dolichopodidae** (Figure 74-Figure 75) (Rampazzi 2002), **Sphaeroceridae** (Figure 76-Figure 77) (Marshall 1994), and multiple other acalyptrate families (Roháček & Máca 1982; Roháček *et al.* 1998).



Figure 73. **Empididae** adult on leafy liverwort. Photo courtesy of Sarah Lloyd.



Figure 74. **Dolichopodidae** larva, one of the wetland inhabitants. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.



Figure 75. **Dolichopodidae** adult, a wetland inhabitant. Photo by Matt Reinbold, through Creative Commons.



Figure 76. Dung inhabited by **Sphaeroceridae**, a family that occurs in wetlands. Photo by James K. Lindsey, with permission.



Figure 77. *Lotophila atra* (Sphaeroceridae) adult, representing a family that is present in peatlands. Photo by James K. Lindsey, with permission.

Autio and Salmela (2010) found 104 species of **Diptera** [**Limoniidae** (Figure 16), **Tipulidae** (Figure 3, Figure 25; Figure 80-Figure 82), **Pediciidae** (Figure 63-Figure 64), **Cylindrotomidae** (Figure 65-Figure 67), **Ptychopteridae** (4; Figure 68-Error! Reference source not found.), **Psychodidae** (Figure 60-Figure 62), and **Dixidae** (9; Figure 11-Figure 12; Figure 17)] in the open mires, wooded mires, rich fens, Baltic shore meadows, ditches, and groves of Åland Islands in Finland. The Baltic shore meadows had the greatest richness, with 44 species. The **Nematocera** of the islands comprised fewer species than did mainland regions of southern Finland, and Autio and Salmela suggested that the theory of island biogeography might explain this lower species number. The island is ~40 km from the nearest continental sites. But they countered this with the fact that some of the most species-rich habitats (e.g. brooks and springs) are lacking on the islands.

Savage *et al.* (2011) found 381 species of **Schizophora** (section of true flies containing 78 families) in temperate Nearctic bogs. Species richness ranged 96-192 per site. The dominant species were usually not peatland specialists. Bog size had no effect on species richness, but vegetation cover at the sampling sites was important. In summary, perhaps referring to the **Diptera** of wetlands is best described as semi-aquatic (Autio & Salmela 2010).

One reason for these seeming contradictions regarding diversity is the paucity of faunal studies in these bog, fen, and mire habitats (Rosenberg & Danks 1987). Salmela and Ilmonen (2005) reiterated this lack of knowledge, specifically for the **Tipuloidea** – the crane flies. They bemoaned the disappearance of many natural mires in Finland. They recorded 29 crane fly species in the Kauhaneva mire system, including some that were regionally threatened. Mesotrophic sites had the highest species richness; **oligotrophic** (having low nutrients) and **ombrotrophic** (dependent on atmosphere for its nutrients) sites had equally low richness.

Loss of peatlands bodes poorly for the invertebrate inhabitants. But this loss is not the only human problem faced by these invertebrates. Peatland crops such as cranberries and other fruits can put them in danger as well. Bayfield (1979) showed that the crane fly *Molophilus ater* (**Limoniidae**) suffers from the compaction of the peat,

especially where trails are developed. Physical crushing in experiments killed large numbers of larvae. It is also possible that eggs were damaged on the foot paths.

Forests

Forest floor bryophytes often harbor **Diptera**. Logs covered with bryophytes are among the important sites. Mosses help to keep them moist and provide safe sites for the **Diptera** (Schuck *et al.* 2005). Others **Diptera** live on roots covered with drier mosses such as *Brachythecium velutinum* (Figure 78) and feed there on the moss (Sevchenko 1966). But these damp logs may have their dangers lurking. It is the site where the parasitic mite *Johnstoniana errans* (Figure 79) larvae and adults actively hunt for **Diptera** larvae and pupae among the damp mosses (Wohltmann 1996). These larvae exclusively parasitize species of *Tipula* (**Tipulidae**) during the pupa (Figure 80-Figure 81) and adult (Figure 82) stages.



Figure 78. *Brachythecium velutinum*, home for **Tipulidae** in forests. Photo by Michael Lüth, with permission.



Figure 79. *Johnstoniana* sp. *Johnstoniana errans* is a parasite on *Tipula* species in forests. Photo by Walter Pfliegler, with permission.



Figure 80. *Tipula* pupa, a stage vulnerable to being parasitized by *Johnstonia errans*. Photo by Ted Kropiewnicki, through Creative Commons.



Figure 81. **Tipulidae** adult emerging from pupal stage among forest mosses. Photo by Janice Gline.



Figure 82. *Tipula* cf. *varipennis* adult, a stage vulnerable to parasites in forests. Photo by Anki Engström at <www.krypinaturen.se>, with permission.

Recently, researchers have attempted to find **surrogates** – species or groups that can serve as predictors for the presence or status of other groups. Smith *et al.*

(2008) found that no one of the species groups in their forest survey could serve as a surrogate for the other species groups. However, they did find that forest bryophytes and saproxylic hoverflies (**Syrphidae**; Figure 83) could possibly serve as surrogates for each other. That is, these groups can indicate the biodiversity of each other.



Figure 83. **Syrphidae** adult, a family one can find among the epiphytes. These flies are bee mimics, but they don't sting. Photo by VladimirZh, through Creative Commons.

Epiphytes

Bar-Ness *et al.* (2006) surmised that *Eucalyptus obliqua* forests have strong age effects in the range of 0-80 years on species composition of bryophytes and tracheophytes. Thus they concluded that the same may be true for canopy invertebrates. The **Diptera** fauna on epiphytes is poorly known. In the Northwest, USA, Nelson and Hauser (1021) used Berlese funnels to extract arthropods. They compared the fauna of mosses and liverworts as pairs from the same tree. **Diptera** were only minor contributors to these communities.

Miller and coworkers (Miller 2006; Wagner *et al.* 2007; Miller *et al.* 2008) found a different picture in the Acadian forest of central Maine, USA. Whereas the **Collembola** and spiders were most abundant at the base of red maple (*Acer rubrum*) of the Acadian forest, correlating with the abundance of bryophytes there, the **Diptera** reached their highest abundance above 2 m on the tree. Miller (2006) found fifteen **Diptera** families, but only eight of these were common. These eight common families used the tree habitats differently, depending on the height above ground. For the **Diptera**, lichens were important. Furthermore, they responded differently to forest gaps. When gaps were created, the bryophytes became less abundant, but the other guilds did not seem to be affected by the loss of canopy. At higher positions on the trees, small foliose lichens were more abundant, whereas in the lower positions the bryophytes and cyanolichens were more abundant. In the first 6 m on the bole of *Acer rubrum* on the south-facing side, they found percent frequencies of

Ceratopogonidae (18; Figure 57-Figure 59), **Chironomidae** (22.5; Figure 7-Figure 10), **Dolichopodidae** (8; Figure 74-Figure 75), **Empididae** (4; Figure 13-Figure 15), **Psychodidae** (9; Figure 60-Figure 62), **Sciaridae** (12; Figure 84), **Phoridae** (35; Figure 85), **Cecidomyiidae** (80; Figure 86), **Chaoboridae** (2; Figure 27), **Culicidae** (7.5; Figure 49-Figure 51), **Drosophilidae** (0.8; Figure 87), **Simuliidae** (7; Figure 88), **Syrphidae** (0.8; Figure 83), and **Tabanidae** (0.8; Figure 52-Figure 54). Only the **Chironomidae** occurred in pitfall traps, suggesting that these taxa were true arboreal dwellers. The suborder **Nematocera** was the most abundant of the **Diptera** in the arboreal habitat above 2 m (Miller *et al.* 2007). These flies may use bryophytes for a drink of water, egg laying, pupation, cover, or escape from wind. And some most likely find food there among the smaller invertebrates. These relationships remain to be elucidated.



Figure 86. **Cecidomyiidae (Lestremiinae)** male feeding. This is a family with some members that live among epiphytes. Photo by Richard Orr, with permission.



Figure 84. ***Bradysia praecox* (Sciaridae)** adult, representing a family in which some members live among epiphytes. Photo by James K. Lindsey, with permission.



Figure 87. ***Drosophila melanogaster*** adult, representing the **Drosophilidae**, a family often found among epiphytes. Photo by André Karwath, through Creative Commons.



Figure 85. **Phoridae** mating in Rock Creek Park, MD, USA. This family can be found among epiphytes. Photo by Katja Schulz, through Creative Commons.



Figure 88. **Simuliidae** larvae. Some members of this family occur among epiphytic mosses. Photo by Steve Marshall, through Creative Commons.

Forest gaps make the terrestrial environment even less inviting for the moisture lovers. Using the red maple tree

(*Acer rubrum*) in the Acadian forest of central Maine, USA, Wagner *et al.* (2007) compared undisturbed red maple forest and forest areas with gaps. Gap harvesting reduced the major groups of arthropods on the trees.

The tree bark habitat with bryophyte mats can provide an ideal habitat for moisture-requiring larvae. Old-growth *Liriodendron tulipifera* in Tennessee exhibited nearly six times as much water in bark under bryophyte mats at the tree base as that in bare bark at about 2 m (Billings & Drew 1938; Ulyshen 2011). We should expect to find **Diptera** taking advantage of these moisture sources.

Harvesting Stowaways

Epiphytes, and especially bryophytes on logs in old-growth forests, are often harvested for use in floral arrangements and other uses. JeriLynn Peck became concerned at the massive amounts of bryophytes being removed, and was furthermore concerned about the invertebrates that were being shipped with the bryophytes to their place of sale. Peck and Moldenke (2011) reported that more than 3.7 million kg yr⁻¹ of fresh epiphytic bryophytes are harvested from the Coast and Cascade Mountain ranges in the Pacific Northwest of North America.

Peck and Moldenke (2010) researched the processing methods used in the moss trade. Most of the material from the Pacific Northwest is shipped dry, but that is little comfort because many of the invertebrates have means to survive this dry state. One processor tumbles the moss in large cylindrical tumblers with a sieve to remove needles, twigs, and other debris from the mosses. This method seems to have a high degree of success in removing the invertebrates as well. Only a few adult **Sciaridae** (dark-winged fungus gnats; Figure 89-Figure 90), an isopod, and a few oribatid mites were present in the tumbled mosses, whereas the non-tumbled fresh mosses had both high diversity and high abundance.

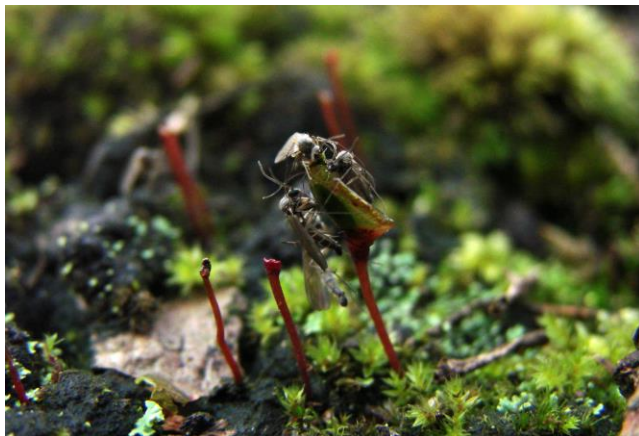


Figure 89. Fungus gnat (**Sciaridae**) herbivory on *Buxbaumia aphylla* capsules. Photo by Jörg Müller, through Creative Commons.

Altitude

Andrew *et al.* (2003) assessed the invertebrate-bryophyte community on four Australasian mountain ranges. The invertebrates were identified only to family, but the bryophytes were identified to species. In total, they

collected six families of **Diptera** [**Ceratopogonidae** (Figure 57-Figure 59), **Chironomidae** (Figure 7-Figure 10), **Cecidomyiidae** (Figure 86), **Tipulidae** (Figure 3, Figure 25; Figure 80-Figure 82), **Psychodidae** (Figure 60-Figure 62), **Phoridae** (Figure 85)], and these were usually among the top five in number of families among the represented groups. **Diptera** comprised 9% of the fauna in both Tasmania and New Zealand.



Figure 90. Fungus gnat (**Sciaridae**) herbivory on *Buxbaumia aphylla*. Photo by Jörg Müller, with permission.

Summary

Diptera differ from other insect orders in having only one pair of wings and a pair of **halteres**. Larvae of various families (especially **Chironomidae** and **Tipulidae**) often develop among bryophytes, and the same is typically true of the pupae. Some larvae even live in the thalli of liverworts.

The bryophytes provide a safe haven from predators and dry air. They serve as an insulating layer against cold. And in some cases they serve as food.

Collecting bryophyte-dwelling **Diptera** in the larval stage can be done with pan traps and pitfall traps, whereas in the adult stage sweep nets, Malaise traps, and windowpane traps are useful. They can be separated from the mosses with Tullgren funnels with sugar flotation, kerosene phase separation, or hand picking. The bryophytes with their inhabitants can be preserved in 95% ethanol, but rearing is often needed to identify the larvae.

The moss family **Splachnaceae** is adapted for spore dispersal by several families of flies, attracting them with odors in the capsules, colors, and having sticky spores. The mosses themselves grow on dung and other organic substrates, hence reaching there via the flies.

Peatlands and other wetlands typically have high diversity of **Diptera**, with many benefitting from the high moisture content. Forests also harbor a number of species among the bryophytes, especially in the larval and pupal stages, but adults may use the bryophytes for regaining moisture, avoiding predators, and oviposition. Even epiphytic bryophytes often house **Diptera**, and harvesting these epiphytes and other forest bryophytes for commercial purposes is a means of introducing invasive species where they are sold. Food may be available among the bacteria, fungi, protozoa, algae, and small invertebrates. Altitudinal differences of bryophyte dwellers seem to be poorly known in most of the world.

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CHAPTER 12-18

TERRESTRIAL INSECTS:

HOLOMETABOLA – DIPTERA

NEMATOCERA: TIPULOIDEA

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CHAPTER 12-18

TERRESTRIAL INSECTS:

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NEMATOCERA: TIPULOIDEA



Figure 1. *Triogma trisulcata* larva among mosses, demonstrating mimicry of mosses with its many leaflike appendages protruding. The moss is probably *Calliergonella cuspidata*. Photo by J. C. Schou <www.biopix.com>, with permission.

NEMATOCERA

The **Nematocera** are elongated flies that have thin, segmented antennae. Their larvae are mostly aquatic, but some are able to live on land, often using the limnoterrestrial habitat of mosses to maintain their hydration.

Using transplant experiments at the Moor House National Nature Reserve, UK, Briones *et al.* (1997) noted that **Diptera** larvae responded to changes in climate. The larvae depended on the moisture in the upper soil layers and populations diminished at higher temperatures and lower moisture levels.

Using Malaise and window traps as well as sweep netting, Salmela (2001) surveyed the **Nematocera** associated with 27 springs and springbrooks in Southern

Finland. Among the 2714 individuals collected, Salmela found 95 species, comprised of 24 **Tipulidae**, 2 **Cylindrotomidae**, 54 **Limoniidae**, 12 **Pediciidae**, and 3 **Ptychopteridae**. This is a habitat that typically has extensive bryophyte cover.

Cylindrotomidae

The **Cylindrotomidae** is one of the families of the **Tipulomorpha**, an infraorder whose families were once included in the family **Tipulidae**; then the family **Cylindrotomidae** and others were separated. But the trend today is that most researchers include these 115 species in the **Cylindrotominae**, back in the family **Tipulidae**. I have maintained the separation here for ease of discussion.

The flies are yellowish to pale brown, 11-16 mm long. Most of the larvae are herbivores, and some are adapted for living among and eating bryophytes (Figure 2-Figure 3).



Figure 2. *Cylindrotomidae* eating *Cratoneuron filicinum*. Photo courtesy of Misha Ignatov.



Figure 3. *Cratoneuron filicinum* eaten by Tipulidae. Photo courtesy of Misha Ignatov.

Adaptations

The *Cylindrotomidae* larvae often occur among bryophytes and appear to exhibit camouflage to that habitat by their coloration and numerous horizontal, elongated, cuticular lobes on the integument. Imada (2021) explored the selective pressures and functions that might be responsible for the retention of these characters. He challenged the notion that this apparent camouflage protected the larvae from predators because of the apparent absence of visual predators such as birds. Could it be that the camouflage is so good that the birds never find these larvae?

So of what importance, if any, are the lobes? Imada (2021) noted that these moss dwellers tended to crawl among the mosses, with movement starting at the posterior end and shifting to the anterior end. Imada then considered that these lobes might contribute to that movement on the soft moss beds. He found that the musculature of the larvae seems to support this movement, but he has not yet been able to demonstrate whether or not this is the case. The coloration of greens and browns, while adaptive as camouflage among the mosses, is common among plant-eating larvae in general and therefore may represent an evolutionary leftover from related families of Diptera.

Triogma

Triogma trisulcata (Figure 1, Figure 5-Figure 4) is one such mimic from upland seepage bogs and streams (Falk 1991), mosses of springs (Hemmingsen 1968), and eutrophic fens (Mannheims 1965; Salmela 2002). In streams the larvae hook themselves onto mosses such as *Fontinalis antipyretica* (Figure 6) or *Calliergonella cuspidata* (Figure 7). This species lives among the mosses and feeds on them, resembling the mosses where they live (Alexander 1920).



Figure 4. Posterior end of *Triogma trisulcata* showing the structures that resemble moss leaves. Photo by Walter Pfliegler, with permission.



Figure 5. *Triogma trisulcata* on *Plagiomnium* sp. Photo by Janice Glime.



Figure 6. *Fontinalis antipyretica*, aquatic home for *Triogma trisulcata*. Photo by Chris Wagner, with permission.



Figure 7. *Calliergonella cuspidata*, home for *Triogma trisulcata*. Photo by Michael Becker, through Creative Commons.

Diogma

The genus *Diogma* (Cylindrotomidae) is a terrestrial version resembling the more aquatic *Triogma trisulcata* (Figure 5-Figure 4) (Brinkmann 1997). It often lives near the water in humid terrestrial mosses and like *T. trisulcata* has dorsal processes that help to camouflage it, along with its green color (Müggenburg 1902). The larvae remain small throughout winter, reaching 2 cm at maturity. The pupae likewise live among the mosses. Müggenburg reported that *Diogma glabrata* (Figure 8) not only lived among leaves of the moss *Rhytidiadelphus squarrosus* (Figure 9) as larvae and pupae, but also that it ate them and laid its eggs there in the leaf axils. Adults emerge from the pupae in only a few days.



Figure 8. *Diogma glabrata* adult. Green larvae and pupae live among mosses and eat *Rhytidiadelphus squarrosus*. Photo by Louis Boumans, with permission.



Figure 9. *Rhytidiadelphus squarrosus*, home, food, and oviposition site for *Diogma glabrata*. Photo by Johan N, through Creative Commons.

Cylindrotoma

The terrestrial members of this genus (Figure 10) likewise spend their larval stage among terrestrial mosses or on marsh plants (Brinkmann 1997).



Figure 10. *Cyindrotoma* sp. larva, often a terrestrial moss inhabitant. Photo by Walter Pfliegler, with permission.



Figure 12. *Sphagnum capillifolium*, food for larvae of *Phalacrocer replicata*. Photo by Bernd Haynold, through Creative Commons.

Phalacrocer

This genus is fairly restricted in its range with the exception of *Phalacrocer replicata* (Figure 11). This moss dweller is a cosmopolitan species, occurring in North America, northern Europe, and northern Asia (Wikipedia 2014). *Phalacrocer replicata* larvae (Figure 15) feed on *Sphagnum* (Figure 12) (Clymo & Hayward 1982) and also live on *Warnstorfia exannulata* (Figure 13-Figure 14).



Figure 13. *Warnstorfia exannulata* habitat and home for *Phalacrocer replicata*. Photo by J. C. Schou, with permission.



Figure 11. *Phalacrocer replicata* adult, a moss dweller. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 14. *Warnstorfia exannulata*, home for *Phalacrocer replicata*. Photo by J. C. Schou, with permission.

The young larvae of the genus *Phalacrocer* (Figure 15) are transparent, permitting the green coloration of the moss to show through (Alexander 1920). Older larvae are

a brownish green with a striping that somewhat resembles the light and dark shades of moss branches. Long filamentous processes on the larvae help provide disruptive coloration that makes them more difficult to see. The larvae can survive for a long time under water, but also can survive a long time out of water. They can even survive frozen in ice for the duration of winter. They are sluggish and hang onto the mosses with their anal hooks, swaying back and forth. When they do move through the mosses, they alternately grab the moss with their mandibles and anal hooks. When they are disturbed, they roll into a ball like roly-polies. The female deposits her eggs in the leaf axils of the mosses.



