Glime, J. M. 2017. Arthropods: Mite Habitats, Minor Arachnids, and Myriapods. Chapt. 9-2. In: Glime, J. M. Bryophyte Ecology. 9-2-1
Volume 2. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated
18 July 2020 and available at <http://digitalcommons.mtu.edu/bryophyte-ecology2/>.

CHAPTER 9-2
ARTHROPODS: MITE HABITATS, MINOR ARACHNIDS, AND MYRIAPODS

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ARTHROPODS: MITE HABITATS
AND MINOR ARACHNIDS

Figure 1. Red mite (**Stigmaeidae**) on *Riccia ciliata*. Photo by Michael Lüth, with permission.

Mites occur among bryophytes in a variety of habitats (Figure 1). These can be grouped into forests, aquatic, peatlands, polar/alpine, and tropics to define the major differences in community structure. Within those categories, communities are divided both vertically and seasonally, as well as divisions into niches that differ in light, moisture, and sometimes temperature. This defines those that are generalists and those that are specialists in food or cover type.

Forest Bryophytes

Forests offer a variety of microhabitats for both bryophytes and mites. Monson (1998) found more than 100 species of mites among mosses in Slapton Wood and nearby in the United Kingdom. And the dominant mite species can exhibit considerable variability. For example, *Minunthozetes pseudofusiger* (**Punctoribatidae**) can be very common among mosses in one site and nearly absent in another (Monson 1998). In his study of oribatid mites in mosses at Slapton Wood, UK, Monson found a number of species new for the UK, including *Minunthozetes pseudofusiger* (**Punctoribatidae**), *Cepheus tuberculosus* (**Cepheidae**; see Figure 2), *Microzetes petrocoriensis* (**Microzetidae**), *Liochthonius perfusorius* (**Brachychthoniidae**; see Figure 3), and *Quadroppia pseudocircumita* (**Quadroppiidae**).
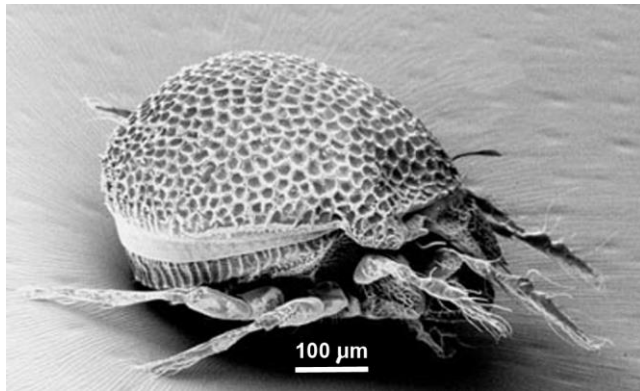
Figure 2. *Cepheus corae* SEM. *Cepheus tuberculosus* is a moss dweller in the UK. Photo by Christopher Taylor. PERMISSION PENDING

Figure 4. SEM of *Eueremaeus tetrosus*, member of a forest bryophyte-dwelling genus. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.
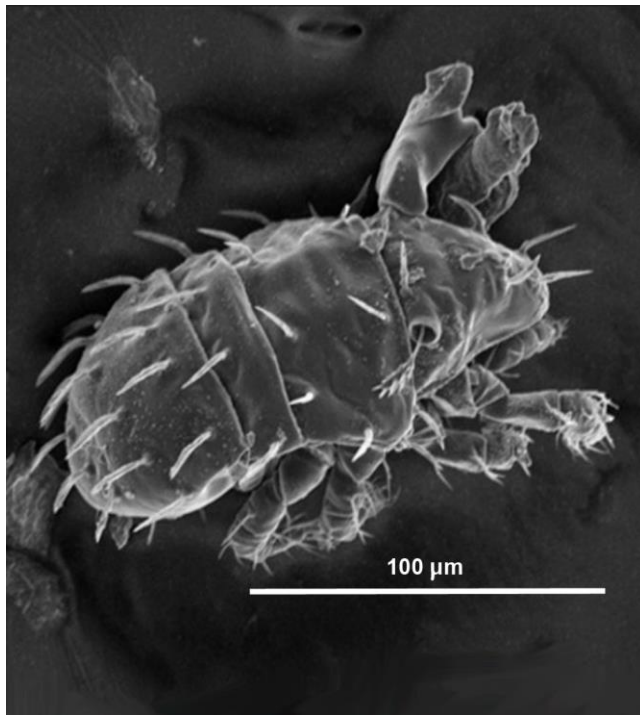

Figure 3. *Liochthonius propinquus*. *Liochthonius perfusorius* is a moss dweller in the UK. Photo by Christopher Taylor. PERMISSION PENDING
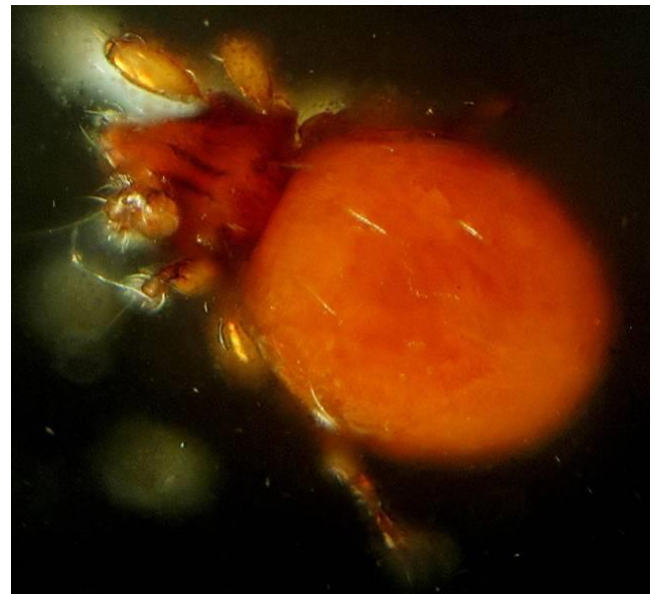

Figure 5. *Eremaeus* sp., member of a forest bryophyte-dwelling genus Photo by Walter Pfliegler, with permission.