Figure 15. *Phalacrocer replicata* larva, a moss dweller and moss consumer. Note the green color of the digestive tract and the transparency of the larva. Photo by Paul T, through Creative Commons.

Not surprisingly, these larvae remain in the mosses to pupate (Figure 16). When they emerge, they climb out the pupal encasement in its upright position (Figure 17), emerging from the top.



Figure 16. *Phalacrocer replicata* pupa on moss in Michigan, USA. Photo by Janice Glime.

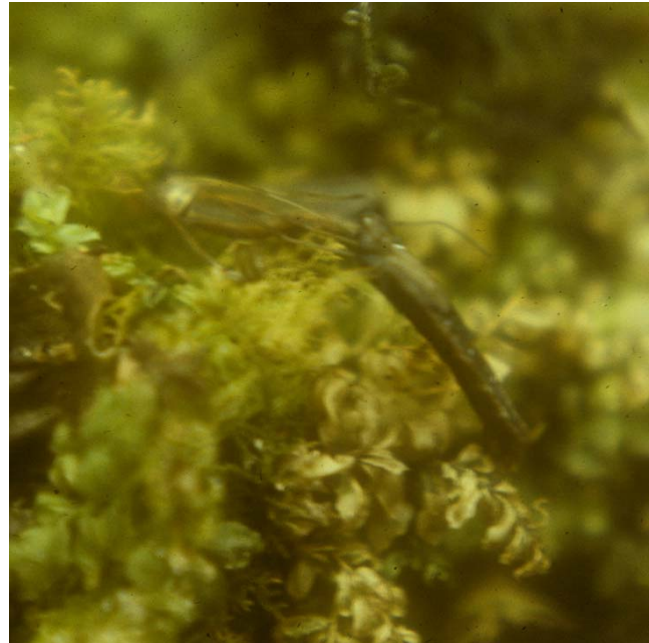


Figure 17. *Phalacrocer replicata* adult emerging from its pupa on moss in Michigan, USA. Photo by Janice Glime.

Phalacrocer tipulina (Figure 18) is another bog dweller in this family. It lives in or near the mountain peat bogs and as a larva eats mosses and other plants (Alexander 1942; Fetzner 2007).



Figure 18. *Phalacrocer tipulina* adult, a bog dweller. Photo by Chen Young, through Creative Commons.

Liogma

Liogma is one of the genera that exhibits cryptic coloration. The larvae live among mosses and feed on them (Alexander 1920; Byers 1961; Fetzner 2007). And they look like mosses in coloration and markings (Alexander 1920). One of these is *Liogma nodicornis* (Figure 19-Figure 21), a species that lives in *Hypnum cupressiforme* (Figure 22-Figure 23) as larvae and pupae.



Figure 19. *Liogma* sp. larva, a moss dweller with disruptive filaments. Photo by Bob Barber, through Creative Commons.



Figure 22. Typical habitat of *Hypnum cupressiforme* and home for *Liogma nodicornis*. Photo by Michael Lüth, with permission.



Figure 20. *Liogma nodicornis*, a species that spends its larval and pupal life in mosses such as *Drepanocladus*. Photo by Stephen Cresswell, with permission.



Figure 23. *Hypnum cupressiforme*, home for *Liogma nodicornis*. Photo by Michael Lüth, with permission.

Limoniidae

This family is often included as a subfamily in the **Tipulidae**. The species *Limnophila alleni* (Figure 24- Figure 25) was among early reports of members of this family that made use of mosses. Alexander (1919) reported that the females laid their eggs in mosses, flying low over the substrate until they find a suitable place.



Figure 21. *Liogma nodicornis* mating, a species that spends its larval and pupal life in mosses such as *Drepanocladus*. Photo by Stephen Cresswell, with permission.



Figure 24. *Limnophila* larva; some species hatch among mosses. Photo by Tom Murray, through Creative Commons.



Figure 25. *Limnophila alleni* adult, a species that oviposits among mosses. Photo by Chen Young, through Creative Commons.

The **Limoniidae** species tend to be in moist habitats. *Paradelphomyia fuscata* (Figure 26) was among the four most common species along springs in southern Finland (Salmela 2001).



Figure 26. *Paradelphomyia fuscata* adult, a common species along springs in Finland. Photo by Marko Mutanen, through Creative Commons.

Geranomyia vitiella has an unusual habit worth noting. Its larvae live on leaves of *Pandanus* in moist habitats of Fijian rainforest (Beaver & Ryan 1988). The larva makes a tube of jelly on the upper surface of the leaf, living and moving in it and emerging to feed on dead **epiphylls** (mosses, liverworts, fungi, algae, and lichens that live on the leaves) and the associated decaying matter and microbes (Beaver & Ryan 1988). When it is mature, it changes its position to the lower surface, producing an even

larger mass of jelly. It pupates in the jelly. These jelly masses protect both larvae and pupae against both desiccation and natural enemies. Beaver and Ryan assumed that the eggs are laid among the epiphylls.

Hancock (2008) reports that Falk (1991) reared *Gnophomyia viridipennis* from moss collected from a fallen tree trunk of beech in Great Britain. Previous records indicate the species may prefer *Populus* species.

Arroyo-Rodríguez *et al.* (2007) experimented with *Geranomyia recondita* feeding in the lab. They offered three species of **Lejeuneaceae** – small leafy liverworts that are common among epiphylls. Only 30% of the larvae consumed the offered liverworts, but this demonstrates that they can eat live liverworts. They fed mostly on *Lejeunea* (Figure 27) and never ate *Leptolejeunea* (Figure 28). Arroyo-Rodríguez and coworkers suggested that this avoidance indicates they avoid liverworts with aromatic compounds. The larvae also consumed other epiphylls on the leaves. The jelly mass area had a negative correlation with the temperature, a relationship the authors interpreted as an indication the larvae are more active at night since the masses were larger at that time. The larger jelly mass would give them a larger foraging area.



Figure 27. *Lejeunea cf. epiphylla* on *Blechnum wattsii* leaf; this liverwort is food for *Geranomyia recondita*. Photo by Tom Thekathyl, with permission.



Figure 28. *Leptolejeunea elliptica*, member of a genus rejected as food by *Geranomyia recondita*. Photo by Yan Jia-dang, through Creative Commons.

Geranomyia sexocellata near Cape Town, South Africa, uses a similar gelatinous tube, but it adds minute sand grains and attaches the tube to mosses in small trickles of water (Harrison & Barnard 1972). *Limonia capicola* larvae live among mosses at the edge of rapidly flowing small streams. Similarly, larvae of *L. rostrata* (= *Geranomyia rostrata*; Figure 29) live among mosses, liverworts, and filamentous algae on wet rocks (Rogers 1927). The larvae occur between the layers of liverwort thalli or in contact with stems of the mosses where they feed on the leaves. They seem to prefer the terminal leaves on the smaller stems in the lab, but in the field they are mostly found deep within the mat. Their translucent greenish color and slow movement make them hard to see. The larvae construct a tube and feed from its safety. Pupation occurs at the distal ends of the larval tubes. *Limonia annulata* (Figure 30-Figure 31) adults tend to occur on the moss-covered tree bases in forests (Fetzner 2008).



Figure 29. *Limonia rostrata* adult, a species whose larvae live between layers of liverworts or along stems of mosses that they feed on. Photo by Stephen Luk, with permission.



Figure 30. If you are having trouble finding the *Limonia annulata* adult on this moss, you can understand the value of its coloration. This species spends much of its adult time on moss-covered tree bases. Photo by Katja Schulz, through Creative Commons.



Figure 31. *Limonia annulata* adult, a species that hangs out on mosses at tree bases in its adult stage. Photo by Tom Murray, through Creative Commons.

The genus "*Gonomyia*" has been split into a number of genera, several of which include bryophyte dwellers. Byers (1961) reported use of bryophytes as habitat by at least some *Erioptera* larvae. Salmela (2001) found *Erioptera pederi* (Figure 32) among the *Nematocera* along springs and springbrooks in southern Finland.



Figure 32. *Erioptera pederi* adult, a species that lives along springs and springbrooks and larvae can occur among the bryophytes. Photo by Marko Mutanen, through Creative Commons.

Falk (1991) found that *Ellipteroides alboscuteallatus* (previously in *Gonomyia*; Figure 33) seemed to be associated with wooded mossy calcareous seepages. Several of the *Limoniidae* were published just as *Gonomyia*, so other bryophyte dwellers may be lurking in

that former genus. In their search for indicator species, Salmela and Ilmonen (2005) recorded 29 species of craneflies (**Tipuloidea**) from Malaise traps in the Kauhaneva mire system in Finland. They found the highest diversity in mesotrophic sites, with the oligotrophic and ombrotrophic sites having equally low diversity. *Erioptera flavata* (Figure 34) and *Phylidorea squalens* (Figure 35) were indicators of mesotrophic sites (Figure 36), but they found no indicators for the low-nutrient sites.



Figure 33. *Ellipteroides alboscuteallatus* adult, a species associated with wooded mossy calcareous seepages. This museum specimen is unfortunately missing its long legs. Photo by Jukka Salmela, with permission.



Figure 34. *Erioptera flavata* adult, an indicator of mesotrophic sites. Photo by James K. Lindsey, with permission.



Figure 35. *Phylidorea squalens* adult male, an indicator of mesotrophic sites. Photo by James K. Lindsey, with permission.



Figure 36. *Phylidorea squalens* habitat in wet forest with mosses. Photo by James K. Lindsey, with permission

Elephantomyia aurantiaca (see Figure 37) is a limoniid that lives among damp mosses and liverworts near streams (Harrison & Barnard 1972).



Figure 37. *Elephantomyia westwoodi* male adult. *Elephantomyia aurantiaca* lives among damp mosses and liverworts near streams. Photo by Tom Murray, through Creative Commons.

Pediciidae

The **Pediciidae** (Figure 38) is another family that is often included as a subfamily in the **Tipulidae**. In addition to the two members of **Limoniidae**, Salmela and Ilmonen (2005) found that *Pedicia rivosa* (Figure 39-Figure 40) and *Tricyphona immaculata* (Figure 41) indicated mesotrophic sites in the Kauhaneva mire system, but there were no indicators for the low-nutrient sites. These two species and *Pedicia straminea* (Figure 42) were among the four most common species and often the most abundant species of the **Diptera** collected around southern Finnish springs (Salmela 2001).



Figure 38. *Pedicia albivitta*, member of a genus that often occurs among mosses. Photo by Jason Neuswanger, with permission.



Figure 39. *Pedicia rivosa* adult, an indicator of mesotrophic sites, camouflaged here against the vegetation. James K. Lindsey, with permission.



Figure 40. *Pedicia rivosa* adult, an indicator of mesotrophic systems. Photo by Roger S. Key, with permission.



Figure 41. *Tricyphona immaculata* adult, indicator of mesotrophic sites. Photo by Malcolm Storey at <www.discoverlife.org>, through Creative Commons.



Figure 42. *Pedicia straminea* adult, an indicator of mesotrophic sites. Photo by Marko Mutonen, through Creative Commons.

Stephen Cresswell observed *Pedicia auripennis* (Figure 43) resting on a mossy rock overhang in the bed of a ravine in West Virginia, USA (Fetzner 2008). Flies can use such resting places to rehydrate and to maintain lower temperatures.



Figure 43. *Pedicia auripennis* adult resting. Mosses make good resting sites, especially cool, damp ones. Photo by Stephen Cresswell, with permission.



Figure 44. *Tipula oleracea* larval respiratory organ showing small papillae, but this species does not seem to be a moss dweller. Photo by Malcolm Storey, through Creative Commons.

Tipulidae – Craneflies

Most of the craneflies associated with bryophytes are aquatic, but a few terrestrial taxa give the bryophytes special importance. Alexander (1919) considered the **Tipulidae** family to serve as a major food group for the vertebrates. *Tipula* species on the Pribilof group in the Bering Sea are abundant in the summer. Larvae are especially common under mosses where they feed on the rhizoids. As many as 20 larvae can occur in a 30-cm square; considerable areas of mosses are killed by their activity (Figure 3). To add to destruction by the larvae, foxes dig up large areas of mosses to find the juicy larvae for food. Hofsvang (1997) noted the wide range of larval habitats, from water to mosses to dry logs. As adults, the **Tipulidae** typically live only a few days and some don't eat as adults.

In West Germany, changes in some of the fly populations are directly linked to changes in bryophyte cover (Wagner 1980). Morris (1986) reports on "an unusual habitat" for the overwintering of European cranefly larvae, but it appears that craneflies are the most important group utilizing the terrestrial bryological habitat. Craneflies are those insects that tend to cling around the ceiling and look like giant mosquitoes.

Adaptations

Some craneflies (**Tipulidae**) are highly adapted to their mossy habitat, with some taxa colored in such a way as to resemble a moss branch, as discussed under the various genera. Brindle (1957) observed that the **Tipulidae** that live among bryophytes have special anal papillae (Figure 44-Figure 45) to help them gain oxygen. I have been unable to verify that with the more recent data available.



Figure 45. *Tipula abdominalis* larval respiratory disk with large grey papillae. This species likewise is not a moss dweller. Photo by Thomas Palmer (Ophis), with permission.

Among the bryophytes they select, growth form is important (Gerson 1982). The compact species like *Bryum argenteum* (Figure 46) and *Ceratodon purpureus* (Figure 47-Figure 48) hinder tunnelling by the larvae, whereas loose growth forms like those of *Climacium* (Figure 49), *Polytrichum* (Figure 50), and *Plagiomnium cuspidatum* (Figure 51) are too diffuse for making tunnels (Byers 1961). Byers also concluded that *Polytrichum* and thallose liverworts were not soft enough. I have to wonder if secondary (antiherbivory) compounds might be important for protecting the thallose liverworts.



Figure 46. *Bryum argenteum*, a compact species that hinders tunnelling by *Tipulidae* larvae. Photo by Michael Becker, through Creative Commons.



Figure 49. *Climacium dendroides* showing openness of the clump, spaces unsuitable for tunnelling by *Tipulidae*. Photo by Janice Glime.



Figure 47. *Ceratodon purpureus* cushions, a compact species that hinders tunnelling by *Tipulidae* larvae. Photo by Michael Lüth, with permission.



Figure 50. *Polytrichum juniperinum* showing open leaf overlap and open spaces in clump, unsuitable for tunnelling by *Tipulidae*. Photo by Janice Glime.



Figure 48. *Ceratodon purpureus* cushion, a compact species that hinders tunnelling by *Tipulidae* larvae. Photo by Janice Glime.



Figure 51. *Plagiomnium cuspidatum* showing the openness of the branches, unsuitable for tunnelling by *Tipulidae*. Photo by Michael Lüth, with permission.

Mosses can be a major portion of the diet of *Tipulidae* larvae (Richardson 1981; Pritchard 1983). However, the feces of some species have undigested vegetable particles in the feces, including mosses, suggesting that the food value may be from periphyton on the mosses and that the

mosses are not digested (Pritchard 1983). At least *Tipula abdominalis* (Figure 52-Figure 53) larvae have a high pH in the gut that permits them to digest leaf litter (Martin *et al.* 1980; Sharma *et al.* 1984). But leaf litter typically has fungi that begin the process to prepare them for digestion (Barlocher 1985). The mosses are living cells and thus gaining access to the contents inside the cell walls is more difficult.



Figure 52. *Tipula abdominalis* adult, a crane fly whose larvae have a high gut pH to digest detritus. Photo by Stephen Cresswell, with permission.



Figure 53. *Tipula abdominalis* larva, a species with a high gut pH to digest detritus. Photo by Tom Murray, through Creative Commons.

Tipula

Tipula (Figure 55-Figure 60) is a worldwide genus with 59 species in Britain alone (Freeman 1967). It is a typical wet habitat fly, especially in its larval stage. Using sweep nets (catching adults), Freeman (1968) found more species in wet or woodland habitats than in dry or non-woodland habitats. Not surprisingly, it feeds on the mosses in these habitats. And it is also not surprising that in the open and drier habitats the peak in number of species present occurs in spring and late summer, whereas in the more moist and shaded habitats the diversity remains relatively constant during the entire period of spring to late summer. And of course Freeman found more species in the more shaded or moist habitats.

Sevchenko (1966) found that larvae of *Tipula stigmatella* (Figure 55) / *T. submaculata* (Figure 56) live among dry mosses, especially *Brachythecium velutinum* (Figure 54) on tree roots, and feed on the moss. Savchenko

(1964) likewise found that *Tipula benesignata* (Figure 57) feeds on mosses living under the forest cover. In fact, the association of fly larvae, and especially the crane flies (*Tipulidae*), is so strong that Oldroyd (1964) suggested that flies arose from ancestors that had larvae that lived in wet moss.



Figure 54. *Brachythecium velutinum* with capsules, a common home for *Tipula stigmatella/submaculata* on tree roots. Photo by Dick Haaksma, with permission.



Figure 55. *Tipula stigmatella* adult, a species whose larvae live among dry mosses such as *Brachythecium velutinum*. Photo by James K. Lindsey, with permission.



Figure 56. *Tipula submaculata* adult, a species whose larvae live among dry mosses. Photo by Tom Murray, through Creative Commons.



Figure 57. *Tipula benesignata*, a species that feeds as larvae on mosses under forest cover. Photo by Marko Mutanen, through Creative Commons.

Brindle (1960) found a correlation that may be a moss adaptation for moss-dwelling *Tipula* (Figure 58-Figure 59). The moss feeders always have four pairs of short anal papillae at the posterior end. They never have long papillae like the ones on larvae from wetter environments. On the other hand, this may simply be an evolutionary correlation of two divergent groups. But spiracular disk size also differs (Todd 1993) and it would be interesting to compare the size of this respiratory organ with available airspace within the bryophyte mat inhabited.



Figure 58. *Tipulidae* – herbivore on the moss *Cratoneuron filicinum*. Photo courtesy of Misha Ignatov.



Figure 59. *Cratoneuron filicinum* – food for a *Tipulidae* larva. Photo courtesy of Misha Ignatov.

Zasyapkina and Ryabukhin (2001) described the insects that lived in intermediate habitats in northeast Asia. They reported that the larvae of *Tipula glaucocinerea* live in wet depressions with no open water, living in moss litter under snowfields as well as those on the banks of bog pools and small lakes. Larvae of *T. melanoceros* live in boggy forest clearings, in peat mosses, or in decaying *Sphagnum* where they occur in groups.

Tipula confusa (Figure 61-Figure 60) not only chose to live in clumps of *Brachythecium rutabulum* (Figure 62) on walls and buildings, but it also consumed its mossy housing (Todd 1993). *Tipula confusa* had a significant preference for *Dicranella heteromalla* (Figure 63-Figure 64) ($70.0 \pm 1.4\%$ S.E. of observations), with *Brachythecium rutabulum*, a woodland species, preferred second ($47.3 \pm 1.3\%$ S.E.); both a woodland species, *Mnium hornum* (Figure 65) ($41.7 \pm 1.5\%$ S.E.), and a moorland species, *Sphagnum recurvum* (Figure 66) ($40.0 \pm 1.4\%$ S.E.) were third in preference. *Tipula subnodicornis* (Figure 67) spent significantly more time on *Eurhynchium praelongum* (Figure 68) than on *Sphagnum recurvum*, and exhibited the greatest preference for *Eurhynchium praelongum* ($42.8 \pm 1.7\%$ S.E. of obs), but not significantly higher than for *Dicranum scoparium* (Figure 69-Figure 70) ($40.6 \pm 1.5\%$ S.E.), for which preference was not significantly higher than that for *Sphagnum recurvum* ($38.0 \pm 1.4\%$ S.E.). Both *Tipula confusa* and *T. subnodicornis* preferred *Polytrichum commune* (Figure 71) significantly less than any other moss studied. Brindle (1960) found that on moorlands *T. subnodicornis* is typically associated with semi-aquatic mosses such as *Sphagnum* and "*Hypnum*" (presumably *Drepanocladus* s.l.; Figure 72).



Figure 60. *Tipula confusa* adult, a species whose larvae live among and feed upon *Brachythecium rutabulum* on walls. Photo by Janet Graham, through Creative Commons.



Figure 61. *Tipula confusa* adult, a species whose larvae live among and feed upon *Brachythecium rutabulum* on walls. Photo by James K. Lindsey, with permission.



Figure 64. *Dicranella heteromalla*, a choice habitat and food for *Tipula confusa*. Photo by Michael Lüth, with permission.



Figure 62. *Brachythecium rutabulum* with capsules, habitat and second choice of mosses as food for *Tipula confusa*. Photo by J. C. Schou, with permission.



Figure 65. *Mnium hornum*, a moss that is eaten by *Tipula confusa*. Photo by Michael Lüth, with permission.



Figure 63. *Dicranella heteromalla* habitat where one might find *Tipula confusa*. Photo by Michael Lüth, with permission.



Figure 66. *Sphagnum recurvum*, among the food sources for *Tipula confusa*. Photo by Malcolm Storey <www.discoverlife.com>, through Creative Commons.



Figure 67. *Tipula subnodicornis* adult, a species whose larvae prefer the moss *Eurhynchium praelongum* as food. Photo by James K. Lindsey, with permission.



Figure 70. *Dicranum scoparium*, home and food for *Tipula subnodicornis*. Photo by Janice Glime.



Figure 68. *Eurhynchium praelongum*, home and food source for *Tipula subnodicornis*. Photo by Blanka Shaw, with permission.



Figure 71. *Polytrichum commune*, one of the least preferred moss species for food by *Tipula confusa* and *T. subnodicornis*. Photo by Malcolm Storey <www.discoverlife.com>, through Creative Commons.



Figure 69. *Dicranum scoparium* habitat and home for *Tipula subnodicornis*. Photo by Janice Glime.



Figure 72. *Drepanocladus exnnulatus*, a typical emergent moss home for *Tipula subnodicornis*. Photo by Michael Lüth, with permission.

In lab choice experiments, Todd (1993) showed that *Tipula confusa* (Figure 61-Figure 60) preferred mosses from woodland habitats, whereas *Tipula subnodicornis* (Figure 67) did not show any overall preference for either woodland or moorland mosses. Todd found that eight (of 11 studied) species of *Tipula* were moss feeders, seven of which were in the subgenus *Savtshenkia* [*Tipula rufina* (Figure 73), *T. confusa*, *T. pagana* (Figure 74), *T. staegeri*, *T. limbata* (Figure 75), *T. alpium* (Figure 76), *T. subnodicornis*]. Only *Tipula montana* (Figure 90) was in the separate subgenus *Vestiplex*. On recently burned *Calluna* heath larvae live among and feed on dead introduced mosses, *Campylopus introflexus* (Figure 77). Falk (1991) reported that *Tipula limbata* also occurs in boggy forests in Scotland.



Figure 75. *Tipula limbata* adult, a species whose larvae are moss feeders. Photo by Derek Sikes, through Creative Commons.



Figure 73. *Tipula rufina* adult; larvae of this species have small mandibles and eat small particles of moss. Photo by Malcolm Storey, through Creative Commons.



Figure 76. *Tipula alpium* adult, a species whose larvae eat mosses. Photo by James K. Lindsey, with permission.



Figure 74. *Tipula pagana* adult, a moss feeder in Europe. Photo by Malcolm Storey, through Creative Commons.

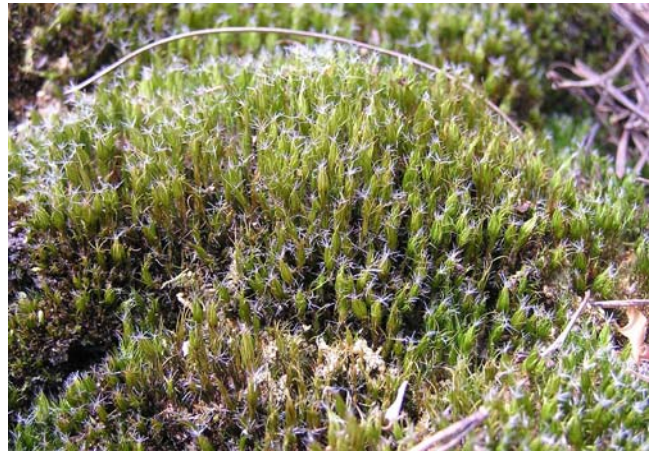


Figure 77. *Campylopus introflexus*, an introduced moss in Europe that serves as home and food for some *Tipula* species. Photo by Michael Becker, through Creative Commons.

Approximately one fourth of the British species of *Tipula* feed on mosses, but in some species the ingested mosses depart in the feces with no evidence of breakdown (Todd 1993). That does not appear to be the case for *Tipula montana* (Figure 90) – it feeds exclusively on mosses. This species does not grow at temperatures below 7°C (Todd 1996). Perhaps the moss maintains a higher temperature where it can successfully complete its life cycle in a timely manner.

Mandible size seems to be an important character in bite size. **Grass feeders** typically have longer mandibles than moss feeders. *Tipula paludosa* (Figure 78-Figure 82) has significantly larger mandibles and ingests larger particles than the smallest mandibles of this group, exhibited by *T. rufina* (Figure 73), a species that ingests smaller particles. There was no evidence that the cell walls had been broken down, indicating that crushing of cells by the mandibles was the only means by which larvae could obtain the nutrients within the cells. Furthermore, biflavonoids in the cell walls of mosses apparently resist fungal invasion, thus making it difficult or impossible for the larvae to digest the cell walls. This explains the reason for the approach of taking the same size of particles throughout their growth because larger particles would not offer much more digestible food. Other kinds of insect larvae are known to increase particle size as they grow. The larvae apparently, as one might expect, eat from edge inward on the leaf, leaving less damage in the mid-cell region. Some *Tipula* species do switch moss species as they grow. Heavy metals accumulated by the bryophytes from pollution can also deter feeding.



Figure 78. *Tipula paludosa* larva, a species with large mandibles that feeds on mosses. Photo by Roger S. Key, with permission.



Figure 79. *Tipula paludosa* blending in with the surrounding twigs and needles. Photo by James K. Lindsey, with permission.



Figure 80. *Tipula paludosa* adult. Photo from <www.aphotofauna.com>, with permission.



Figure 81. *Tipula paludosa* mating. Photo by Anki Engström <www.krypinaturen.se>, with permission.



Figure 82. Head, thorax, and halteres of *Tipula paludosa*. Photo by Anki Engström at <www.krypinaturen.se>, with permission.

To these members of the subgenus *Savtshenkia*, Savchenko (1964) adds *Tipula benesignata* (Figure 83). This species likewise feeds on mosses under forest cover.



Figure 83. *Tipula benesignata*, a moss feeder under forest cover. Photo by Marko Mutanen, through Creative Commons.

It is of interest that the tipulid populations do not appear to support **Gause's law**. That is, in this group, closely related species tend to occur together. However, several factors may actually separate their niches. The adults in the same subgenus may be separated in time. Other factors such as mating behavior also help to keep the species from interbreeding.

Freeman (1967) explored **Gause's law** in the **Tipulinae**. Using a 350 x 350 m area, Freeman was able to demonstrate that each of the 23 species of *Tipula* was restricted to one or occasionally two of the five plant communities represented. Within each of those plant communities there was no evidence of competition for food in the soil-dwelling *Tipula* species, but some species, especially *T. paludosa* (Figure 78-Figure 81), became aggressive, directly attacking competitors. Ten species of *Tipula* were able to co-exist for nine years in one plant community, the **carr** (waterlogged wooded terrain). They seemed to accomplish this co-existence through use of microhabitats.

Coulson (1962) found that *Tipula paludosa* (Figure 78-Figure 81) was restricted to mineral soils in the Pennine, UK, moorland. Morris (1986) found a more unusual habitat for *Tipula paludosa*. These crane fly larvae, known as leatherjackets in their larval stages and numbering in the hundreds, were living among mosses on the roof of a covered picnic table in Newfoundland, Canada. The roof shingles had accumulated sand and organic matter that sustained the mosses.

Tipula subnodicornis (Figure 67) has wide occurrence in the Pennine moorland of the UK, but it occurs only in areas with peat (Coulson 1962). It demonstrates niche separation from *T. paludosa* (Figure 78-Figure 81) in the moorland by emerging mostly within an 11-day period, whereas for *T. paludosa* emergence is spread mostly over 23 days in late July and early August. The time of day for emergence differed, with *T. subnodicornis* emerging around mid-day and *T. paludosa* emerging at 21:00 h, shortly after sunset. Mating of both species occurred shortly after emergence, thus separating the two species in time. Both species began laying eggs immediately after mating, with *T. subnodicornis* occurring deeper than those of *T. paludosa*. Densities of final instar larvae of *T. subnodicornis* reached more than 100 per m² on *Juncus squarrosus* moorland (Figure 84) but was much lower on the *Sphagnum* (Figure 12; Figure 84) bog areas. In dry

spells such as that of 1955, there was high mortality among eggs and first instars in *T. subnodicornis*. Density similar to previous years was maintained only in areas such as *Sphagnum* flushes (Figure 84) where water was retained.



Figure 84. *Sphagnum* in flush with *Juncus* on Mt. Snowdon, Wales. Photo by Janice Glimme.

With so many *Tipula* species occurring among mosses as larvae, we must assume that the mosses are suitable, perhaps preferred or exclusive egg-laying sites for many species (Figure 85). One such species that was identified early was *Tipula nobilis* (Figure 86) that laid eggs in mosses (Alexander 1919).



Figure 85. *Tipula williamsiana* female laying eggs on mosses. Photo by Chen Young, through Creative Commons.



Figure 86. *Tipula nobilis* adult, a species that uses mosses for oviposition. Photo by Chen Young, through Creative Commons.

Among this group are crane flies that eat mosses. Sevchenko (1966) found that crane flies live among and feed on dry *Brachythecium velutinum* (Figure 54) on tree roots. The larvae of *Tipula oropezoides* (Figure 87) are regular feeders on *Rhizomnium punctatum* subsp. *chlorosum* (see Figure 88) along streams in eastern deciduous forests of the United States (Wyatt & Stoneburner 1989). The larvae typically strip the leaves of their lamina, leaving the costa and border. Could it be that borders discourage feeding by some invertebrate herbivores?



Figure 87. *Tipula oropezoides* male, a species whose larvae feed on mosses such as *Rhizomnium punctatum* along streams. Photo by Tom Murray, through Creative Commons.



Figure 88. *Rhizomnium punctatum*, home and food for *Tipula oropezoides* along streams in the eastern USA. Photo by J. C. Schou, with permission.

Some of the crane flies require 4 years to complete larval development, especially in Arctic ecosystems (MacLean 1980). The soil organisms there, and especially the **Diptera**, support the breeding populations of many breeding bird species, with crane flies being the most important prey. Hence, timing is important and the bird breeding is timed so that the young birds can feed on the emerging adult **Diptera** in early to mid July. In June and again in August, the **Diptera** larvae, especially crane flies, become the most important prey items. An overproduction of crane flies is necessary to compensate for the predation. These birds consume 35-70% of the annual production of *Tipula carinifrons* (Figure 89) and 50% of the peak emergence of all adult crane flies.



Figure 89. *Tipula carinifrons* male adult, a moss dweller in dry *Sphagnum* hummocks. Photo by Ashley Bradford, through Creative Commons.

In the blanket bogs of British moorland, larvae of *Tipula subnodicornis* (Figure 67) feed on liverworts (Coulson & Whittaker 1978; MacLean 1980). In a *Sphagnum* (Figure 12) bog, Smirnov (1958, 1961) found large quantities of *Sphagnum* leaves in gut analyses only in

Tipula larvae. In the coastal tundra of Barrow, Alaska, USA, *Tipula carinifrons* (Figure 89) is common in dry moss hummocks. Smirnov estimated that more than 25% of the energy consumed by crane fly larvae came from living plants.

Smith and coworkers (Smith 1997; Smith *et al.* 2001) examined the balance between the need for food and the need for shelter in the crane fly *Tipula montana* (Figure 90). Larvae were reared on single genera of mosses and the resulting growth in weight differed by a factor of two. When the larvae were given a choice between two genera, they chose the moss that had the most beneficial food quality. However, their response to *Pleurozium schreberi* (Figure 91-Figure 92) was a surprise. Although this food had the best food quality and resulted in the best growth, it was among the least eaten by the larvae. Fecal pellet analysis gave different results from those of observations, perhaps due to differences in digestibility. The sedge *Carex bigelowii* was eaten in preference to any of the mosses during the experiments, suggesting that the crane flies benefitted from using the bryophytes as a refuge, overriding the importance of dietary quality and making the trek to sedges less advantageous.



Figure 90. *Tipula montana verberneae* adult; larvae choose mosses as food based on quality. Photo by Pila Partanen, through Creative Commons.



Figure 91. *Pleurozium schreberi* habitat, displaying a habitat that appears suitable for *Tipula* larvae, but that is avoided by them as food. Photo by Michael Lüth, with permission.



Figure 92. *Pleurozium schreberi*, a moss that is typically avoided as food for *Tipula* larvae. Photo by Bob Klips, with permission.

Tipulids are important contributors to the food web, and *Tipula montana* (Figure 90) is no exception. In Scotland the Dotterel (*Charadrius morinellus*; Figure 93) adults and chicks feed selectively, with adults eating mostly beetles, sawflies, and both adults and larvae of *T. montana* (Galbraith *et al.* 1993). The adult Dotterels contained a high proportion of beetles. The chicks, on the other hand, took more soft-bodied food. Every two years the adults of *T. montana* emerge *en masse*. At that time, both chicks and adults feast on tipulids. In one case, the larvae of *T. montana* formed much of the diet soon after the birds arrived at their breeding grounds and again just before they left in the autumn. The preferred feeding habitats were the moss *Racomitrium lanuginosum* (Figure 94) or the rush *Juncus trifidus* (Figure 95) heaths or the transition zone between the moss heath and montane bog. When the montane bogs were close to the *R. lanuginosum* heaths, they met the feeding needs of both the chicks and adults, respectively.



Figure 93. *Charadrius morinellus* (European Dotterel) male with chicks, consumers of moss inhabitants. Photo by Helwig Brunner, through Creative Commons.



Figure 94. *Racomitrium lanuginosum* hummocks in old drainage channels, home for *Tipula montana*. Photo by Alan Silverside, with permission.



Figure 95. *Juncus trifidus*, one of the preferred feeding habitats for *Tipula montana*. Photo by Opiola Jerzy, through Creative Commons.

Tipula borealis (Figure 96) is a species of wet woodlands. The larvae occur in well-rotted logs, often occupying the interface space under the surface mosses (Gelhaus 1986).



Figure 96. *Tipula borealis* adult, a species whose larvae often live under mosses on rotten logs. Photo by Chen Young, through Creative Commons.

One of the more unusual relationships is the use of the hornworts *Anthoceros agrestis* (Figure 97) and *Phaeoceros carolinianus* (Figure 98) (Bisang 1996). *Tipula* sp. larvae consumed both the gametophytes and sporophytes of these hornwort species. *Bryum* sp. (see Figure 99) and several seedlings in the same pots were not eaten.



Figure 97. *Anthoceros agrestis*, food for some *Tipula* larvae. Photo by Bernd Haynold, through Creative Commons.



Figure 98. *Phaeoceros carolinianus* with sporophytes, a hornwort that is food for some *Tipula* larvae. Photo by Hermann Schachner, through Creative Commons.



Figure 99. *Bryum capillare*, a food source refused by hornwort-dwelling *Tipula*. Photo by Michael Lüth, with permission.

Prionocera

In the coastal tundra at Barrow, Alaska, USA, *Prionocera recta* (Figure 100) is restricted to mossy depressions (MacLean 1980).



Figure 100. *Prionocera recta* adult, a species that in Alaska is restricted to mossy depressions. Photo by Jukka Salmela, with permission.

Dolichopeza

Alexander (1920 in Gerson 1982) and Byers (1961) reported that *Dolichopeza* lives in and eats the mosses. Like several other *Tipulidae* (*s.l.*), larvae of *Dolichopeza americana* (Figure 101) has cryptic coloration of green with irregular markings and dark lines, permitting it to blend with its mossy environment (Byers 1961).



Figure 101. *Dolichopeza americana* adult, a species whose larvae have cryptic coloration among bryophytes. Photo by Tony Gallucci, through Creative Commons.

Dolichopeza americana (Figure 101) and *Oropeza* larvae, also crane flies, have color patterns that make them inconspicuous among the mosses and permit them to browse without being easily detected by predators (Byers 1961). *Dolichopeza barnardi*, *D. hirtipennis*, and *D. peringueyi* live in wet moss and liverwort cushions on the sides of waterfalls on Table Mountain, South Africa (Harrison & Barnard 1972). *Dolichopeza* females lay eggs in mosses (Gerson 1982). *Dolichopeza* larvae are bryophagous (Byers 1961).



Figure 102. This crane fly adult is emerging from its pupal case where it has spent the last few months in the moss mat. Photo by Janice Glime.

Lauren Russell (pers. comm.) found species of *Dolichopeza* in the Pacific Northwest, USA, to feed on living tissues of mosses and occasionally on liverworts. Roper (2001) reported *Dolichopeza albipes* (Figure 103) as a bryophage on mosses and liverworts in ghyll woodlands in Sussex, UK.



Figure 103. *Dolichopeza albipes* adult, a species whose larvae are bryophages on both mosses and liverworts. Photo by Janet Graham, through Creative Commons.

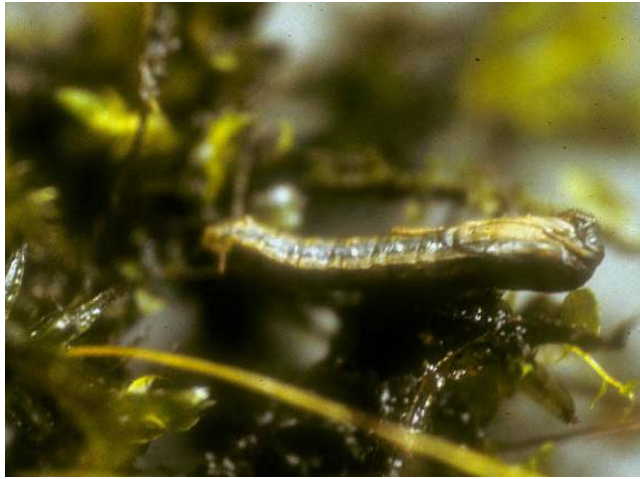


Figure 104. This pupa of a cranefly (**Tipulidae**) can be found among mosses. Photo by Janice Glime.

Dicranomyia

It is not unusual for bryophytes to house rare species. This habitat is time-consuming to sample, and sampling is destructive of the habitat, so the inhabitants are often overlooked. Most members of *Dicranomyia* (Figure 105) are aquatic, but *D. lackschewitzi* lives in seepages where there are sparse mosses in slumping coastal cliffs (Falk 1991). The species is considered extremely rare in Europe (Stubbs 1998).



Figure 105. *Dicranomyia chorea* adult; *D. lackschewitzi* lives in mosses in seepages on coastal cliffs. Photo by James K. Lindsey, with permission.

Dicranomyia goritiensis has a sporadic distribution (Kolcsár *et al.* 2015). It is associated with mosses and algae on rocks around waterfalls and rocky coastlines of Croatia and Greece.

***Nephrotoma* – Tiger Craneflies**

Immature stages of *Nephrotoma* typically occur among mosses, in soil, and in decaying wood (Alexander & McAtee 1921). *Nephrotoma virescens* (Figure 106) larvae live among wet mosses (Johannsen 1969).



Figure 106. *Nephrotoma virescens* adult, a species whose larvae live among wet mosses. Photo by Odin Toness, through Creative Commons.

Summary

Many species of **Diptera** lay their eggs among bryophytes, develop as larvae there, and pupate there. Some eat the mosses. And some eat the associated algae, bacteria, fungi, and microorganisms. And they are often selective in their food choices. Others have looser associations, landing there for moisture regulation or hiding there to avoid predation or escape wind and cold. Bryophyte structure affects colonization, with very compact mosses making tunneling difficult, and very loose structure providing too little protection for some.