Eremaeus stiktos (**Eremaeidae**; see Figure 5-Figure 4) was described from moss-covered logs and other forest habitats in Washington state, USA (Higgins 1962). Other members of this genus and segregates of the genus also occur on mossy logs and among bryophytes on the forest floor (Figure 6-Figure 4). Woolley (1968) reported *Liacarus bidentatus* (**Liacaridae**; see Figure 7) on the forest floor among mosses in Washington state, USA, and in mosses in Wyoming. *Liacarus spiniger* (see Figure 7) also occurs among mosses. In Illinois, USA, *Platynothrus peltifer* (**Camisiidae**; Figure 9; formerly *Hermannia bistriata*) lives among mosses and under logs (Ewing 1909).

Figure 6. SEM of *Eueremaeus foveolatus*, member of a moss-dwelling genus on logs and the forest floor. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.
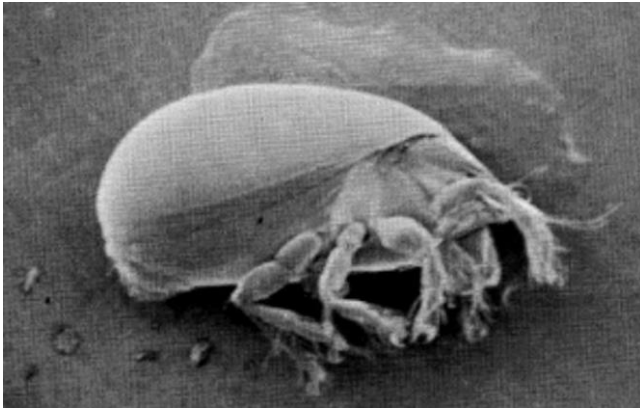
Figure 7. *Liacarus* nr. *robustus*. *Liacarus bidentatus* and *L. springeri* are moss dwellers. Photo from <www.fs.fed.us> through public domain.

Figure 8. *Platynothrus peltifer* (**Camisiidae**) dorsal view, a moss dweller. Photos from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Figure 9. *Platynothrus peltifer*, a moss dweller. Photos from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Forest Floor

Mites are a common component on the forest floor, where they may inhabit soil, leaf litter, logs, or moss (Sywestrowicz-Maliszewska *et al*. 1993; Proctor *et al*. 2002). *Epicriopsis rivus* (**Ameroseiidae**) lives among mosses and litter in pine forests in northern Latvia (Salmane 2011). Members of *Epicrius* (**Epicriidae**; Figure 10) live among mosses (David E. Walter, pers. comm. 1 September 2011). Some members of the genus

Epidamaeus (**Damaeidae**; Figure 11) occur among leaf litter and mosses on soil. (Ermilov & Łochyska 2009). **Labidostommatidae** live on and in the soil, as well as in overlying vegetation and litter, including mosses (Krantz & Walter 2009). From this vantage point, they prey on smaller invertebrates (Figure 12). This soil/moss interface provides a moist environment where fungi and other micro-organisms can provide food sources.

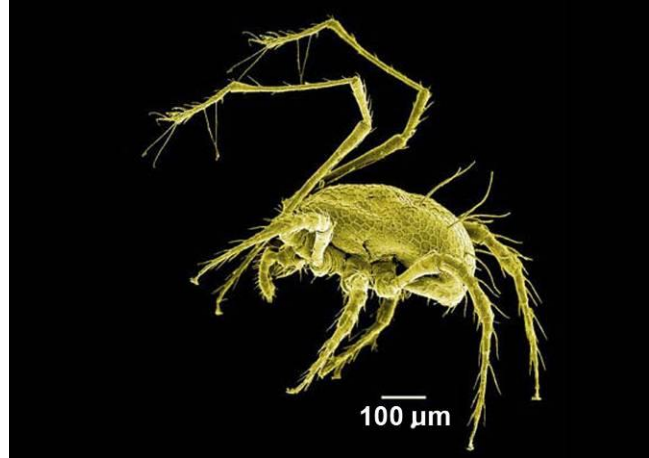Figure 10. *Epicrius* sp., member of a mite genus that can live among forest bryophytes. Photo by David E. Walter, with permission.

Figure 11. *Epidamaeus* sp., a forest floor bryophyte dweller, on leaf litter. Photo by Walter Pfliegler, with permission.

Figure 12. *Labidostomma mamillata* eating a springtail amid dead moss. Photo by Roy A. Norton, in Smith *et al*. 2011, with permission.

Salmane and Brumelis (2008) demonstrated the importance of the moss layer to the diversity of the predatory mites in the **Gamasina** group (an infraorder within the **Mesostigmata**; Figure 13) in the coniferous forest. In coniferous forests, bryophytes are able to establish on the forest floor because the narrow conifer leaves permit them to gain sufficient light to grow through the litter. In these forests, bryophytes are often the predominant forest floor vegetation and provide a moist haven for invertebrates. And, as seen in the previous sub-chapter, the bryophytes can serve as food.