The several families that were once **Tipulidae** have numerous species that live among bryophytes both in the water and on land. Some of these (especially *Triogma trisulcata*) are adapted to bryophyte living by being bryophyte mimics. Often members of *Tipula* seem to defy Gause's law, but on closer inspection we find they mate at different times of the day or in different time periods, live in different parts of the moss, or have other needs that separate their niches.

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CHAPTER 12-19

TERRESTRIAL INSECTS:

HOLOMETABOLA – DIPTERA

NEMATOCERA 2

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CHAPTER 12-19

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NEMATOCERA 2



Figure 1. Fungus gnat herbivory on *Buxbaumia aphylla* capsules. Note the topless setae. Photo by Jörg Müller, with permission.

Cecidomyiidae – Gall Midges

Some members of this family that are typical of trees can be found in moss tussocks or among the mosses on tree trunks. These include members of the genus *Peromyia* (Figure 2) (Perkovsky & Fedotova 2004). Mosses are so important to some species as to be the source of the name – including *Bryocrypta dubia*, *Cryptoneurus muscicola*, *Bryomyia bergrothi*, and *Peromyia muscorum*, as well as *Peromyia palustris* (Mamaev & Krivosheina 1993).

Stabaev (in Mamaev & Krivosheina 1993) found that larvae of gall midges comprised an important part of the fauna in primary soils under mosses. But Mamaev and Krivosheina comment that there has been little study of the moss-inhabiting gall midges, promising surprises for those who explore them.



Figure 2. *Peromyia* adult, a genus that sometimes lives among bryophytes on the ground and on tree trunks. Photo by Charley Eiseman, through Creative Commons.

Mycetophilidae – Fungus Gnats

This family primarily feeds on fungi, but a few species eat algae, mosses, and liverworts, while others are **saprophagous** (feeding on or obtaining nourishment from dead or decaying animal matter) in bird nests (Hackman *et al.* 1988; Økland 1994). *Cordyla fusca* (see Figure 3) is significantly correlated with mosses (Økland 1994). On the other hand, *Boletina gripha* (Figure 4) and *Acnernia nitidicollis* have high negative correlations with mosses. The correlation of some members of this family with mosses may relate to a concentration of host fungi in the soil that likewise correlates with the mosses or their habitat.



Figure 3. *Cordyla fissa* adult; the presence of *C. fusca* correlates with mosses in European forests. Photo by Hanna Koivula, through Creative Commons.

Pettet (1967) reported that larvae in the **Mycetophilidae** parasitize the thallose liverwort *Riccia frostii* (Figure 5). The infestation occurred when the Nile floodwaters receded in Sudan. The infestation spread and increased until virtually all thalli were infected and remained so until flooding returned. The infestation then completely disappeared and although Pettet watched for it closely for the next five years, it never returned. The larvae eat the internal tissues of the thalli, causing the thallus to become non-turgid and flabby. In the last stages of the infestation, the liverwort surface disintegrates. Each rosette revealed 5-25 small, yellow-orange larvae. Pupation likewise occurred inside the thallus. Such interactions can easily go unnoticed and close observation may reveal other interesting bryological habitats for insects.



Figure 4. *Boletina gripha* adult, a species that is negatively correlated with mosses. Photo by Hanna Koivula, through Creative Commons.



Figure 5. *Riccia frostii*, a species that is parasitized by **Mycetophilidae**. Photo by Rosemary Taylor, with permission.

Müller (2012) found several adult fungus gnats (Figure 1, Figure 6) feeding on spores in capsules of *Buxbaumia aphylla* (Figure 7) in Germany. It is likely that at least some of the spores escape being eaten and are transported by the fungus gnats, later being deposited elsewhere.



Figure 6. Fungus gnat herbivory on capsules of *Buxbaumia aphylla*. Photo courtesy of Jörg Müller.



Figure 7. *Buxbaumia aphylla* with fly. Photo courtesy of Sabovljevic.

Sciaridae – Dark-winged Fungus Gnats

Fungus gnats (Sciaridae) deposit eggs in organic matter, including mosses (Hurley 2006). When such habitats are present in greenhouses, the fungus gnats become pests. Shin *et al.* (2012) reported that these gnats inhabit peat bogs, thus making this a source of the gnats in nurseries and greenhouses. Peck and Moldenke (2010) are concerned with invertebrate invasions through commercial uses of mosses. Among those invertebrates, they found a few adult sciarid flies.

Ponge (1991) found that some of the **Sciaridae** larvae on the Scots pine (*Pinus sylvestris*) forest floor consumed mosses, but they also consumed fungi. But not all interactions of this family with bryophytes are so casual. Sawangproh (2014) notified me of finding the larvae of a black-winged fungus gnat, *Scatopsciara cunicularius* (Figure 8-Figure 14), feeding and tunnelling on a liverwort thallus, *Marchantia polymorpha* (Figure 8-Figure 10), in the greenhouse. The feeding causes serious damage to both growth and survival of the liverwort. The gnat population expands when the ambient temperature increases in early spring. When it is cool (12°C), the larvae take longer to develop and consequently do more damage to the thalli than when reared at 22°C (Sawangproh & Cronberg 2016; Sawangproh *et al.* 2016). Following the larval damage, the thalli are more susceptible to secondary attacks by other pests and fungal infections.

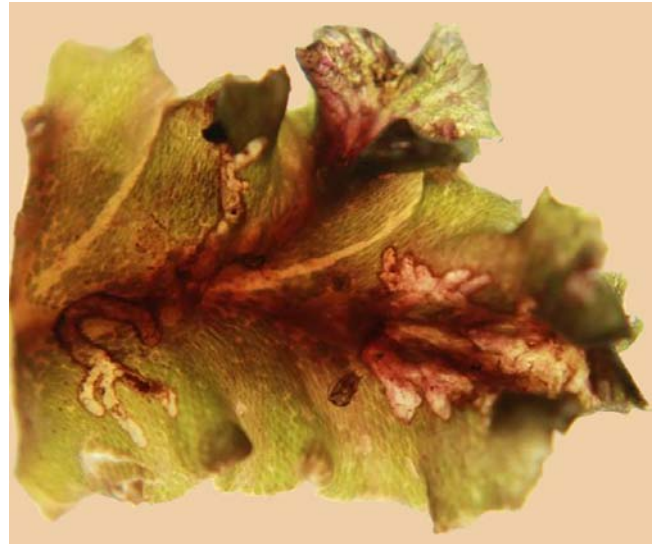


Figure 8. *Scatopsciara cunicularius* damage to *Marchantia polymorpha* by two third-instar larvae at 22°C in culture. Photo courtesy of Weerachon Sawangproh.



Figure 9. *Scatopsciara cunicularius* damage to *Marchantia polymorpha* by a group of larvae at day 2 after hatching. Photo courtesy of Weerachon Sawangproh.

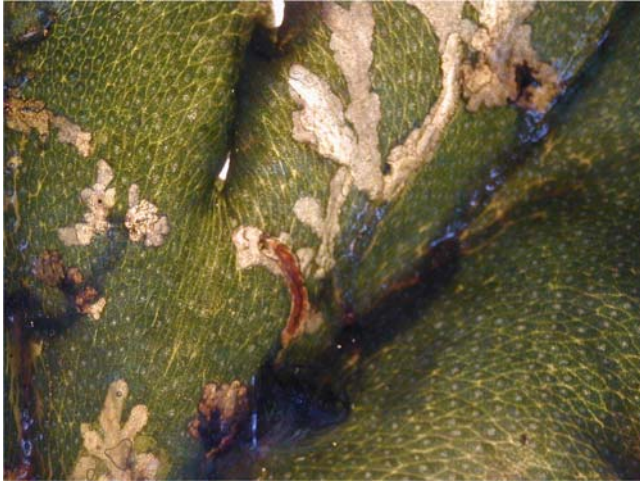


Figure 10. *Scatopsciara cunicularius* larva on one of the wounded patches of *Marchantia polymorpha*. Photo courtesy of Nils Cronberg.



Figure 11. *Scatopsciara cunicularius* larva from *Marchantia polymorpha*. Photo courtesy of Weerachon Sawangproh.



Figure 12. *Scatopsciara cunicularius* mature pupal stage on a liverwort thallus. Photo by Weerachon Sawangproh.



Figure 13. *Scatopsciara cunicularius* pupa from *Marchantia polymorpha*. Photo courtesy of Weerachon Sawangproh.

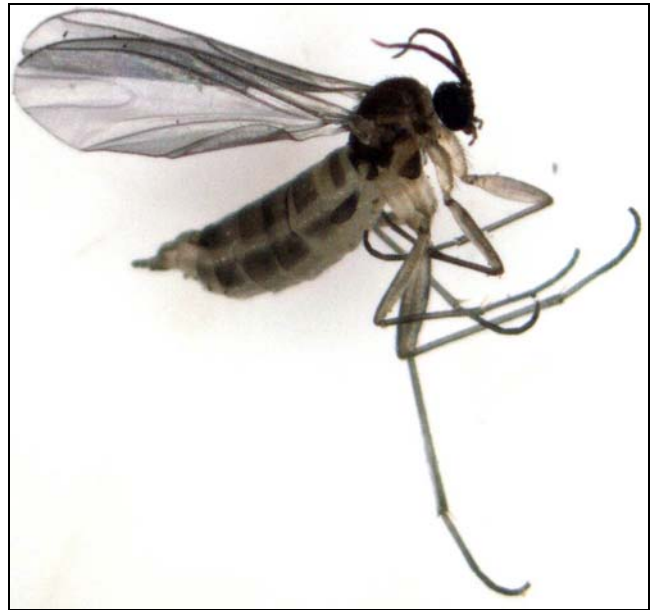


Figure 14. *Scatopsciara cunicularius* female adult. Photo courtesy of Weerachon Sawangproh.

It does not appear that these bryophagous fungus gnats need fungi. *Scatopsciara cunicularius* (Figure 8-Figure 14) can complete its entire life cycle with only liverworts as food (Sawangproh & Cronberg 2016; Sawangproh *et al.* 2016). This is an unusual relationship because few insects are known to eat liverworts. Sawangproh and coworkers (2016) suggested that the liverwort oil bodies with their essential oils may serve as a deterrent to herbivory. We still have little understanding of the mechanisms that permit some insects to eat the bryophytes, especially those with antiherbivore compounds, whereas most insects seem unable to. Just imagine what the world might be like with no insects. Bryophytes would most likely be far more speciose, whereas the insects may have eliminated those that did not develop antiherbivore compounds early in their evolution.

Bradysia sp. (Figure 15-Figure 16) larvae (Figure 15) can be found under several species of *Bryum* [*B. argenteum* (Figure 17), *B. dichotomum* (Figure 18), and *B. pachythea* (Figure 19)], at least in flower pots (Downing & Selkirk 1996). Downing and Selkirk observed that the mosses had a rough, patchy appearance, "like they had been ploughed." These larvae eat the moss rhizoids. My surprise was that after drenching the pots with a solution of 2 g Alsystriin in 10 L water the bryophytes grew back in two weeks!



Figure 15. *Bradysia* sp. larvae, *Bryum* inhabitants. Photo by David Cappaert, through Creative Commons.



Figure 16. *Bradysia praecox*; some members of this genus live among the moss *Bryum* as larvae. Photo by James K. Lindsey, with permission.



Figure 17. *Bryum argenteum*, a species where *Bradysia* sp. larvae hide under the clump. Photo by Janice Glime.

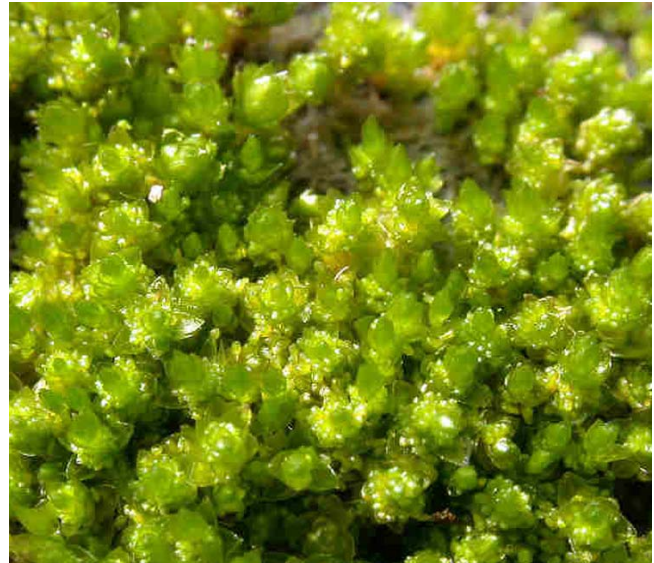


Figure 18. *Bryum dichotomum* with gemmae, home for some species of *Bradysia*. Photo by David T. Holyoak, with permission.



Figure 19. *Bryum pachythea* with capsules, cover for some *Bradysia* species. Photo by David Tng, with permission.

Ceratopogonidae – Biting Midges

One might not expect chocolate to be involved in this chapter, but certain members of the **Ceratopogonidae** (Figure 20) are associated with cacao (chocolate) flowers as important pollinators (Winder 1977). On the same trees, among the epiphytic mosses, one can find *Atrichopogon* (Figure 21-Figure 22), *Stilobezzia* (Figure 23), and *Dasyhelea* (Figure 24-Figure 26), all members of **Ceratopogonidae**.

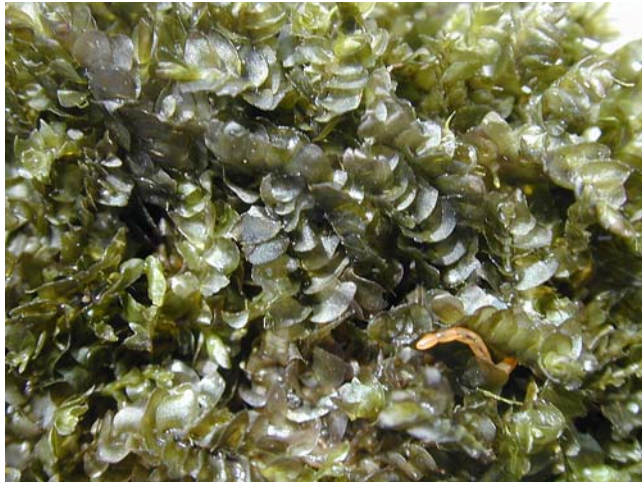


Figure 20. *Jungermannia exertifolia* ssp. *cordifolia* with **Diptera** larva (*Ceratopogonidae*?). Photo by Michael Lüth, with permission.



Figure 21. *Atripogon* larva, a dweller among epiphytic mosses. Photo from Waterbugkey, through EPA public domain.



Figure 22. *Atripogon* female adult, a species associated with epiphytic bryophytes. Photo by Tom Murray, through Creative Commons.



Figure 23. *Stilobezzia* female adult, a genus known from epiphytic mosses. Photo by Tom Murray, through Creative Commons.



Figure 24. *Dasyhelea flavifrons* larva weaving its way under the bark. Photo by Walter Pfliegler, with permission.



Figure 25. *Dasyhelea flavifrons* larvae; for some members of the genus this stage is spent in bryophytes on trees. Photo by Walter Pfliegler, with permission.



Figure 26. *Dasyhelea* male adult, a genus that can be found among bryophytes on trees. Photo by Christophe Quintin, through Creative Commons.

Many of the **Ceratopogonidae** have aquatic larvae, so it is natural that the adults hang out in moist conditions, near the water sources where they can lay eggs. Hence, some will naturally land on mosses to rest or obtain moisture (Figure 27).



Figure 27. **Ceratopogonidae** male on moss. Photo by Christophe Quintin, through Creative Commons.

Kolenohoelea calcarata occurs among mosses in springs, and *Serromyia femorata* (Figure 28) occurs among damp mosses (Strenzke 1950). But *Culicoides impunctatus* (Figure 29) (biting midge) larvae at one site in western Scotland actually avoided most mosses (Blackwell *et al.* 1999). Their distribution and larval counts had a significantly negative correlation with all mosses other than species of *Sphagnum*. This species increases its number of eggs when provided with *Sphagnum* egg-laying sites (Carpenter *et al.* 2001). Members of the genus *Forcipomyia* (Figure 30), another biting midge, also builds nests in *Sphagnum* (Oldroyd 1964).



Figure 28. *Serromyia femorata* female, a species associated with damp mosses. Photo by James K. Lindsey, with permission.



Figure 29. *Culicoides impunctatus* adult, a species that avoids mosses, except *Sphagnum*. Photo by Orikrin, through Creative Commons.



Figure 30. *Forcipomyia bipunctata* adult, member of a genus that builds nests in *Sphagnum*. Photo by James K. Lindsey, with permission.

Chironomidae – Midges

Bettis (2008) compared the abundance of invertebrate fauna in two different *Grimmia* (Figure 31) morphotypes, one on exposed granitic outcropping and one at a protected seasonal riparian habitat. In both cases, **Chironomidae** larvae were among the major invertebrates present. Some of the **Chironomidae** can emerge from mosses in large numbers (Figure 32), especially in polar regions, and adults cover mosses as they emerge (Figure 33) (pers. obs.).



Figure 31. *Grimmia laevigata* on boulder, potential home for **Chironomidae**. Photo by Alan Cressler, with permission.



Figure 33. **Chironomidae** adults on moss at Helfdi, Myvatn, Iceland. Photo by Janice Glime.

Although **Chironomidae** are abundant aquatic larvae, they also occur on land. The *Cricotopus* (Figure 34-Figure 35) larva occurs with **epilithic** (growing on rocks) and **epiphytic** (growing on plants, usually trees) liverworts in western Oregon and Washington, USA, and feeds on the leafy liverworts *Calypogeia* (Figure 36), *Gyrothyra underwoodiana* (Figure 37), *Jungermannia rubra* (Figure 38), *Porella navicularis* (Figure 39), and *Scapania bolanderi* (Figure 40) in the lab (Russell 1979). In the field they do considerable feeding damage to *Calypogeia fissa* (Figure 36) and *Jungermannia rubra*.



Figure 32. **Chironomidae** swarming in moss garden, a typical scene in summer. Photo by J. Paul Moore, with permission.



Figure 34. *Cricotopus annulator* complex larva, member of a genus that occurs among liverworts on boulders and trees. Photo © Stroud Water Research Center, through Creative Commons.



Figure 35. *Cricotopus* adult, a genus whose larvae occur among liverworts on trees and boulders. Photo by G Drange, through Creative Commons.



Figure 38. *Jungermannia rubra* with perianth. This species provides home and food for *Cricotopus* larvae among epiphytes. Photo by Ken-ichi Ueda, through Creative Commons.



Figure 36. *Calypogeia fissa*, home and food for larvae of *Cricotopus*. Photo by David T. Holyoak, with permission.



Figure 39. Branch with *Porella navicularis*, home and food for larvae of *Cricotopus*. Photo by Tanya Yoder, through Creative Commons.

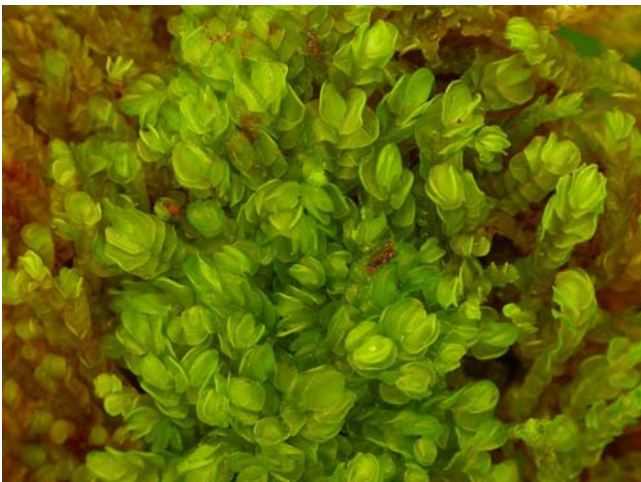


Figure 37. *Gyrothyra underwoodiana*, home and food for *Cricotopus* larvae. Photo by Li Zhang, with permission.



Figure 40. *Scapania bolanderi* with capsules, a species that is home and food for *Cricotopus* larvae. Photo by Chris Wagner, with permission.

The **Chironomidae** may do an important service to some mosses. Harvey-Gibson and Miller-Brown (1927) reported that these midges, as adults, seem to be agents of fertilization for *Polytrichum commune* (Figure 41-Figure 42). In this species, the **paraphyses** (Figure 43) associated with both antheridia and archegonia exude mucilage (but no sugar). Small midges were among the continuous visitors to these gametangial areas. The insects lap the mucilage and get it on their body parts. If they visit at the right time, sperm may become attached as well and the midges that subsequently visit females may transfer live sperm to the appropriate location.



Figure 41. Field of *Polytrichum commune* with capsules, indicating successful fertilization. Photo by Michael Lüth, with permission.



Figure 42. *Polytrichum commune* with male splash cups that attract adult **Chironomidae** that carry sperm to the female plants that are mixed with them. Photo by Li Zhang, with permission.

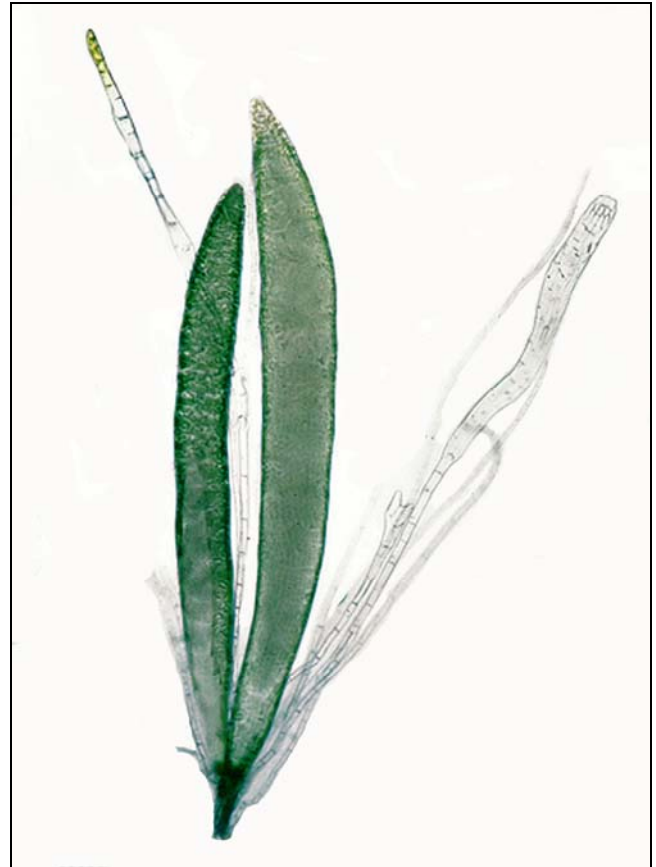


Figure 43. *Polytrichum* showing two antheridia with adjacent paraphyses. Photo by George J. Shepherd, through Creative Commons.

Moss-dwelling **Chironomidae** are abundant in and around springs. Lencioni *et al.* (2011) studied **Chironomidae** distribution in 81 springs in the Italian PreAlps and Alps. In 173 samples they found 26,871 **Chironomidae** representing all life stages except eggs. To illustrate the abundance of moss-dwelling **Chironomidae**, Nolte (1991) sampled and compared mosses that were intermittently out of the water on semi-submersed mosses near a spring with those in permanently submersed locations 700 m downstream. All of these larvae were small, and 98% were less than 5 mm in length. The total sampling revealed 65 species of chironomids in 26 genera, with greater species richness near the source in the semi-submersed mosses. But the mean abundance was 5X higher in the permanently submersed mosses compared to those that were semi-submersed at the spring. On the other hand, the maximum abundance anywhere was 830 larvae per 10 cm² in one semi-submersed sample. The dominance of the various chironomid taxa was dependent primarily on the location of the moss along the stream.

Ponge (1991) examined gut contents of forest floor animals in a 5x5 cm Scots pine litter. The subsequent feces were followed to determine the ultimate fate of the ingested material. Some of the fecal material included bryophytes and was the primary material in feces of both enchytraeid and lumbricid worms. In turn, the chironomid larvae consumed and digested the fecal material.

Chironomidae may play an important role in initial stages of both primary and secondary succession. These species specialize on open patches created by these

successional conditions and live in the early stage that is fallow, having mosses and lichens as pioneers (Frouz & Kindlmann 2001). The habitat generally has good quality food, but it is prone to severe desiccation in the summer that can decimate the larval population. In the Czech Republic and elsewhere, winter conditions permit the populations to replenish. The larvae are poor dispersers, but winged adults have the opportunity to move about. To explore the ability of these species to survive in this hostile environment, Frouz and Kindlmann studied *Smittia aterrima* (Figure 44), an abundant species in old fields. They found that eggs laid by the females from adjoining more developed vegetation were sufficient to replenish the lost populations.



Figure 44. *Smittia aterrima* adult, a species that includes mosses in its diet. Photo by James K. Lindsey, with permission.

Smittia aterrima (Figure 44) is common in disturbed areas, with up to 12,000 individuals per m² (Delettre & Lagerlöf 1992). These larvae live in the surface soil horizon and feed on plant litter, fungi, soil algae, and mosses (Frouz & Lukešová 1995). In České Budějovice, Frouz and Kindlmann (2001) tested the **source-sink hypothesis** [idea that organisms move from a favorable habitat (source), often as a result of overcrowding, to a sink that is less favorable, where they remain and accumulate] with this species and demonstrated that as their preferred open habitat became unsuitable, the larval population disappeared there. Ducrotoy (1980) and Delettre (1986) had observed the same phenomenon for terrestrial chironomids living among mosses on rocks, again as a result of drought. The larvae continue to exist in sub-optimal habitats during the drought and re-colonize the preferred habitats (including mosses) when favorable conditions return (Frouz & Kindlmann 2001). This migration maintains the source-sink survival strategy.

Other **Chironomidae** species have similar abundance patterns in these pioneer habitats. *Bryophaenocladus* cf. *illimbatus* (Figure 45) is a **parthenogenic** (having unfertilized eggs that develop into new individuals) moss dweller that lives in habitats with open and low vegetation (Frouz 1997). Both *Bryophaenocladus* cf. *illimbatus* and *Smittia aterrima* (Figure 44) decreased from the first to third year of the study as the field became less open and forbs taller than 20 cm became more prominent. Soil algae and mosses form an important component of food for both species (Frouz & Lukešová 1995).



Figure 45. *Bryophaenocladus illimbatus* adult, a species of mosses in sites with low, open vegetation. Photo by Marko Mutanen, through Creative Commons.

Sometimes one can find exciting new species by knowing the general habits of the genus. The snow-dwelling adults of *Bryophaenocladus thaleri* were discovered in barren areas of Dolomite Alps in Italy above 3100 m altitude. This species probably mates in **leks** (assembly areas where males gather during mating season to exhibit competing mating displays and attract females) on the ground because their males cannot fly (Willassen 1996). But the immature (larval) stages are so far unknown. Willassen suggests that we look for them among terrestrial mosses because that is a preferred habitat of other members of the genus. *Bryophaenocladus virgo* lives among mosses as larvae and adults and solves the flight problem by being **parthenogenetic** (giving birth without fertilization) (Cranston 1987). *Bryophaenocladus vernalis* (Figure 46) has been caught in the act of damaging rare mosses growing in chalk quarries in southern England.



Figure 46. *Bryophaenocladus* cf. *vernalis* adult male, a species that damages rare mosses in chalk quarries in England. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Limnophyes minimus (Figure 47-Figure 49) is likewise a pioneer that lives in the shallow soil that is formed by the mosses, lichens, and raw humus (Delettre 1986). On rocks, mosses trap dust and soon accumulate a thin soil on rock surfaces. This provides suitable habitat for *Limnophyes minimus* in Brittany, France. This species also occurs in the sub-Antarctic where the adult females are parthenogenic (Hänel & Chown 1998). And these females do not feed. As larvae, this species joins *Pringleophaga marioni* (Lepidoptera, Tineidae; Figure 50) in their contribution to nutrient recycling on sub-Antarctic Marion Island.

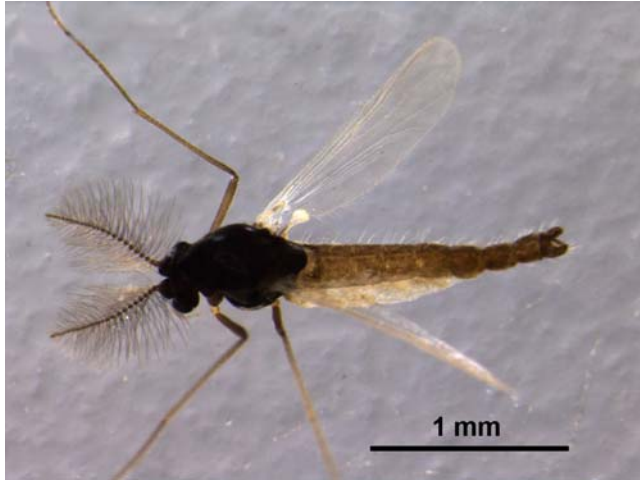


Figure 47. *Limnophyes minimus*, a pioneer species in mosses on newly colonized areas. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.



Figure 48. *Limnophyes minimus*, a pioneer among mosses. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.



Figure 49. *Limnophyes minimus* adult, a pioneer species among mosses in early succession stages. Photo by James K. Lindsey, with permission.



Figure 50. *Pringleophaga marioni* adult, a lepidopteran moss-dwelling contributor to nutrient cycling on Marion Island in the sub-Antarctic. Photo by Steven L. Chown, with permission.

The females of *Eretmoptera murphyi* (Figure 51) from the Antarctic and sub-Antarctic are **brachypterous** (short-winged), making dispersal difficult. Not only is the female apparently parthenogenic, but males are unknown (Cranston 1985). This species has terrestrial larvae that live among damp mosses and peat.



Figure 51. *Eretmoptera murphyi* on a leafy liverwort, Prince Olav Harbour, South Georgia. Photo courtesy of Roger S. Key.

As already seen in the aquatic midges, living among mosses could present a danger from parasitic mites (Stur *et al.* 2005). But when those mosses are semi-terrestrial, the **Chironomidae** become unavailable to those aquatic parasitic mites.

Belgica

One of the best known of the moss-dwelling **Chironomidae** is *Belgica antarctica* (Figure 52-Figure 54). These larvae are abundant in damp mosses, grass roots, detritus, and around penguin rookeries and seabird nests in the Antarctic (Wirth & Gressitt 1967; Cranston 1985). The species overwinters as larvae (Strong 1967); all four larval instars overwinter (Benoit *et al.* 2007). Some also occur in meltwater pools and small ponds with algae.

Belgica antarctica (Figure 52-Figure 54) is the largest arthropod in Antarctica and is wingless (Gressitt 1967). The females lay their eggs in a gelatinous mass in damp mosses and the larvae disperse among the mosses about 10 days later. The mosses most likely make survival of this larger animal possible by providing a warmer refuge than the ambient temperature. Gressitt showed that temperatures in *Polytrichum* (Figure 41-Figure 42) there exceed that of the air by as much as 13°C. The temperatures in *Drepanocladus* (probably *Sanionia uncinata* – Figure 55) were closer to those of the air.



Figure 52. *Belgica antarctica* eggs among mosses in Antarctica. Photo by Rick Lee, through Creative Commons.



Figure 53. *Belgica antarctica* larvae in Antarctica, a species that often lives among mosses. Photo by Rick Lee, through Creative Commons.



Figure 54. *Belgica antarctica* mating in Antarctica. Photo by Rick Lee, through Creative Commons.



Figure 55. *Sanionia uncinata*, potential home for *Belgica antarctica*, but temperatures in this moss differ little from that of the air. Photo by Franz Xaver, through Creative Commons.

Temperature is not the only factor limiting the distribution of *Belgica antarctica* (Figure 52-Figure 54). Hayward *et al.* (2007) considered moisture to be as important as cold resistance in these polar invertebrates. With temperatures most of the year below 0°C, water is hence inaccessible for a long period of time. Hayward and coworkers found that when the larvae were desiccated at a high relative humidity (98.2%) they were more tolerant of desiccation and also exhibited increased freezing tolerance to -10 and -15°C. Nevertheless, all larvae were frozen at -10°C. Slow drying was important for this acclimation. The researchers found that osmolality increased, reaching its highest levels after five days at 98.2% RH, but that these values returned to predesiccation values with just one hour of rehydration, well before water content returned to predesiccation levels. They found no evidence of heat-shock proteins contributing to desiccation tolerance. Membrane phospholipid adaptation and metabolite synthesis appeared to be the important physiological mechanisms that enhanced both cold tolerance and desiccation tolerance, a conclusion also supported by Lee *et al.* (2006). I would consider it likely that the mosses are important in ensuring a high initial humidity and a slow rate of desiccation, permitting the larvae to acclimate.

Teets *et al.* (2011) examined the effects of repeated cold exposure on survival, energy content, and stress protein expression of the larvae of *Belgica antarctica* (Figure 53). Most of the larvae (>95%) survived a single 12-hour stint of -5°C when frozen in both the presence of

water and in a dry environment. However, after five cycles of repeated cold exposure to -5°C , survival of frozen larvae dropped to below 70%. On the other hand, survival of controls and supercooled (dry) larvae remained unchanged. Freezing during these repeated cold exposures resulted in a drastic reduction in energy reserves. After five of these cold exposures, the larvae had 25% less lipid, 30% less glycogen, and nearly 40% less trehalose than supercooled larvae. There were further indications of protein damage in this frozen group. There seemed to be no difference in larvae frozen for 60 continuous hours and those that had a total of 60 hours accumulated from repeated cold exposure. Teets and coworkers concluded that both survival and energy conservation benefitted from a dry microhabitat that remained unfrozen during repeated cold exposures. Do bryophytes provide such an environment, or must the larvae migrate into the soil to survive?

The larvae of *Belgica antarctica* (Figure 53) spend most of the year (7-8 months) encased in ice with soil (Elnitsky *et al.* 2008; Lopez *et al.* 2009), creating desiccating conditions. Elnitsky *et al.* (2008) explored the possibility that they use cryoprotection to survive. They found that after 14 days of subzero exposure in the lab the larval survival remained above 95%. They interpreted this as an indication that the larvae underwent cryoprotective dehydration. But they also considered that in their natural environment **cryoprotection** (low-temperature protection) may be constrained by **inoculative freezing** (process in which organisms actually freeze) because of the close contact of the larvae with environmental ice. Their ability to undergo cryoprotective dehydration during slow cooling within frozen soil is dependent on the soil moisture. The percentage of larvae that were able to resist inoculative freezing increased as the soil moisture decreased. The researchers suggest that the larvae are likely to undergo cryoprotection under the right conditions.

Lee and coworkers (2006) demonstrated that rapid **cold-hardening** (physiological or anatomical preparation for cold) increases freezing tolerance in *Belgica antarctica* (Figure 53). Larvae that were summer acclimated had less cold tolerance at -10°C for 24 hours than those that were cold-acclimated. Cold-acclimated larvae had higher supercooling points than summer larvae. But when summer-acclimated larvae were maintained at 4°C , then transferred to -5°C for 1 hour prior to exposures to -10 , -15 or -20°C , rapid cold hardening occurred; rapid cold hardening significantly increased larval freeze tolerance to both -15 and -20°C . Adults, which typically live for only a week, did not respond to rapid cold hardening. Living among mosses can protect the larvae from sudden changes in temperature, permitting them to acclimate.

But even during the summer the larvae are subject to summer storms, osmotic stress from salt spray, and desiccation due to wind and sunlight (Lopez-Martinez *et al.* 2009). In contrast to Hayward *et al.* (2007), Lopez-Martinez and coworkers found that the genes that were the most responsive to hydration changes were the ones encoding heat-shock proteins, as well as those for antioxidants, detoxifications, and those involved in altering cell membranes. Fast dehydration elicited both the

highest expression and the greater number of genes expressed. As the larvae were rehydrated, most of the same genes were once again expressed. Fatty acid desaturase was the only gene upregulated during rehydration.

Strong (1967) considers the living mosses to serve only as shelter for *Belgica antarctica* (Figure 52-Figure 54), providing little nourishment. Instead, detritus, algae, lichens, and fungal hyphae are the primary food sources. Other researchers include mosses as part of the diet during the two-year life cycle (Sugg *et al.* 1983; Convey & Block 1996). But there is no comprehensive food study to indicate the diet throughout the life cycle and seasonal changes. The larvae demonstrate cryoprotectants, including erythritol, glucose, sucrose, and trehalose, but adults are freezing-susceptible and lack adequate quantities of these cryoprotectants (Baust & Edwards 1979). Maintenance on artificial diets indicate that cryoprotectant complexes are dependent on food source and temperature. We have seen how gene expression changes as freezing occurs. Could it be that these new compounds are supported by a change in diet to one that includes more bryophytes?

Leaf Miners

Most of us have seen the evidence of leafmining activity on deciduous leaves or herbaceous plants. But have you ever seen it on liverwort thalli? It is a world needing exploration.

Eisman *et al.* (2023) have just described the behavior of *Paraphaenocladus exagitans* in the thalli of *Marchantia polymorpha* (Figure 56). They discovered that unlike the miner *Metriocnemus*, which scatters its frass throughout its mines, the mines of *P. exagitans* are clean; the frass instead accumulates around the rim of the entry hole. These larvae were first noticed in Iowa in mid-October. On 23 November, the first adult emerged from an oblong, dark brown cocoon made of frass and located on the thallus of the liverwort. The larva had apparently fed on the surface of the thallus. However, two larvae were seen mining the fresh thallus in late December.

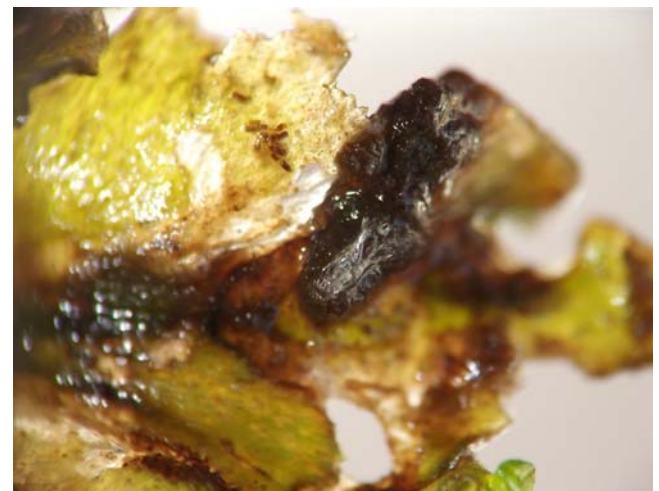


Figure 56. *Paraphaenocladus exagitans* pupa on a *Marchantia polymorpha* thallus. Photo courtesy of John van der Linden.

In a different collection, Eisman *et al.* (2023) found larvae of *Paraphaenocladus exagitans exagitans* and adults of *Boreochlus persimilis* in association with *Marchantia polymorpha* in Oregon, this time in late April. However, the authors were unable to determine what the midges were feeding on.

Culicidae – Mosquitoes

Gert Mogensen told an interesting mosquito story on Bryonet (13 March 2011). Arctic mosquitoes (Figure 57) struggle with low moisture on sunny days. They compensate for this dry atmosphere by spending much time on mosses, keeping in the shadows when possible. They are able to shelter on the undersides of leaves of shrubs (Figure 57), but there they are subject to spider predation. These spiders, in turn, are food for the group of birds called waders (Figure 58). The chicks of these waders benefit from the dwarfed nature of the shrubs. The females migrate south again once the eggs are laid and the males remain behind to care for the young!



Figure 57. Mosquito adult, member of a family (Culicidae) that struggles with low moisture in the Arctic. Photo by Brad Smith, through Creative Commons.



Figure 58. The Common Gallinule (*Gallinula galeata*), a wading bird that is part of the food chain of moss inhabitants (Culicidae→spiders→wading birds). Photo by Jim Rathert, USFWS, through public domain.

Simuliidae – Blackflies

I have discussed this family in the chapter on aquatic insects. But when I began researching the terrestrial Diptera, I was quite surprised to find that not all Simuliidae begin life in the water. *Prosimulium hirtipes* (see Figure 59-Figure 61), *P. tomosvaryi*, and *P. subrufipes* all oviposit on moist terrestrial mosses, usually about 20 cm above streams (Zwick & Zwick 1990). This is no small contribution as they lay up to 20,000 eggs per cm². The eggs form a dense crust on mosses with small leaves, especially *Brachythecium rivulare* (Figure 62). These eggs are dependent on moisture and cannot survive complete desiccation.