Feather mosses [*Hylocomium splendens* (Figure 14), *Pleurozium schreberi* (Figure 15), *Ptilium crista-castrensis* (Figure 16)], common boreal forest mosses, harbor a diversity of predatory **Gamasina** mites (Figure 13; Salmane & Brumelis 2008). Salmane and Brumelis removed the feather mosses, then compared species richness, **Shannon diversity**, and equitability. In the spring, these all decreased where the moss layer was removed, but not in the autumn. Moss plots housed 31 mote species, plots with mosses turned over housed 24, and removal plots housed only 16 species. The mosses buffer the temperature (Skre & Oechel 1979; Startsev *et al*. 2007), a possible reason for those mites that lived only among the mosses. It is also likely that the **Collembola**, nematodes, and enchytraeids (annelid worms) among the mosses provided food (Karg 1983; Moore *et al*. 1988; Koehler 1999). The **Collembola** move down into the soil to avoid drought stress (Huhta *et al*. 1986; Pflug & Wolters 2001; Juceviča & Melecis 2002), and mites can easily follow them.
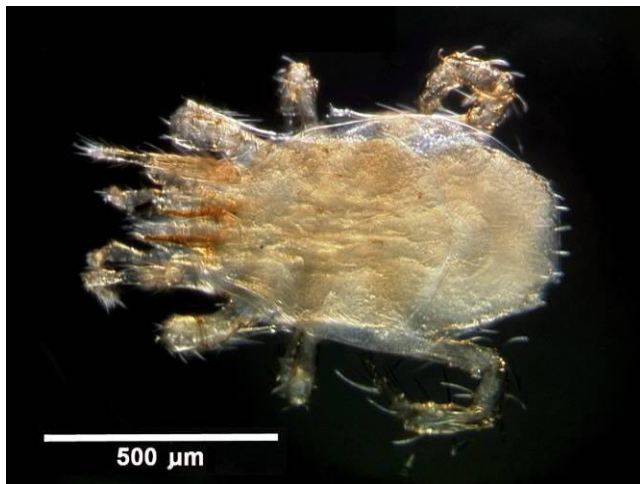

Figure 13. *Veigaia nemorensis* (**Veigaiidae**), a **Gamasina** (**Mesostigmata**) mite that depends on mosses for its habitat. Photo by Derek Tan from Diane Srivastava's online Mite Classification Guide at <http://www.zoology.ubc.ca/~srivast/mites/>, with permission.

Although many species of mites occupy both leaf litter and bryophytes on the forest floor, bryophytes can provide unique habitats unlike those of the forest floor leaf litter. Womersley (1961) reported a new species of trachytid mite, *Acroseius tuberculatus* (as *Polyaspinus tuberculatus*; **Ascidae**; see Figure 17; see Bloszyk *et al*. 2005) from Queensland, Australia, noting that it occurred only in the leaf litter and not among the mosses, indicating the uniqueness of the two habitats. David Walter later found

another member of the genus in litter (including mosses) in Queensland (pers. comm. 15 September 2011; Figure 17).

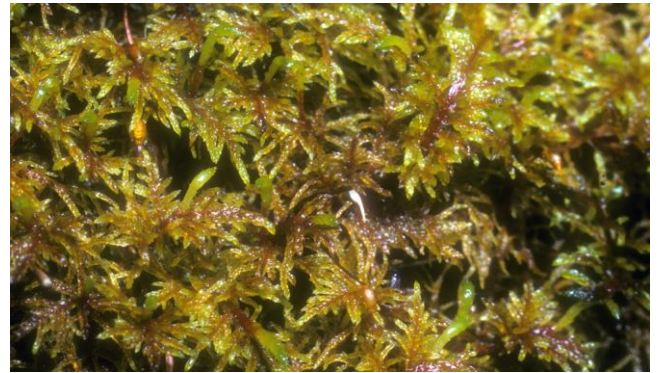Figure 14. *Hylocomium splendens*, a feather moss known to harbor a number of predatory **Gamasina** mites. Photo by Janice Glime.

Figure 15. *Pleurozium schreberi*, a feather moss known to harbor a number of predatory **Gamasina** mites. Photo by Janice Glime.

Figure 16. *Ptilium crista-castrensis*, a feather moss known to harbor a number of predatory **Gamasina** mites. Photo by Janice Glime.
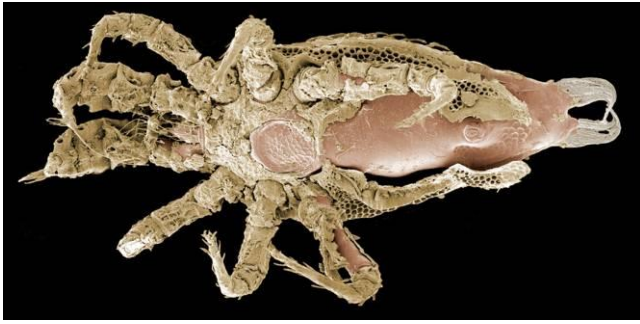
Figure 17. *Acroseius*, new species from litter (including mosses), from Queensland, Australia. Photo by David E. Walter, with permission.

Arboreal Habitats

Canopy communities of mites are distinct from those of the forest floor (Arroya *et al*. 2010). In an old-growth Sitka spruce (*Picea sitchensis*) forest on Vancouver Island, Canada, Behan-Pelletier and Winchester (1998) found 36 oribatid mite species in the canopy and forest floor. In Ireland, 22 species occupied the Sitka spruce forest in the canopy or moss growing on the tree or on the soil.

The canopy community is more homogeneous than that on the soil surface. Five of these species occurred exclusively in the canopy. Three members of **Zerconidae** lived only in the canopy and in moss mats on tree branches. Among these moss-dwelling bryophytes is *Trachytes aegrota* (Figure 18), recorded by Arroya *et al*. (2010) for the first time in Ireland, despite being known since 1841.
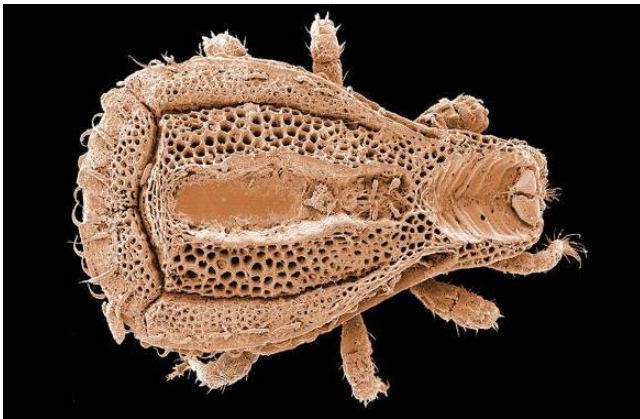

Figure 18. *Trachytes* sp., member of an arboreal genus with bryophyte-dwelling members. Photo by David E. Walter, with permission.

Epiphytes

Epiphytic bryophytes serve as habitat for a number of oribatid mites (Travé 1963; Walter & Behan-Pelletier 1999). In arboreal habitats, bryophytes can provide both 3-dimensional structure and a safe haven that protects against desiccation and predation. In these habitats, one can find a variety of arboreal oribatid mites, with differences occurring among habitat types within the forests (Seniczak 1974). Even within the same Sitka spruce (*Picea sitchensis*) forest, those species occurring in canopy moss mats can differ significantly from those located elsewhere in the canopy (Behan-Pelletier & Winchester 1998).

Figure 19. Red mite on moss *Dicranum montanum* on bark near tree base. Photo by Michael Lüth, with permission.

André (1984) found that 34% of the arthropod epiphyte dwellers in the Belgian Lorraine were oribatid mites, represented by 19,000 individuals in 36 species. The typical *Zygoribatula exilis* (**Oribatulidae**; see Figure 20) association (Pschorn-Walcher & Gunhold 1957; Travé 1963; Lebrun 1971; Gjelstrup 1979) was not present. This mite association is most typical among mosses, liverworts, and foliose lichens in the shade and requires a continuous high humidity (Travé 1963). Thus, it did not find suitable habitat here.
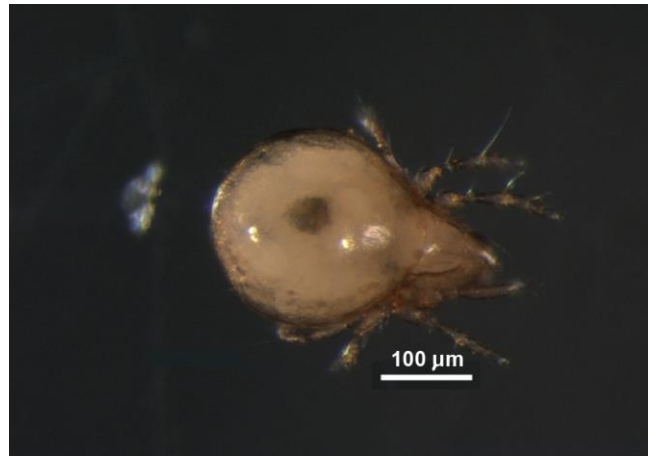
Figure 20. *Zygoribatula* *bulanovae*. *Zygoribatula exilis* is a typical moss dweller among mosses, liverworts, and lichens in shaded, moist areas. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

The activities of mites on the bole of forest trees (which are often covered by bryophytes) raised the question of the role of the tree bore and its bark. As asked by Proctor *et al.* (2002), "Are tree trunks habitats or highways?" In their Australian study of oribatid mites on the hoop pine (*Araucaria cunninghamii*), they found that indeed the bark of the bole harbors a unique community compared to the forest floor. Using insecticides to immobilize the communities, they collected from leaf litter and tree bole. Not only did they find unique communities, but they were nearly 100% distinct! Only *Pseudotocepheus* sp. (**Tetracondylidae**) occurred in both litter and bark habitats. The richness of litter was greater,

but on the bark the oribatid mites comprised the greater percentage of total mites. The researchers were surprised that, contrary to their expectations, the more consistent physical nature of bark as a substrate did not result in greater similarity of oribatid faunas among trunks compared to litter. Rather, greater similarity occurred among litter faunas. They suggested that tree trunks act as islands and that faunal differences represent dispersal challenges that result from traversing across different habitats to reach a new "island." The conclusion: tree boles are not highways from the ground layer to the canopy, at least in this Australian system.

Trapping experiments by Behan-Pelletier and Winchester (1998) in the Sitka spruce canopy on Vancouver Island, Canada, support the hypothesis that dispersal of mites among canopy habitats is due to random movement. Nevertheless, single unidentified species in the genera *Eporibatula* (**Oribatulidae**), *Sphaerozetes* (**Ceratozetidae**), and *Dendrozetes* (**Ceratoppiidae**; Figure 21) had a frequency greater than 50% in canopy traps, suggesting that random dispersal is a successful means for these taxa. One might conclude that the same random dispersal is likely for the bole, but the boles of the individual trees are not touching, whereas the canopies are. Furthermore, bryophytes often provide the dispersal unit, and they are more likely to become attached on a horizontal surface than on a vertical one.

there seemed to be differences in communities that related to the location of the moss mats.