Figure 59. *Prosimulium hirtipes* larva, a species that begins life on land among mosses at streamside. Photo by Janice Glime.



Figure 60. *Prosimulium arvum* adult, member of a genus in which some members lay their eggs among streamside mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 61. *Prosimulium* female adult, member of a genus in which some members lay their eggs among streamside mosses. Photo by Tom Murray, through Creative Commons.



Figure 62. *Brachythecium rivulare*, a site for egg-laying by *Prosimulium hirtipes*, *P. tomosvaryi*, and *P. subrufipes*. Photo by Norbert Stapper, with permission.

Two Japanese blackfly species, *Simulium japonicum* and *S. rufibasis* (see Figure 63-Figure 66), lay their eggs in bryophytes (Baba & Takaoka 1989). These do not make large masses and lay their eggs singly on bryophytes on water-splashed rocks. Later, Baba and Takaoka (1991) discovered that *Prosimulium kiotoense* likewise oviposited on land, using mosses on riverbank rocks as their oviposition sites. They likewise laid eggs singly, but the females deposited many eggs in small areas, often forming large, irregular egg masses. These wet oviposition sites had dense bryophyte cover and were 0-15 cm above water level. If you want to watch, the event occurs mostly between 12:00 and 14:00 hours in the latter part of April on Kyushu Island, Japan.



Figure 63. *Simuliidae* larvae, a stage that is spent in fast water. Photo by Sarah Gregg, through Creative Commons.



Figure 64. *Simulium heiroglyphicum* pupa, an aquatic stage that is often on mosses. Photo by Luis Hernandez Triana, through Creative Commons.

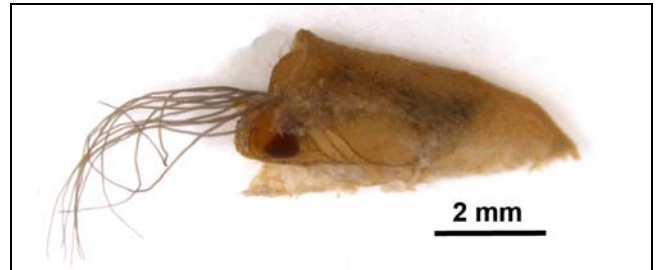


Figure 65. *Simulium* nr. *metallicum* pupa, a stage that is spent in fast water, often on bryophytes. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 66. *Simulium equinum* adult, member of a genus in which some species oviposit on land among mosses. Photo by Ladislav Tábi, with permission.

Psychodidae – Drain Flies, Sink Flies, Moth Flies, or Sewer Gnats

This family includes species with aquatic larvae, so it is not surprising that terrestrial species are often associated with bryophytes in locations where they can maintain high moisture. Roper (2001) reports several of these species in the ghyll woodlands (linear valley features cut into the sandy beds of the Weald of south-eastern England where temperatures are buffered and moisture levels are high; they have a rich flora of bryophytes). In Sussex, England, the very ornate *Sycorax* species occur among mosses near springs and "trickles" (Roper 2001).

Sycorax silacea larvae are wormlike and live on wet stones or mosses near cascades, springs, trickles (Andersen 1992), on mosses in the neighborhood of streams (Omolkova & Ježek 2012), and on mosses on half-submerged tree branches (Kroča & Ježek 2015), making them semiaquatic. Their decorations are quite ornate, permitting them to blend well among the mosses (Roper 2001).

Like *Sycorax silacea*, many of the **Psychodidae** are semi-aquatic. *Peripsychoda fusca* lives in wet mosses and leaf litter piles in Europe (Kroča & Ježek 2015). Another European psychodid, *Feuerborniella obscura*, lives among wet moss cushions, springs, and small streams. *Parabazarella subneglecta* (Figure 67) similarly prefers wet moss cushions, springs, and streams. *Pneumia stammeri* (Figure 68) lives among mosses in wetlands. Larvae of *Bazarella neglecta* occur among mosses around mill races and waterfalls (Roper 2001). This species has been reared successfully on the moss *Platyhypnidium riparioides* (Figure 69-Figure 70), a moss that typically occurs around the water-air interface where it is almost constantly wet or submerged. *Parajungiella longicornis* is a widespread and common species in Europe and western Siberia (Omolkova & Ježek 2012; Kroča & Ježek 2015). This species lives in both shaded and unshaded habitats in moss cushions on banks of streams, as well as ponds and forest seepages.



Figure 67. *Parabazarella subneglecta* adult, a species whose larvae prefer wet moss cushions and mosses of springs and streams. Photo from Bergen Museum, through Creative Commons.



Figure 68. *Pneumia stammeri* adult, a species that lives among mosses in wetlands. Photo by Aina Maerk Aspaas, NTNU University Museum, through Creative Commons.



Figure 69. *Platyhypnidium riparioides*, showing its partly submersed and partly emergent location. Photo by Hermann Schachner, through Creative Commons.



Figure 70. *Platyhypnidium riparioides*, home and food for *Bazarella neglecta*. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Pericoma larvae (Figure 71-Figure 72) and pupae both live in damp locations along streams in the UK, frequently

among mosses (Satchell 1949). Suitable habitats can often support several species within a few meters. *Pericoma* species, including *P. nubila* (Figure 73-Figure 74), *P. fuliginosa* (Figure 75), and *Tonnoiriella pulchra* (syn.=*P. pulchra*) emerge in ghyll woodlands from rotting vegetation and mosses along streambanks (Roper 2001). *Pericoma blandula* (Figure 76) and *P. fallax* are both widespread species in Europe and parts of Asia, living among mosses in both shaded and unshaded locations (Omelkova & Jezek 2012; Kroča & Ježek 2015). The latter species is mostly aquatic, but also occurs in swampy meadows and bottomlands. *Pericoma blandula* is more common among mosses on riverbanks and the banks of springs (Duckhouse 1962).



Figure 71. *Pericoma* larva, a stage that often lives among bryophytes in damp places and along stream margins. Photo from <www.shl.uiowa.edu>, through public domain.



Figure 72. *Pericoma* larva, a stage that often lives among bryophytes in damp places and along stream margins. Photo from <www.dfg.ca.gov>, through public domain.



Figure 73. *Pericoma nubila* adult, a terrestrial stage often closely associated with aquatic habitats and mosses. Photo by Malcolm Storey, through Creative Commons.



Figure 74. *Pericoma nubila* adult, a stage often closely associated with aquatic habitats and mosses. Photo by Malcolm Storey, through Creative Commons.



Figure 75. *Pericoma fuliginosa* adult, a species that pupates in rotting vegetation and mosses on streambanks. Photo by James K. Lindsey, with permission.



Figure 76. *Pericoma blandula* adult, a species whose larvae live among mosses in both shaded and unshaded situations. Photo ©Nick Upton <www.diptera.info>, with permission.

For *Psychoda cinerea* (Figure 77) larvae, moisture is important, accounting for their habitat in mud and among mosses (Ježek 1990). *Paramormia ustulata* is more ubiquitous, living in a variety of habitats in both fresh and salt water, but it also includes mosses and moist soil (Vaillant 1971).



Figure 77. *Psychoda cinerea* adult. Larvae of this species live in mud and among mosses. Photo by Luis Miguel Bugallo Sanchez, through Creative Commons.

In some cases we don't know why the flies visit the mosses. Martin Cooper found a species of *Philosepedon* (Figure 78) resting on the capsules of a moss, but perhaps it was just a convenient resting place, serving no other purpose. Its larvae are known from dead snails (Corbet 2006)! It is clear that we need more behavioral studies on these flies and their interactions with bryophytes.



Figure 78. *Philosepedon*, probably *P. humeralis* adult, on moss capsule. Photo by Martin Cooper, through Creative Commons.

Anisopodidae (=Rhyphidae) – Wood Gnats

I was introduced to the larvae (Figure 79) of this family when I found a larva feeding on mosses on a wet ledge. The larva was green and blended well with the bright green mosses. I watched for a time and found that mosses went in the mouth covered with detritus and came out the other end clean. It appeared the the larva was unable to digest the moss leaves it consumed.



Figure 79. *Anisopodidae* larva; some larvae in this family eat wet mosses, apparently to obtain the detritus and associated organisms on the moss surface. Photo by Walter Pfliegler, with permission.

Summary

Some adult members of fungus gnats (*Mycetophilidae*) feed on spores in the capsules of *Buxbaumia aphylla*. Others, as larvae, develop within the thalli of liverworts, also completing pupation there. The dark-winged fungus gnats (*Sciaridae*) tunnel in liverwort thalli.

The midge (*Chironomidae*) adults include some members that are attracted to exudates from antheridia and archegonia of mosses, accomplishing the transfer of sperm to the eggs. And even the blackflies (*Simuliidae*) have some members that begin their lives among mosses on land. The moth flies (*Psychodidae*) live among bryophytes as larvae in both aquatic and terrestrial habitats. The biting midges (*Ceratopogonidae*) live in moist places and are common on mosses. Few mosquitoes (*Culicidae*) or gall midges (*Cecidomyiidae*) are known to use mosses.

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cunicularius. Irene Bisang answered my questions about the liverwort thallus parasite. As usual, many photographers provided kind permission for use of their images.

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CHAPTER 12-20

TERRESTRIAL INSECTS:

HOLOMETABOLA – DIPTERA

BRACHYCERA

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CHAPTER 12-20

TERRESTRIAL INSECTS:

HOLOMETABOLA – DIPTERA

BRACHYCERA



Figure 1. Beefly (*Syrphidae*) on *Cratoneuron filicinum*. Many flies use bryophytes for resting sites where the bryophytes reduce the danger of dehydration or the flies take a drink of water. Photo by Serhat Ursavas, with permission.

BRACHYCERA



Rhagionidae sensu stricto – Snipe Flies

The *Rhagionidae* is a worldwide family that has some members among the most primitive of the **Brachycera**. One of its diagnostic characters is that its head points downward when at rest (Figure 2), earning it the name of "downlooker flies."

In the Czech Republic, *Rhagio latipennis* (Figure 2) is a predaceous fly that prefers moist soil rich in organic matter (Farkač *et al.* 2005). Some prefer decaying wood, mosses, or liverworts along the sides of water courses.

Figure 2. *Rhagio latipennis* adult, a species that sometimes is associated with streamside mosses or liverworts. Note the downward-pointing head. Photo by João Coelho, through Creative Commons.

Spaniidae

Members of the **Spaniidae** family are often included in the **Rhagionidae**. The **Spaniidae** feeding habits may be assumed to be similar, in most cases, to those of the **Rhagionidae**.

Both adults and larvae typically eat small insects. The adults live in forests, especially near moist places. Larvae occur in moist meadow soil, among mosses, in decaying wood, under bark, and a few in water.

Imada and Kato (2016a) investigated **Diptera** in the **Rhagionidae/Spaniidae** to determine apparent adaptations to bryophyte consumption. The **Spaniidae** has larval members with multiple bryophyte-feeding habits. *Spania* (Figure 30-Figure 34) and *Litoleptis* (thallus-miners of thallose liverworts; Figure 3, Figure 17) both have a toothed form of apical mandibular sclerite with an orifice on its dorsal surface, contrasting with those of the members of **Rhagionidae** that possess a blade-like mandibular hook with an adoral groove. On the other hand, the moss stem borer *Ptiolina* (Figure 25) has a weak groove on the adoral surface of the mandible and has a highly sclerotized maxilla with toothed projections. Imada and Kato hypothesized that the toothed mandibles with the dorsal orifice would facilitate the leaf miners in scraping plant tissue and imbibing it along with a large quantity of cell sap. Their phylogenetic analysis indicated that the loss or reduction of the adoral mandibular groove and mandibular brush coincides with the evolution of bryophyte feeding.

Litoleptis (Figure 3)

Imada and Kato (2016b) reported the feeding strategy for *Litoleptis* (Figure 3, Figure 17) in Japan. The larvae of this genus mine the thalli of thallose liverworts in the families **Aytoniaceae** and **Conocephalaceae**. These include species of *Conocephalum* (Figure 4), *Reboulia* (Figure 5), and *Asterella* (Figure 6). It is clear that bryophyte miners are an overlooked group of species. While I was working on the original preparation of this chapter, Imada and Kato (2016b) provided me with six new species they described in the genus *Litoleptis*, all from thallose liverworts, in Japan.



Figure 3. *Litoleptis japonica* adult on *Conocephalum* sp. Photo courtesy of Yume Imada.



Figure 4. *Conocephalum conicum* on wet rock; the dipteran *Litoleptis japonica* deposits eggs on its thallus and the larvae mine the interior. Photo by Fotis Samaritakis, through Creative Commons.



Figure 5. *Reboulia hemisphaerica* with archegoniophores, a potential host plant for species of *Litoleptis*. Photo by Michael Lüth, with permission.

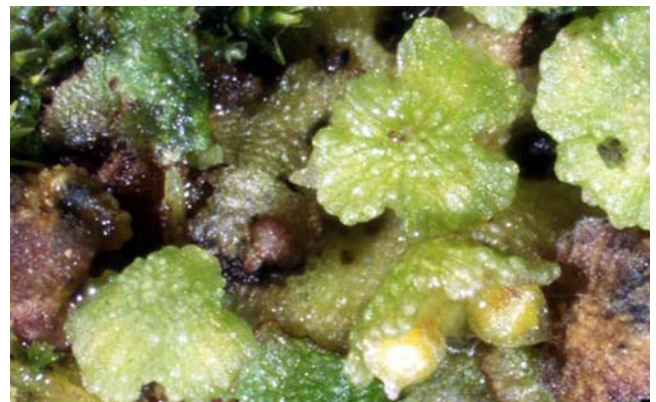


Figure 6. *Asterella cruciata*, an endangered species in Japan and home of *Litoleptis asterellaphile*. Photo by Misao Ito, with permission from Digital Museum of Hiroshima.

Litoleptis japonica (Figure 3) larvae occur in thalli of *Conocephalum conicum* (Figure 4) in shaded habitats in Japan (Figure 7-Figure 8). The adult female deposits eggs on the thallus of *Conocephalum conicum* (Figure 9-Figure 11), and its larvae (Figure 12-Figure 14) subsequently mine the thallus of this liverwort.



Figure 7. *Litoleptis japonica* habitat at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.



Figure 8. *Litoleptis japonica* habitat in Nanataki in Wakayama Pref., Japan. Photo by Yume Imada, with permission.



Figure 9. *Litoleptis japonica* adult on *Conocephalum conicum*. Photo by Yume Imada, with permission.



Figure 10. *Litoleptis japonica* ovipositing on *Conocephalum conicum* at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.



Figure 11. *Litoleptis japonica* eggs (arrows), deposited on liverwort thallus. Photo by Yume Imada, with permission.



Figure 12. *Litoleptis japonica* first instar larva (arrow) mining in a thallus of *Conocephalum conicum*. Photo by Yume Imada, with permission.



Figure 13. *Litoleptis japonica* larva. Photo by Yume Imada, with permission.



Figure 14. *Litoleptis japonica* larva mining *Conocephalum conicum*. Photo by Yume Imada, with permission.



Figure 15. *Litoleptis japonica* pupa (arrow) on *Conocephalum conicum*. Photo by Yume Imada, with permission.

Litoleptis küiensis (Figure 16-Figure 17) occurs in *Reboulia hemisphaerica* (Figure 5) on rocky or clayey slopes in both evergreen and deciduous forests (Imada & Kato 2016b). *Litoleptis küiensis* is a thallus miner on *Reboulia hemisphaerica* (Figure 5). The larvae mine the middle layer of the thalli, making mines nearly invisible from outside the thallus. The final instar of the larvae individually mine along the mid-vein and pupate near the adaxial layer of thalli in that mine in early spring. In their observations, this pupa was visible from the outside of the thallus. Adults emerge from the thallus later in the spring.

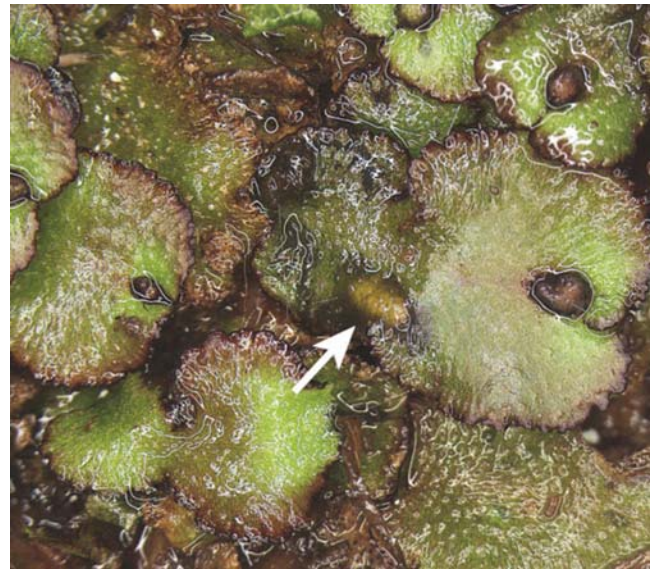


Figure 16. *Litoleptis küiensis* larva (arrow) on thallose liverwort. Photo by Yume Imada, with permission.



Figure 17. *Litoleptis küiensis* larva, a bryophyte inhabitant. Photo courtesy of Yume Imada.

Litoleptis niyodoensis occurs in *Reboulia hemisphaerica* (Figure 5) (Imada & Kato 2016b). *Litoleptis himukaensis* occurs along streams in *Reboulia hemisphaerica*. *Litoleptis izuensis* occurs in *Reboulia hemisphaerica* on shaded clayey slopes along streams and roads in evergreen *Castanopsis* forests. *Litoleptis asterellaphile* (Figure 18) occurs in *Asterella cruciata* (an endangered species in Japan; Figure 6) on rocky cliffs along streams and roads in deciduous forests.



Figure 18. *Litoleptis asterellaphile* pupa (arrow) among liverworts. Photo by Yume Imada, with permission.

***Ptiolina* (Figure 19)**

Lane and Anderson (1982) found immature adults of *Ptiolina* cf. *zonata* (Figure 19) by hand sorting moss-covered soil samples (Figure 20). Apparently mosses also provide oviposition sites for the genus (Figure 21-Figure 23), hence also providing homes for the larvae (Figure 24-Figure 26).



Figure 19. *Ptiolina* sp. on moss. Photo by Pristurus, through Creative Commons.



Figure 20. *Ptiolina* habitat at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.



Figure 21. *Ptiolina* sp. ovipositing on *Brachythecium buehnanii* at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.



Figure 22. *Ptiolina* sp. ovipositing on moss; the two yellow areas at the tip of the abdomen are egg masses. Photo by Pristurus, through Creative Commons.



Figure 23. *Ptiolina* sp. eggs (arrow), deposited on *Brachythecium buchananii*. Photo by Yume Imada, with permission.



Figure 24. *Ptiolina* sp. larva. Photo by Yume Imada, with permission.



Figure 25. *Ptiolina* sp. larva, a bryophyte inhabitant. Photo courtesy of Yume Imada.



Figure 26. *Ptiolina* sp. second-instar larva (arrow), boring a shoot of the moss *Plagiomnium vesicatum*. Photo by Yume Imada, with permission.

Since that publication, we have learned that a number of species in this family are adapted to mining bryophytes, and they seem to be very specific about their choice of bryophyte. Furthermore, they deposit their eggs on the same bryophyte that the larvae will later eat. *Ptiolina* sp. (Figure 19-Figure 22) deposits eggs (Figure 21, Figure 23) on the moss *Brachythecium buchananii* (Figure 27), and the larvae (Figure 25) are stem borers on this same species (Imada & Kato 2016a).



Figure 27. *Brachythecium buchananii*; *Ptiolina* deposits eggs on this species and larvae are stem borers in it. Photo by Michael Lüth, with permission.

Spania

The original record I found of a member of **Spaniidae** among bryophytes is that of *Spania nigra* (Figure 29-Figure 34). Larvae of this species live on mosses and liverworts in damp shade such as the ghyll woodlands of Sussex (Roper 2001). Boyce (2002) reported it from the

thallose liverwort *Pellia* (Figure 35) in England. Yume Imada (pers. comm.) has also found *Spania* sp. tunnelling in *Conocephalum* (Figure 34).



Figure 28. *Spania* sp. habitat. Photo by Yume Imada, with permission.



Figure 29. *Spania nigra* adult, a species whose larvae live among forest mosses and liverworts in the UK. Photo by Marko Mutanen, through Creative Commons.