Figure 22. *Acer circinatum*, understory home for moss-dwelling mites. Photo from <www.nwplants.com> through Creative Commons.
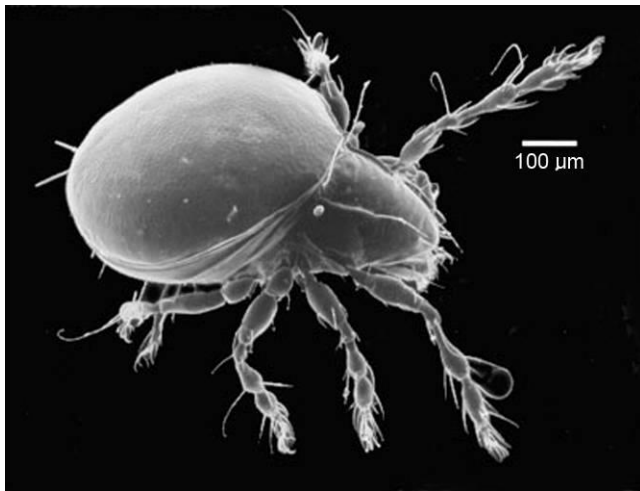
Figure 21. SEM of *Dendrozetes* sp., member of a genus known from Sitka spruce canopy bryophytes. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Peck and Moldenke (2010) became concerned with the role of moss harvesting on the movement of invertebrate communities, including many mites, to new locations. They used Berlese funnels to assess the fauna of bryophyte mats on two shrub species [vine maple (*Acer circinatum*; Figure 22) and huckleberry (*Vaccinium parvifolium*; Figure 23)] in the Pacific Northwest, USA. This method revealed 205 morphospecies of arthropods, and it is likely that there was a portion of the fauna that did not respond to the Berlese funnel arrangement, hence were not counted. The communities between the tree species did not differ, but

Figure 23. *Vaccinium parvifolium* with fruit, home for moss-dwelling mites. Photo by Walter Siegmund, through Creative Commons.

Lobule Mites

Leafy liverworts are common on the boles and canopy branches of forest trees. Among these, *Radula* (Figure 24-Figure 25), *Porella* (Figure 26-Figure 27), *Frullania* (Figure 28-Figure 29), and others have lobes. In *Frullania*, these lobes are modified into **lobules** (Figure 28-Figure 29) that trap and hold water through capillarity.

Figure 24.   *Radula buccinifera* on tree, showing growth habit.   Photo   by   David   Tng   <www.davidtng.com>,   with permission.

Figure 26. *Porella platyphylla* showing growth habit on tree. Photo by Tigerente, through Creative Commons.

Figure 27. *Radula complanata* ventral side showing lobes where mites may hide. Photo by Hermann Schachner, through Creative Commons.

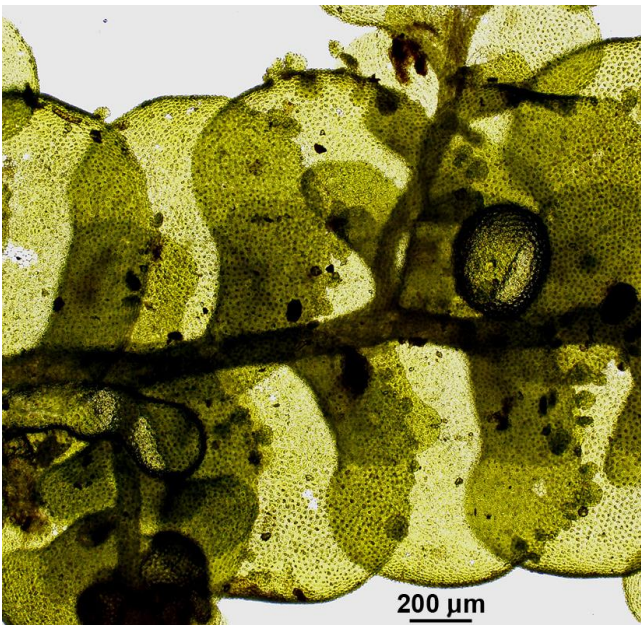Figure 25. *Radula complanata* ventral view showing folded lobes   where   mites   hide.   Photo   from   Dale   A.   Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 28. Leafy liverwort *Frullania rostrata* ventral view showing dark brown lobules where some mites are able to live in members   of   the   genus.   Photo   by   Matt   von   Konrat,   with permission.

Figure 29. *Frullania dilatata*, showing the arrangement of leaves, underleaves, and **lobules** that provide a nearly continuous route of moisture to help mites move about. Photo by Michael Lüth, with permission.

Andi Cairns, Tamás Pócs, Saci Pócs, Chris Cargill, and Elizabeth Brown discovered tiny oribatid mites moving about in the lobules of *Frullania ferdinandi-muelleri* (Figure 30-Figure 31) in the Australian Wet Tropics (Andi Cairns, pers. comm.). Andi later found similar mites in other specimens of *F. ferdinandi-muelleri* they had collected. Matt Colloff determined these to belong to the genus *Birobates* (Figure 31-Figure 33), the first record for the genus in Australia. Because of its association with liverwort lobules, Colloff and Cairns (2011) named this mite *Birobates hepaticolus* (**Oripodidae**; Figure 31-Figure 33). The lobules of the *Frullania* (Figure 31-Figure 32) buffer the mite against moisture loss. The lobules have an opening, giving mites free access, and generally are close to each other and the underleaves, providing a nearly continuous moist enironment. Hence, the liverwort provides a moist habitat that permits these mites to live in otherwise dry habitats. Colloff and Cairns (2011) point out that even if the mites die during periods of liverwort desiccation, the population is likely to survive through its eggs.