Imada and Kato (2016a) observed that *Spania* sp. (Figure 29) deposited eggs exclusively on the thallus of the liverwort *Pellia endiviifolia* (Figure 35), a species it also mines.



Figure 30. *Spania* sp. adult on *Brachythecium buehnerii*, Japan. Photo courtesy of Yume Imada.



Figure 31. *Spania* sp. ovipositing on *Pellia endiviifolia*, at Higashiyoshinomura, Nara Pref., Japan. Photo by Yume Imada, with permission.



Figure 32. *Spania* sp. eggs (arrows) on *Pellia endiviifolia*. Photo by Yume Imada, with permission.



Figure 33. *Spania* sp. larva. Photo by Yume Imada, with permission.



Figure 34. *Spania* sp. larva tunnelling in *Conocephalum*. Photo courtesy of Yume Imada.



Figure 35. *Pellia endiviifolia* males and females; thalli are home for some *Spania* larvae that mine the interior. Photo by David T. Holyoak, with permission.

Dolichopodidae – Long-legged Flies

The **Dolichopodidae** is likewise a family of water-loving species. I mention here a few that are somewhat amphibious. *Dolichopus maculipennis* (Figure 36) lives in calcareous wet habitats near small permanent pools, in bryophyte flushes (Figure 37), flushed grasslands, and wet mires (Horsfield & MacGowan 1997), but it also occurs in bogs (Ringdahl 1928). *Hydrophorus rufibarbis* (see Figure 39-Figure 38) seems to prefer small, peaty pools, but it also lives in grassy flushes and bryophyte springs (Horsfield & MacGowan 1997).



Figure 36. *Dolichopus maculipennis* adult, a species whose larvae live in bryophyte flushes. Photo by I. Grichanov, with online permission.



Figure 37. Bryophyte flush in Wales, potential home for some **Dolichopodidae**. Photo by Janice Glime.

Empididae – Dance Flies

The **Empididae** are somewhat common on aquatic bryophytes (Gootaert 2004), so it is no surprise that some terrestrial species likewise find bryophytes to be suitable homes. Plant (1993) found adult females of *Monodromia fragilis* (Figure 40) by sweeping the damp mosses on a cloud forest floor at 550 m asl in New Zealand. In Malaysia the adults are only 3-5 mm long and are mostly yellow or black (Gootaert 2004). These seem to prefer boulders covered with mosses or a splash zone where there is constant high humidity.



Figure 38. *Hydrophorus litoreus* adult; *H. rufibarbis* lives in bryophyte springs and peaty pools. Photo by James K. Lindsey, with permission.



Figure 39. *Hydrophorus oceanus* larvae; *H. rufibarbis* lives in bryophyte springs and peaty pools. Photo by Hans Hillewaert, through Creative Commons.

The larvae of *Hemerodromia* (Figure 41) occur in fast-flowing streams and are predaceous. The adults are yellow or black and occur on moss-covered boulders or in the splash zone, both habitats that ensure moisture.



Figure 40. *Monodromia fragilis* adult, a species whose adults are associated with damp mosses on the floor of a New Zealand cloud forest. Photo modified from one by Stephen Thorpe, through Creative Commons.



Figure 41. *Hemerodromia* adult, a genus whose adults are associated with moss-covered boulders or in the splash zone. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Some insects only use bryophytes as landing and resting places. That appears to be the case with the empidid fly in Sarah Lloyd's pictures below (Figure 42- Figure 44). This family is mostly predaceous on other small invertebrates (Tony Daley, pers. comm. 19 November 2011).



Figure 42. Empidoid fly, possibly *Hybotidae*, on a leafy liverwort. Note the greatly arched thorax and long legs. Photo courtesy of Sarah Lloyd.

Clinocera nivalis (*nivalis* refers to snow; Figure 44) in Scotland is primarily on wet stony and mossy slopes, especially below melting snow, and always above 850 m asl (Edwards 1933a, b; Horsfield & MacGowan 1997). It also is abundant on bryophyte springs and occurs in *Racomitrium* moss heaths (Figure 45) and moss-dominated snowbed communities. Horsfield and MacGowan consider that it might be restricted to areas with bryophyte springs and flushes, common in the highlands. J. M. Nelson found it in an *Anthelia julacea* (leafy liverwort; Figure 46-Figure 47) spring in Coire Raibert at around 1000 m.



Figure 43. Adult member of **Empididae** resting on a moss capsule. Photo courtesy of Sarah Lloyd.



Figure 44. *Clinocera nivalis* adult, a species of wet, stony, and mossy slopes and bryophyte springs. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 45. *Racomitrium lanuginosum* heath, home for *Clinocera nivalis*. Photo by Mike Pennington, through Creative Commons.



Figure 46. *Anthelia julacea*, home for *Clinocera nivalis*. 1 Photo by Jean Faubert., with permission.

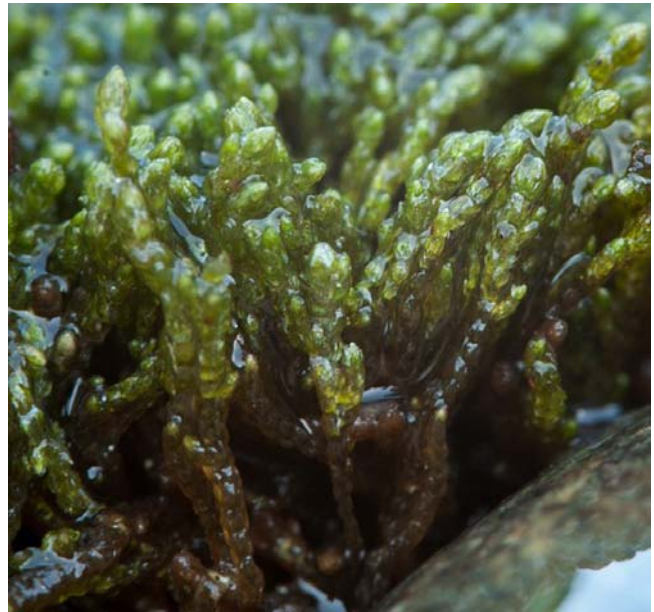


Figure 47. *Anthelia julacea*, home for *Clinocera nivalis*. Photo by Štěpán Koval, with permission.

Larvae of *Wiedemannia impudica* (see Figure 48) probably live in mosses on emergent boulders (Horsfield & MacGowan 1997), again where they will be constantly moist.



Figure 48. *Wiedemannia bistigma* adult; *W. impudica* is a likely moss inhabitant on emergent boulders. Photo by Marko Mutanen, through Creative Commons.



Figure 50. *Stilpon curvipes* adult, member of a genus in which some adults occur in *Sphagnum*. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 51. *Sphagnum warnstorffii*; *Sphagnum* is a genus that is home to adult *Stilpon* (and possibly the unknown larvae). Photo by Michael Lüth, with permission

Hybotidae – Hybotid Dance Flies

Smith (1965) described a new species of *Stilpon* (Figure 49-Figure 50) from Portugal. The immature stages of this genus were still unknown, but the adults occur in grass tufts, heaps of cut sedge, and *Sphagnum* (Figure 51). The new species was similar to *Stilpon nubilus*.



Figure 49. *Stilpon* sp. adult, a genus in which some adults occur in *Sphagnum*. Photo by Tom Murray, through Creative Commons.

Syrphidae – Syrphid Flies

This is a family of flies that often resemble bees. If you find a "bee" with only two wings and a pair of halteres, you have found a bee fly. *Platycheirus melanopsis* (Figure 52) is known from moss-dominated summit heaths (Figure 45) and grasslands in Scotland (Horsfield & MacGowan 1997). *Cheilosia sahlbergi* (Figure 53) occurs in habitats where bryophytes are abundant, including ericaceous dwarf shrub heaths, flushes, and bryophyte springs.



Figure 52. *Platycheirus melanopsis* adult, a species from moss-dominated summit heaths. Photo from America Pink, with online permission.



Figure 53. *Cheilosia sahlbergi* adult, a species that occurs in habitats with abundant bryophytes. Photo by Ladislav Tabi, with permission.

Phoridae – Scuttle Flies

Mosses often provide a safe overwintering shelter. Herbert and Braun (1958) reported moss polsters as the overwintering quarters for adult dipterans in the family **Phoridae** (Figure 54).



Figure 54. **Phoridae** mating in Rock Creek Park, MD. Photo by Katja Schulz, through Creative Commons.

Agromyzidae – Mine Flies

This family has bryophyte specialists, but not on mosses. Rather, these bryobionts are known only from hornworts and liverworts (Spencer 1990). D'Aguilar (1945) described a new species of *Liriomyza* (Figure 55) from the thallose liverwort *Ricciocarpus natans* (Figure 56). *Phytoliriomyza mesnili* (formerly *Liriomyza*; see Figure 57-Figure 58) is known from *Ricciocarpus natans* in France as well as being present on the thallose liverwort *Riccia beyrichiana* (Figure 59). It feeds in the thallus and pupates there and also pupates in the thallus of *Nothoceros vincentianus* (Figure 60-Figure 62) in Peru. In Mexico, it is known on *Dumortiera* (Figure 63) and *Monoclea* (Figure 64).

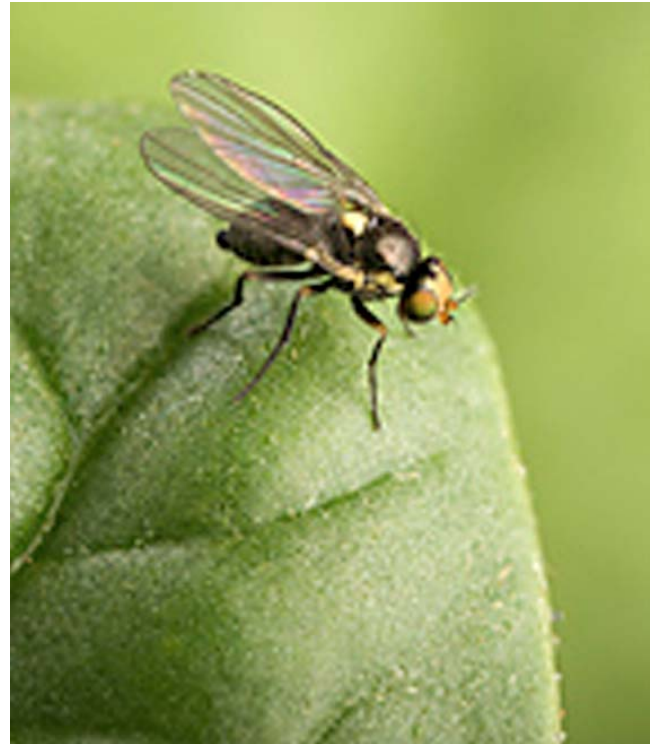


Figure 55. *Liriomyza taraxaci* adult, member of a genus known from the liverwort *Ricciocarpus natans*. Photo by Peggy Greb, USDA, through public domain.

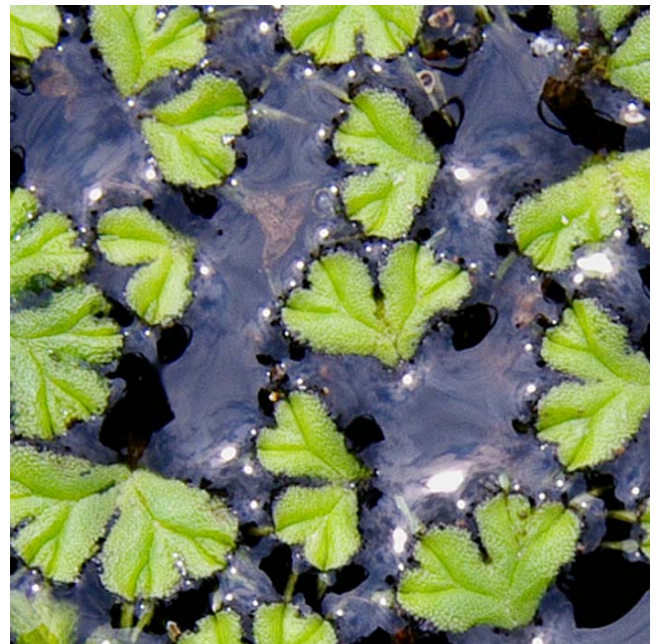


Figure 56. *Ricciocarpus natans*, home for some species of *Liriomyza*/*Phytoliriomyza*. Photo by Christian Fischer, through Creative Commons.



Figure 57. *Phytoliriomyza arctica* adult. Some members of this genus live in liverwort thalli. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 58. *Phytoliriomyza melampyga* larval tunnels in a leaf. Photo from Biodiversity Centre, through Creative Commons.



Figure 59. *Riccia beyrichiana*, home and food for *Phytoliriomyza mesnili*. Photo by Jan-Peter Frahm, with permission.



Figure 60. *Nothoceros*, a genus where *Phytoliriomyza mesnili* is known to live in Peru. Photo by Juan Larrain, with permission.



Figure 61. *Nothoceros* with *Agromyzidae* leaf miners. Photo courtesy of Juan Carlos Villarreal.

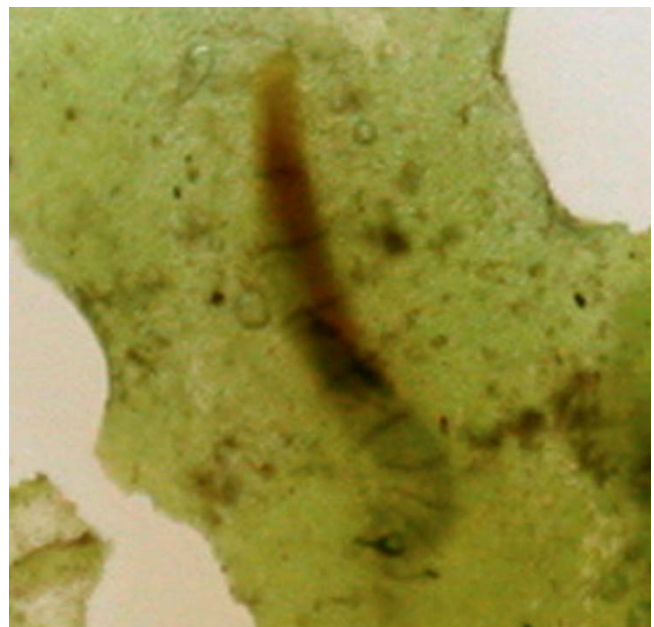


Figure 62. *Nothoceros* leaf miner seen through the thallus. Photo courtesy of Juan Carlos Villarreal.



Figure 63. *Dumortiera hirsuta*, home to *Phytoliriomyza mesnili* in Mexico. Photo by Li Zhang, with permission.



Figure 64. *Monoclea forsteri*, home to *Phytoliriomyza mesnili* in Mexico. Photo by Jan-Peter Frahm, with permission.

Reporting from Spain, Marta Infante and Patxi Heras (Bryonet 2 May 2019) described a larva living in *Riccia cavernosa* (Figure 65). They noted that it tried to defend itself from the dissecting needle. Later, they observed many pupae and larvae inside the thallus. The species proved to be *Phytoliriomyza mesnili* (Figure 66).

Ron Porley (Bryonet 3 May 2019) relayed a similar experience with *Riccia cavernosa* (Figure 65). Although he did not identify the insect, it was present as black pupae in the thalli of this species on the muddy margin of a reservoir in Algarve, Portugal, in November. Pettet (1967) reported a similar parasitism on *Riccia frostii* (Figure 67) by flies. Porley suggested that such habitation may only occur in section *Ricciella* because of its spongy thalli with large air chambers.



Figure 65. *Riccia cavernosa*, home for pupae of *Phytoliriomyza mesnili*. Photo from <www.aphotofauna.com>, with permission.



Figure 66. *Phytoliriomyza melampyga* adult; *P. mesnili* pupates within the thalli of *Riccia cavernosa*. Photo through Wikimedia Commons.



Figure 67. *Riccia frostii*, home for pupae of some *Agromyzidae*. Photo from Earth.com, with permission.

Manju Nair provided me with images of the pupae (Figure 68) of an *Agromyzidae* that appears to be

Phytoliriomyza (Figure 68). This pupa inhabits the thalli of *Riccia beyrichiana* (Figure 69) and *Riccia hasskarliana* (Figure 70).



Figure 68. *Phytoliriomyza* pupa from thallus of *Riccia beyrichiana*. Photo by Manju Nair, with permission.



Figure 69. *Phytoliriomyza* pupa in thallus of *Riccia beyrichiana*. Photo by Manju Nair, with permission.

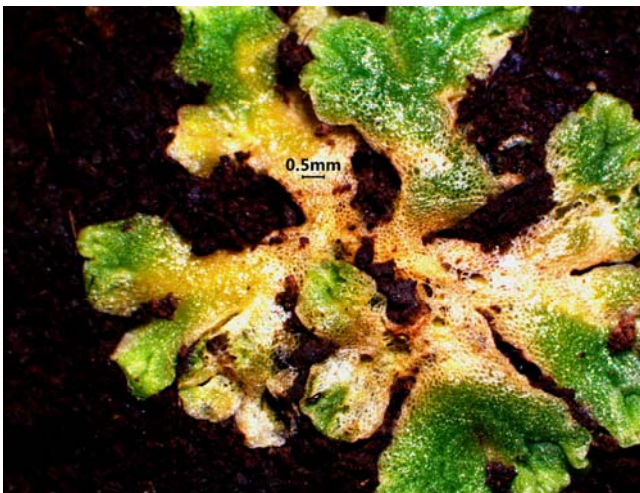


Figure 70. *Riccia hasskarliana* mined by *Phytoliriomyza*. Photo by Manju Nair, with permission.

Some relationships of flies with their bryophyte hosts are obligatory. In Mexico, Juan Carlos Villarreal (pers. comm. 9 September 2014) found the larvae (Figure 71) of leaf-mining flies crawling within the hornwort *Nothoceros aenigmaticus*, making traces. While in his custody, it became a pupa (Figure 72). Then one day a hatchling appeared. But it was not a young leaf miner. It was a parasitoid wasp that lived on the pupa! So far, no one has successfully reared the larvae or pupae of the agromyzid to adults, but using genetic bar-coding he determined it to be close to *Phytomyza* (Figure 73-Figure 78). He found similar *Diptera* from Panamanian *Nothoceros vincentianus* (Figure 75) and sequenced them. They most closely matched *Phytomyza*. But with only an 87% match, perhaps this is a new species or even a new genus.



Figure 71. *Agromyzidae* larva from *Nothoceros* thallus. Photo courtesy of Juan Carlos Villarreal.



Figure 72. *Agromyzidae* pupa grown from larva that was living in *Nothoceros*. Photo courtesy of Juan Carlos Villarreal.



Figure 73. *Phytomyza* egg from *Nothoceros aenigmaticus* Montage Mexico. Photo courtesy of Juan Carlos Villarreal.



Figure 74. *Phytomyza ranunculi* larval tunnels in a leaf, similar to those made by species in liverworts. Photo by James K. Lindsey, with permission.

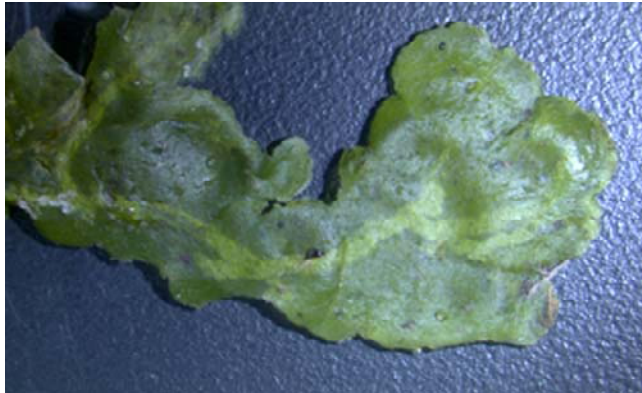


Figure 75. *Nothoceros vincentianus* with leaf miner, possibly *Phytomyza* sp., in Panama. Note the leaf miner trails on the thallus surface. Those are not midribs! Photo courtesy of Juan Carlos Villarreal.



Figure 76. *Phytomyza vitalbae* pupa, member of a genus with some members that live in liverwort thalli. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.



Figure 77. *Phytomyza ranunculi* adult, member of a genus that sometimes lays eggs in liverwort thalli. Photo by Dick Belgers, through Creative Commons.