Figure 30. *Frullania ferdinandi-muelleri* in Ingham, North Queensland, Australia, a leafy liverwort that serves as home to the newly described *Birobates hepaticolus*. Photo courtesy of Andi Cairns.
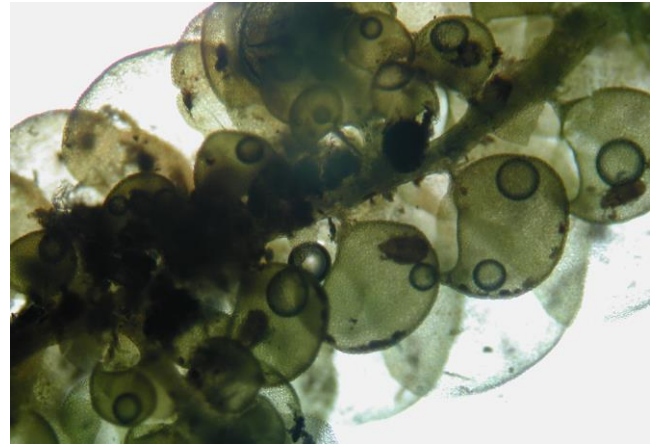
Figure 31. *Frullania ferdinandi-muelleri*. Note the many *Birobates hepaticolus* in lobules, but frequently only one per lobule. Photo courtesy of Tamás Pócs.

Figure 32. *Birobates hepaticolus* mite in the lobule of the liverwort *Frullania ferdinandi-muelleri*. Photo courtesy of Tamás Pócs.

Figure 33. *Birobates hepaticolus* taken from a lobule of the leafy liverworts *Frullania ferdinandi-muelleri*. Photo courtesy of Andi Cairns.

Colloff and Cairns (2011) found that lobules that had mites generally had one to four individuals. The frequency of occupied lobules ranged from contiguous occupation to one in thirty. Every one of the many locality samples had mites in this species of liverwort, although abundance varied widely. It is interesting that only two nymphs were found, whereas there were well over 100 adults.

Furthermore, the liverwort apparently serves as a food source (Colloff & Cairns 2011). Presence of fecal pellets indicated that the mites had been in the lobules for an extended period of time. Consumption of liverworts by mites was not known previously. *Frullania* (Figure 28-

Error! Reference source not found.) is known to have volatile compounds that would discourage eating (Asakawa *et al.* 2003). Dense material in the pellets had the same spectral qualities as the liverworts and appeared to be cells of the same (Colloff & Cairns 2011). In addition to being food itself, the lobules house bacteria, protozoa, rotifers and other small invertebrates that can serve as food.

Figure 34. *Frullania ferdinandi-muelleri* grazed, probably by *Birobates hepaticolus*. Photo courtesy of Andi Cairns.

Semiaquatic Habitats

Terrestrial members of **Parasitengonina** (parasitic mites) may be found among mosses in semiaquatic niches. In particular, members of **Johnstonianidae** all can occur in mosses (Wohltmann 2004). Among these, Wohltmann and co-workers have specifically found *Centrotrombidium* (Figure 35; Wohltmann & Wendt 1996), *Diplothrombium* spp. (Wohltmann 2004), and *Johnstoniana* spp. (Figure 36). Sevsay and Özkan (2005) reported the new species *Johnstoniana hakani* from mosses in Turkey.

Figure 35. *Centrotrombidium schneideri*, a mite whose larva is a parasite on the biting midge *Culicoides*. Photo by Andreas Wohltmann, with permission.

Centrotrombidium schneideri (**Johnstonianidae**; Figure 35) larvae recognize the pupae of the biting midge *Culicoides* sp. (Figure 37) and attach to it to await the emergence of the adult (Wohltmann & Wendt 1996). By attaching to this immobile stage, the larva is guaranteed

that its host won't move to an unfavorable location. As an adult, the *Culicoides* remains in a moist environment that provides the humidity needs of the mite. As the host emerges, the larvae become parasitic on the adult stage.

Figure 36. *Johnstoniana* sp. Photo by Walter Pfliegler, with permission.

Figure 37. *Culicoides* (biting midges) adults, host (as a larva) of the mite *Centrotrombidium schneideri*. Photo by A. J. Cann through Creative Commons.

All developmental stages of these **Johnstonianidae** genera desiccate easily when the air is less than saturated. Mosses, as well as litter, provide the necessary humidity for mating, oviposition, and resting. Other members of **Trombidiae** (**Trombiculidae**, **Trombidiidae**, **Microtrombidiidae**) can burrow into the soil as **deutonymphs** and adults – the mobile stages, but the **Johnstonianidae** are unable to do that. Active stages of all of these **Trombidiae** search among the mosses as well as other locations for prey and for hosts for the next life stage.

Unlike the **Johnstonianidae**, which are confined to amphibious habitats, other mites can occur in such habitats as well as other locations (Andreas Wohltmann, pers. comm. 17 September 2011). These mites that sometimes occur in semiaquatic habitats can be frequent in mosses:

Erythraiae: *Calyptostoma* (Figure 38) in the **Calyptostomatidae**, *Abrolophus* (Figure 39), *Leptus* (Figure 40-Figure 41), *Erythraeus* (Figure 42), and *Charletonia* (Figure 43) in the **Erythraeidae**; **Trombidiae**: *Trombidium* (Figure 44) and *Allothrombium* (Figure 45) in the **Trombidiidae**, *Podothrombium* (Figure 46-Figure 47) in the **Podothrombiidae**, *Microtrombidium* (Figure 48), *Atractothrombium*, *Camerotrombidium* (Figure 49), *Enemothrombium* (Figure 50), *Valgothrombium*, *Echinothrombium rhodinum*, and *Platytrombidium* (Figure 51) in the **Microtrombidiidae**.

Figure 38. *Calyptostoma velutinus* adult, a free-living stage that can occur among mosses in semi-aquatic habitats. Photo by Andreas Wohltmann, with permission.

Figure 39. *Abrolophus* larva, a mite that can occur frequently among mosses when it ventures into semi-aquatic habitats. Photo by Andreas Wohltmann, with permission.

Figure 40. *Leptus trimaculatus* adult. Note the three spots that give it its name. This mite can occur in wet habitats where it becomes frequent among mosses. Photo by Andreas Wohltmann, with permission.

Figure 41. *Leptus beroni*, parasitic larva on the harvestman *Mitopus* sp. Both species can occur among bryophytes. Photo by Andreas Wohltmann, with permission.

Figure 42. *Erythraeus* sp. Some members of this genus are frequent among mosses in semiaquatic habitats. Photo by Tom Murray, through Creative Commons.

Figure 43. *Charletonia* sp. adult feeding on fly (Diptera) eggs. This genus sometimes occurs in semi-aquatic habitats where it can be frequent among bryophytes. Photo by Andreas Wohltmann, with permission.

Figure 44. *Trombidium holosericeum*, velvet mite on soil, where its bright red color makes it easy to see. Photo by Ruth Ahlburg, with permission.

Figure 45. *Allothrombium* sp., a mite shown here on grass, but that can also inhabit bryophytes. Photo by Sankax on Flickr through Creative Commons.

Figure 46. *Podothrombium* sp., a mite of amphibious and other habitats and that can be frequent among bryophytes. Photo by Walter Pfliegler, with permission.

Figure 47. Female *Podothrombium filipes* with eggs visible in her body. However, the eggs in the upper part of the picture are not hers, but eggs of a centipede (*Geophilomorpha*), a source of food for this mite. Photo by Andreas Wohltmann, with permission.

Figure 48. *Microtrombidium pusillum*, a species that maintains its moisture among mosses. Photo by Walter Pfleigler, with permission.
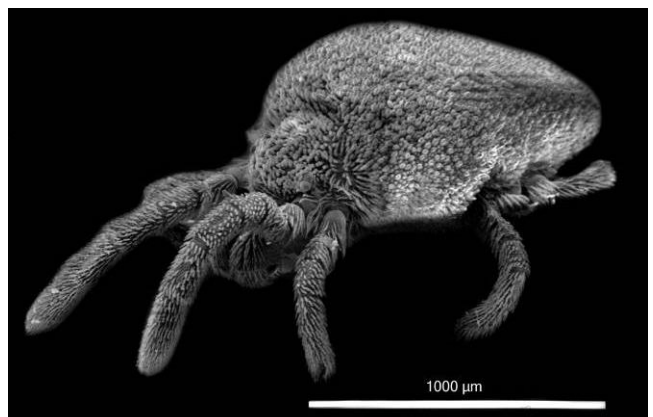

Figure 49. *Camerotrombidium pexatum* adult, a free-living stage that can occur among bryophytes in a variety of habitats. Photo by Andreas Wohltmann, with permission.

Figure 50. *Enemothrombium bifoliosum* adult, a free-living stage that can occur among bryophytes in a variety of habitats. Photo by Andreas Wohltmann, with permission.

Figure 52. *Chaetocladius perennis* adult. Members of this species seem able to avoid being parasitized by aquatic mites by living among mosses. Photo by James K. Lindsey, with permission.

Figure 51. *Platytrombidium fasciatum* adult, a free-living stage that occurs among bryophytes in a variety of habitats, including semi-aquatic ones. Photo by Andreas Wohltmann, with permission.
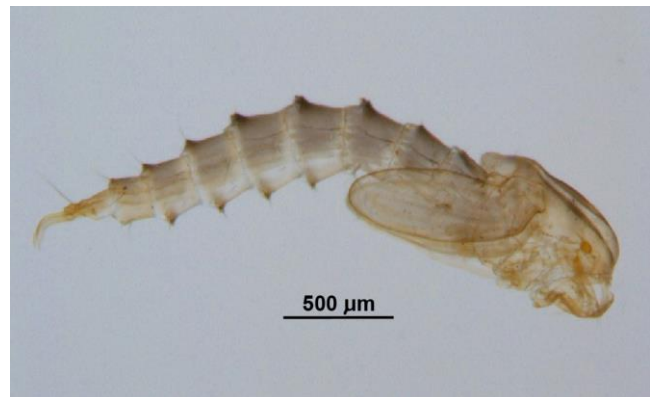
Figure 53. *Tvetenia calvescens* pupa, host for parasitic mites. Photo by P. Kranzfelder, NTNU University Museum, through Creative Commons.

Hosts of parasitic stages of these mites are typically arthropods, and new ones are still being discovered. Stur *et al*. (2005) suggested that the moss-dwelling habit of the midge *Chaetocladius perennis* (Figure 52) may be the reason for absence of mites in their collections. Aquatic mite larvae typically find hosts in the water, not among mosses. This same absence of mites held true for other moss-dwelling midges in these Luxembourg springs. On the other hand, moss dwellers like *Tvetenia calvescens* (**Chironomidae**; Figure 53) and *T. bavarica* (Figure 54-Figure 55) were parasitized in the two springs. Their mossy habitat meant they rarely encountered mites. But Stur and coworkers offered three additional explanations: 1) no water mites parasitize these potential hosts; 2) those water mites that could use these hosts are absent in these springs; 3) the midges are efficient in avoiding colonization by mites.

Figure 54. *Tvetenia bavarica* (**Chironomidae**) larva, host for parasitic mites. Photo by Aina Maerk Aspaas, NTNU University Museum, through Creative Commons.
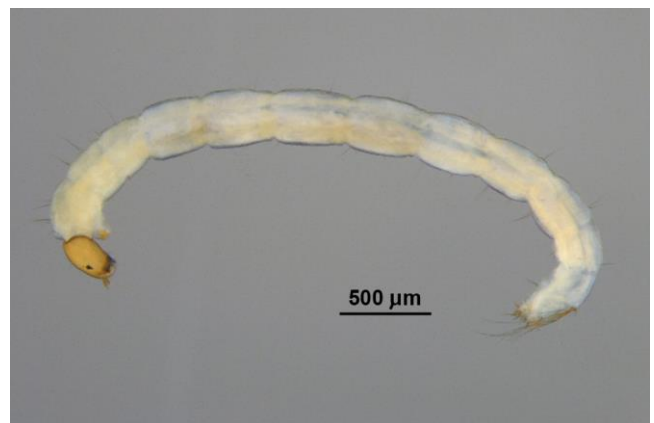
Figure 55. *Tvetenia bavarica* pupa, host for parasitic mites. Sondre Dahle, NTNU University Museum, through Creative Commons.