Figure 78. *Phytomyza ranunculi* adult, member of a genus in which some species live in liverwort thalli. Photo by James K. Lindsey, with permission.

Villarreal was able to determine (via a letter belonging to John Engel) that Proskauer had seen leaf miners in *Megaceros* (Figure 79) and *Nothoceros* (Figure 75). Hering (1957) described *Phytoliriomyza* sp. (see Figure 57-Figure 58) larvae and pupae from *Megaceros*.



Figure 79. *Megaceros* sp. with capsules, home for some of the leaf-mining flies. Photo by David Tng <www.davidtng.com>, with permission.

In the larvae of *Phytoliriomyza mesnili* (see Figure 57-Figure 58), living in the hornwort *Nothoceros vincentianus* (Figure 75), the anterior spiracles of the larva penetrate the epidermis of the thallus to permit breathing (Herring 1966; Spencer 1990). Members of this family also mine *Dumortiera hirsuta* (Figure 63) and *Monoclea* (Figure 64) in Mexico (Spencer 1990). Although their substrate is generally thallose liverworts and hornworts (never mosses), some feed on ferns, but none is known to feed on flowering plants.

Mining flies seem to have a widespread distribution, albeit scattered. Herring (1957) found leaf-mining flies in *Megaceros* spp. (Figure 79) in the West Indies, Juan Fernandez Islands, and New Zealand. Several reports have revealed them in Europe. And Villarreal has found them in Mexico and Panama.

The combination of thallose liverworts or hornworts, mining fly, and parasitic wasp apparently also has far-reaching geographic presence, although the species involved may differ. Sara Altenfelder (pers. comm.) found *Riccia glauca* (Figure 80) and *R. warnstorffii* (Figure 81) with leaf-mining flies in arable fields in Germany, and these, like the ones found by Villarreal, were parasitized by wasps. She determined that the fly is *Phytoliriomyza mesnili* (see Figure 57-Figure 58), first described by Aguilar (1945) feeding on *Ricciocarpos natans* (Figure 56) and later reported by Sellier (1947) from *Riccia beyrichiana* (Figure 59). The larva eats the thallus, then pupates there (Spencer 1990). Fulnek (1962) mentioned a parasitic wasp – *Dacnusa taras* – that lives on some members of *Phytoliriomyza*.



Figure 80. *Riccia glauca*, home for *Phytoliriomyza mesnili*. Photo by Bernd Haynold, through Creative Commons.



Figure 81. *Riccia warnstorffii*, a species that is home to larvae of *Phytoliriomyza mesnili*. Photo by Bernd Haynold, through Creative Commons.

In 2018, Ohgue *et al.* reported the first bryophyte galls (Figure 82) induced by insects. These were created by a species of *Agromyzidae*, probably related to *Phytoliriomyza* (Figure 57-Figure 58, Figure 66, Figure 68). These occur on the thallose liverwort *Monoclea gottschei* subsp. *elongata* (Figure 82) in a tropical mountain forest. The galls form swellings on the thallus surface, but they resemble the thallus, having no ornamentation or sclerotization. The larvae become pupae (Figure 83) within the gall and adult flies (Figure 84) emerge from the gall by making an exit hole in the upper epidermis of the galled thallus. The galls appear in the apical part of the thallus where archegonia or antheridia would normally occur. Although archegonia and antheridia were plentiful in the population, thalli with galls produced no sporophytes. The need to raise larvae to adults for identification has caused many of these thallus-inhabiting larvae to remain unnamed.



Figure 82. *Monoclea gottschei* thallus with a gall of *Agromyzidae*; triangle indicates gall. Photo by Takayuki Ohgue 2018, with permission from Yume Imada.

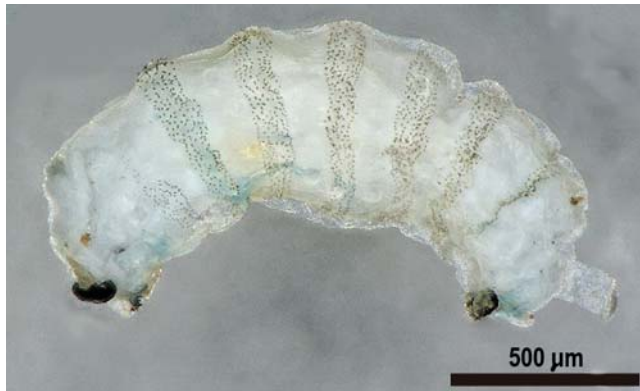


Figure 83. *Agromyzidae* thallus gall larva from *Monoclea gottschei*. Photo by Takayuki Ohgoue, with permission from Yume Imada.



Figure 85. *Marchantia polymorpha*; the genus *Marchantia* serves as home for species of *Phytoliriomyza*. Photo by Denis Barthel, through Creative Commons.



Figure 84. *Agromyzidae* thallus gall larva from *Monoclea gottschei*. Photo by Takayuki Ohgoue, with permission from Yume Imada.



Figure 86. *Plagiochasma* sp., home for species of *Phytoliriomyza*. Photo by Zhang Li, with permission.

Kato *et al.* (2022) found that liverwort-mining *Agromyzidae* were "overwhelmingly widespread and diverse" in the Japanese Archipelago. They found 39 species, 37 of which were new species! All of these were placed in *Phytoliriomyza* (e.g. Figure 57-Figure 58, Figure 66, Figure 68). Five of these were associated with *Marchantia* (Figure 85), two on *Dumortiera* (*Dumortieraceae*; Figure 63), three on *Plagiochasma* (Figure 86), one on *Asterella* (Figure 6), six on *Reboulia* (*Aytoniaceae*; Figure 5), one on *Wiesnerella* (*Wiesnerellaceae*; Figure 87), fifteen on *Conocephalum* (*Conocephalaceae*; Figure 4), and three on *Riccia* (*Ricciaceae*; Figure 59, Figure 65, Figure 67, Figure 70, Figure 80, Figure 81). Another 3 species were associated with hornworts: 1 on *Folioceros* (*Anthocerotaceae*; Figure 88), 1 on *Megaceros* (*Dendrocerotaceae*; Figure 79), and 1 on *Notothylas* (Figure 89), *Phaeoceros* (*Notothyladaceae*; Figure 90), and *Anthoceros* (*Anthocerotaceae*; Figure 91).



Figure 87. *Wiesnerella denudata*, home for species of *Phytoliriomyza*. Photo by Masaki Shimamura, with permission.



Figure 88. *Folioceros cf glandulosus*, a hornwort in a genus that can serve as home for *Phytoliriomyza*. Photo by Li Zhang, with permission.



Figure 89. *Notothylas orbicularis*, a hornwort in a genus that can serve as home for *Phytoliriomyza*. Photo by Blair Young, through Creative Commons.



Figure 90. *Phaeoceros laevis*, a hornwort in a genus that can serve as home for *Phytoliriomyza*. Photo by Oliver S. Beneutzer, through Creative Commons.



Figure 91. *Anthoceros neesii* with sporophytes dehiscing, a hornwort in a genus that can serve as home for *Phytoliriomyza*. Photo from Earth.com, with permission.

Lauxaniidae

Sarah Lloyd described her experiences with some of the mine flies – *Ceratolauxania atrimana* (Figure 92- Figure 94). They like wet places (she never saw them in open, drier areas) and they tend to land on high points, but they sometimes also land on the mosses. That might be a location to rehydrate. They also oviposit on bryophytes, as shown on the *Bazzania adnexa* below (Figure 93).

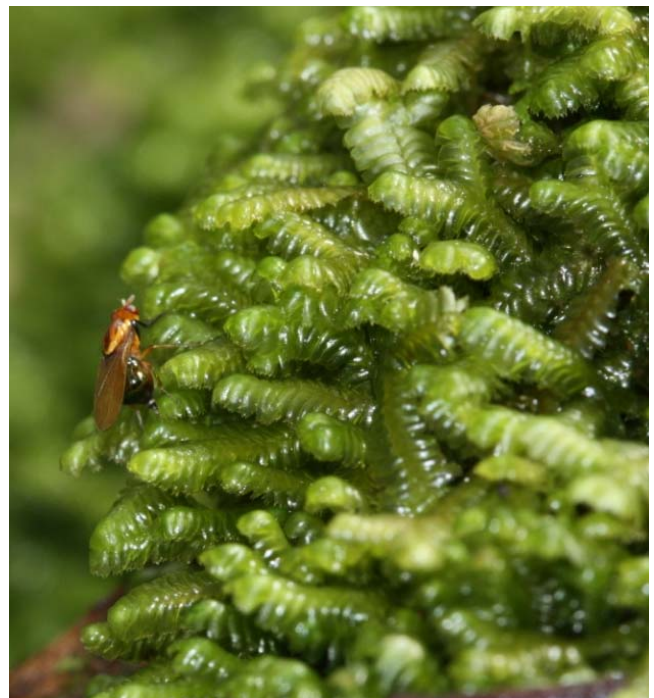


Figure 92. *Ceratolauxania atrimana* laying eggs on *Bazzania adnexa* in Eucalypt forest in Tasmania. Photo courtesy of Sarah Lloyd.



Figure 93. *Ceratolauxania atrimana* laying eggs on *Bazzania adnexa* in Eucalypt forest in Tasmania. Photo courtesy of Sarah Lloyd.

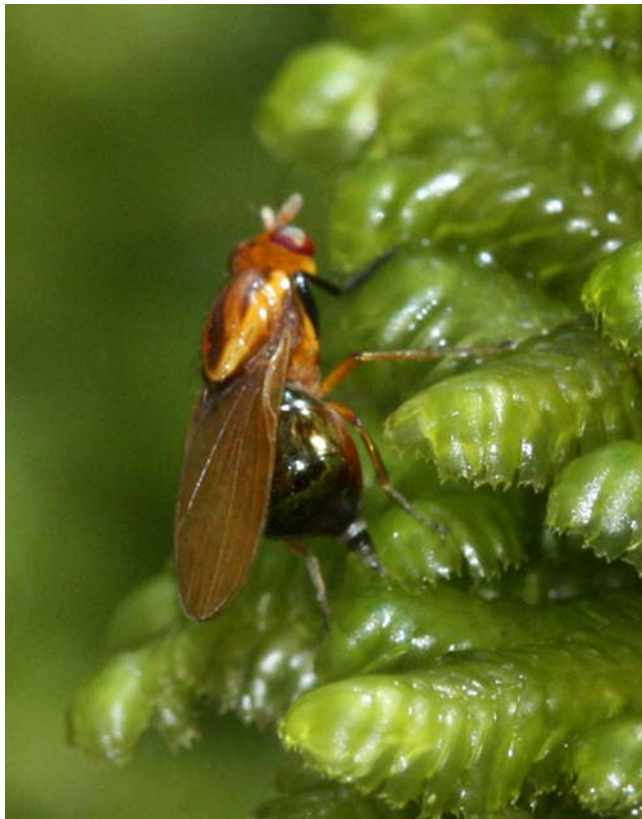


Figure 94. *Ceratolauxania atrimana* adult on *Bazzania adnexa* in a Tasmanian *Eucalyptus* forest. Photo courtesy of Sarah Lloyd.

Anthomyiidae – Root-maggot Flies

Thus far I can find only one paper that discusses the **Anthomyiidae** from bryophytes (Horsfield & MacGowan 1997). From very high altitudes in Britain, *Alliopsis albipennis* (see Figure 95) includes moss-dominated late snow-bed vegetation among its habitats, as well as flushes which are likely to be moss-dominated, but it is not restricted to these mossy habitats. *Alliopsis atronitens* (see Figure 95) exhibits one of its most frequent occurrences in *Racomitrium lanuginosum* moss heaths (Figure 45) on summit plateaus in Scotland.



Figure 95. *Alliopsis billbergi* adult; *Alliopsis albipennis* lives in moss-dominated late snowbeds. Photo by James K. Lindsey, with permission.

Delia caledonica (see Figure 96) occurs in blanket bogs and *Racomitrium lanuginosum* heath (Figure 45), among other montane habitats (Horsfield & MacGowan 1997). *Delia piliventris* (see Figure 96) occurs mostly in the *Racomitrium lanuginosum*, grasslands, and tall herb communities in the montane area of Scotland.



Figure 96. *Delia radicum* adult. *Delia caledonica* is a species living in blanket bogs and *Racomitrium lanuginosum* heaths; *D. piliventris* lives mostly in *Racomitrium lanuginosum* heaths. Photo by Ladislav Tábi, with permission.

Botanophila moriens (see Figure 97-Figure 98) occurs in bryophyte springs and in *Racomitrium lanuginosum* (Figure 45) heaths at high elevations (760-1310 m alt) (Horsfield & MacGowan 1997). *Zaphne spiniclunis* (Figure 99) includes moss heaths (Figure 45) and bryophyte springs among its many habitats, mostly above 800 m near melting snow.



Figure 97. *Botanophila* larva, a species of bryophyte springs and *Racomitrium lanuginosum* heaths. Photo by Malcolm Storey, through Creative Commons.



Figure 98. *Botanophila* cf. *fugax* adult, a species of bryophyte springs and *Racomitrium lanuginosum* heaths. Photo by Martin Cooper, through Creative Commons.



Figure 99. *Zaphne ambigua* adult; *Zaphne spiniculunis* lives in moss heaths and bryophyte springs near melting snow. Photo by James K. Lindsey, with permission.

Heleomyzidae

Only *Scoliocentra scutellaris* (Figure 100) seems to utilize mosses for its habitat. This species in Scotland lives in moss heaths (Figure 45), as well as other montane habitats.



Figure 100. *Scoliocentra scutellaris* adult, a species of moss heaths. Photo by Gunnar M. Kvifte, through Creative Commons.

Muscidae – House Flies

This is one of the families you are undoubtedly familiar with because it includes the common housefly. The **Muscidae** have been discussed in part in the first of the **Diptera** subchapters because of their role in dispersing spores of the **Splachnaceae**. Hence we have already seen a relationship with *Myospila meditabunda* (Figure 101), *Eudasyphora cyanicolor* (Figure 102), *Palpibracus chilensis*, and *Palpibracus* spp.



Figure 101. *Myospila meditabunda* female, one of the flies that facilitates transfer of spores in the **Splachnaceae**. Photo by James. K. Lindsey, with permission.



Figure 102. *Eudasyphora cyanicolor* adult male, one of the flies that facilitates transfer of spores in the **Splachnaceae**. Photo by Tristram Brelstaff, through Creative Commons.



Figure 104. *Spilogona falleni* adult; *Spilogona triangulifera* lives in *Racomitrium lanuginosum* heaths. Photo by James K. Lindsey, through Creative Commons.

In montane areas of Scotland, Horsfield and MacGowan (1997) both *Phaonia subfuscineris* (Figure 103) and *Spilogona triangulifera* (see Figure 104) from *Racomitrium lanuginosum* heath (Figure 45), as well as other non-mossy habitats. These two flies have a habit of sunning themselves on rocks and typically associate with snowbeds. In Lithuania, the predaceous larvae of *Phaonia fuscata* (Figure 105-Figure 107) live in soil and mosses of broad-leaved forests (Gregor *et al.* 2002; Lutovinovas & Rozkošný 2009).



Figure 105. *Phaonia subventa* larva, pupa, adult male. Photo by Martin Cooper, through Creative Commons.



Figure 103. *Phaonia subfuscineris* adult, a species of *Racomitrium lanuginosum* heaths. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 106. *Phaonia fuscata* adult female, a species whose larvae live among and under mosses in broad-leaved forests in Lithuania. Photo by James K. Lindsey, with permission.



Figure 107. *Phaonia fuscata* adult male, a species whose larvae live among and under mosses in broad-leaved forests in Lithuania. Photo by James K. Lindsey, with permission.

Limnophora is mostly aquatic in the larval stage (Roper 2001), but some are more limnoterrestrial. The carnivorous *Limnophora exurda* (current name not found) larvae and pupae live in tufts of wet mosses and liverworts that receive direct water or spray from waterfalls (Tate 1939). *Limnophora riparia* (Figure 108-Figure 109) adults occur singly on stones or mosses or algae in Armenia, but occasionally they may occur as small groups (Pont *et al.* 2011). Roberts (1971) suggested that the mouth parts and musculature of the carnivorous *Limnophora riparia* larvae (Figure 108) were adapted to the type of food they consumed. Larvae of this species are aquatic and prefer mosses as a substrate. They attach to their substrate to anchor themselves as they attack their prey, which includes other invertebrates, especially **Chironomidae** and **Simuliidae** larvae. *Limnophora petallifera* (Figure 110) females and others in the genus use mosses for oviposition, as well as algae (Werner & Pont 2006; Pont *et al.* 2011). They arrived for this purpose at about midday when the rock substrate was in direct sunlight with a temperature of 42°C (Werner & Pont 2006). The female was "running around the rock close to the water and stopped when she found a small indentation, then injected her eggs many times in the mosses and algae. Her forelegs were pointed upward and her abdomen pushed into the wet mosses. She laid the eggs singly, but each egg was placed next to the first one so that ultimately the eggs were in clusters.



Figure 108. *Limnophora riparia* larva, a species whose larval mouthparts are adapted for eating vegetable matter. Photo by Niels Sloth, with permission.



Figure 109. *Limnophora riparia* adult, a species whose adults often hang out on mosses. Photo by Marko Mutanen, through Creative Commons.



Figure 110. *Limnophora petallifera* adults eating larva of *Obuchovia popowae* (Simuliidae). *Limnophora petallifera* oviposits among mosses. Photo by Doreen Werner, permission pending.

Scathophagidae – Dung Flies

This is another poorly represented family in bryophytic habitats. *Gonatherus planiceps* (Figure 111) is a montane species in Scotland, and like many others there, one of its habitats is in *Racomitrium lanuginosum* heaths (Figure 45) (Horsfield & MacGowan 1997).



Figure 111. *Gonatherus planiceps* adult, a species of *Racomitrium* heaths. Photo by Marko Mutanen, through Creative Commons.

Bratton (2012) swept two females of *Gimnomera tarsea* (Figure 112) from mosses beside Loch a' Roe in the Outer Hebrides.



Figure 112. *Gimnomera tarsea* adult, a species whose adults hang out near mosses beside lakes. Photo by Marko Mutanen, through Creative Commons.

Calliphoridae – Blow Flies

And another! For the **Calliphoridae** I found only *Calliphora stelviana* (Figure 113) (Horsfield & MacGowan 1997). Like many other flies in the montane Scotland, these included *Racomitrium lanuginosum* among their habitats.



Figure 113. *Calliphora stelviana* adult, a species that lives in *Racomitrium lanuginosum* heaths. Photo by Marko Mutanen, through Creative Commons.

Summary

The **Rhagionidae** may live among bryophytes and lay their eggs there. The **Spaniidae** are leaf miners and *Litoleptis* species and some *Spania* species mine the thalli of thick thallose liverworts. The **Dolichopodidae** tend to be amphibious, living in wet bryophytes. The **Empididae** may be found on damp mosses as well as aquatic ones. Some **Hybotidae** live among *Sphagnum* as adults. The **Syrphidae** are likewise often aquatic, but some live among terrestrial mosses as larvae. The **Phoridae** are not normal bryophyte inhabitants, but they do overwinter in moss polsters. Several members of **Agromyzidae** are leaf miners in large thallose liverworts and hornworts. The **Lauxaniidae** like wet places and often land on protruding mosses; others oviposit on species of the leafy liverwort *Bazzania*. **Anthomyiidae** live among mosses in late snow-bed vegetation; others live in *Racomitrium* heaths. One **Heleomyzidae** lives in moss heaths. The **Muscidae** are among the important spore dispersers for the moss family **Splachnaceae**. Others occur in *Racomitrium* heaths. The **Scathophagidae** and **Calliphoridae** also sometimes live in *Racomitrium* heaths.

Hence, *Racomitrium*, with its often large hummocks, serves as a home for some members in many of the **Nematocera** families. This habitat is well insulated and capable of maintaining moisture for a longer time than most other terrestrial habitats.

Acknowledgments

Thank you to Yume Imada for sharing his research and images of the **Spaniidae**. Thank you to for alerting me to the mine flies (*Ceratolauxania atrimana*) that live on liverworts and sharing her research and images with me. Likewise, I appreciate Juan Carlos Villarreal for sharing his research on **Anthocerotophyta** and the flies that live in them, providing me with images for this chapter.

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