Calyptostoma velutinus (**Calyptostomatidae**; Figure 38) is a mite that lives on the cranefly *Tipula* (Andreas Wohltmann, pers. comm. 17 September 2011) and probably others. The larvae live on the pupae of *Tipula* (Figure 56), a genus in which the pupal stage often occurs among mosses. This species of mite can also be found on the thorax of the cranefly *Limonia* (Figure 57). Similarly, *Johnstoniana eximia* (Figure 57) lives on the abdomen of *Limonia*. Both of these mites take advantage of the aquatic stages of craneflies for their early development, then emerge when the adult craneflies emerge (Figure 58).

Figure 56. *Tipula* sp. pupa, the stage in the cranefly life cycle that is sought by larvae of the mite *Calyptostoma velutinus*. Several members of *Tipula* pupate among mosses. Photo by Ted Kropiewnicki, through Creative Commons.

Figure 57. Mites *Calyptostoma velutinus* on the thorax and *Johnstoniana eximia* on the abdomen of *Limonia* (cranefly). This genus of cranefly is known to pupate among mosses, permitting the mites to develop there and emerge with the adult craneflies. Photo by Andreas Wohltmann, with permission.

Figure 58. Larva of mite *Calyptostoma velutinus* on thorax of the cranefly *Tipula*. *Tipula* is a common inhabitant of mosses in both its larval and pupal stages. Hence, it is available to moss-dwelling mites as it emerges into the terrestrial habitat. Photo by Andreas Wohltmann, with permission.

Even in the juvenile stage, mites can be subjected to decreased water availability. Although eggs and protonymphs of members of the **Trombidioidea** can take in water vapor from the atmosphere, Wohltmann (1998) demonstrated that this does not occur in **Erythroidea**, including *Calyptostoma velutinus* (**Calyptostomatidae**; Figure 38). Rather, the **Parasitengona** (including *Calyptostoma velutinus*) may have had this character early in their evolution, but have subsequently lost it. Nevertheless, *Calyptostoma velutinus* and others in the **Erythraeoidea** have a higher drought resistance in both instars than do the **Trombidioidea**. Although water uptake seems to be absent in eggs and protonymphs, water uptake prior to the protonymph stage has been observed in post-parasitic larvae of **Trombidioidea** as well as in *C. velutinus*.

Wohltmann (1998) suggests that instead of preventing desiccation by this mechanism of water uptake, drought protection is achieved by a greater sealing of body openings with lipids, as well as reduction in body openings. Together, these result in reduced water loss. This apparently facilitates the consequent increase in body fresh mass by 50% before the protonymph stage begins by increasing the size of the cuticle. For *Calyptostoma velutinus* (**Calyptostomatidae**; Figure 38), this results in "a considerable increase in fresh mass at the end of the post-parasitic larval phase." This may be important in explaining the longer (several days long) post-parasitic stage in this species.

Larval mortality is a high selection pressure among the **Parasitengona**. Two evolutionary traits – larger eggs or more eggs – can help to give the species an advantage against this selection pressure. In the case of **Parasitengona**, evolutionary constraints apparently have kept the egg numbers low (100-300) (Wohltmann 1999). These constraints include difficulty of finding a suitable host in time and restriction to only three growth periods during development that limits adult size. However, some

of the terrestrial and aquatic subgroups have indeed adapted by producing 1000 or more eggs per female.

But reproductive problems do not stop there. Finding a mate can be problematic due to the small numbers of individuals in a single bryophyte clump. Witte (1991) examines the indirect sperm transfer in prostigmatic mites. Important considerations include adaptation of **spermatophores** (protein capsule containing mass of **spermatozoa** (motile sperm, transferred during mating in several invertebrate groups) to low or changing humidities. Like the eggs of some mites, the spermatophores may also exhibit passive uptake of atmospheric water vapor. A second consideration is osmotic protection of sperm cells. Other important factors include spermatophore viability, types of signals used to guide individuals to spermatophores or to a partner, and deposition of spermatophores in absence of a female.

Aquatic Habitats

Figure 59. Pearling (air bubbles) on the brook moss *Fontinalis* sp. Photo by Loh Kwek Leong, with permission.

Aquatic mosses have their own mite fauna, the most common being **Hydrachnidia** (Vlčková 2001/2002) [=**Hydracarina** (Clifford 2012)]. These don't look like aquatic organisms with their chubby morphology, suggesting they often need plants for clinging to avoid being swept away. Furthermore, special adaptations may be needed to permit life in this low-oxygen environment. Smith *et al*. (2011) described the mite *Tegeocranellus muscorum* (**Tegeocranellidae**; Figure 60) in eastern North America as having special structures above the middle two pairs of legs for holding an air bubble when submerging (Figure 61). These bubbles, formed in a condition known as **pearling** (Figure 59) when they come from underwater plants (Benito Tan, pers. comm. 6 June 2011), work like a diving bell into which the mite can exchange CO_2 for O_2 gases. When the bubble gets too small, the mite must return to the surface or the plant for another bubble. Oxygen bubbles produced during plant photosynthesis can provide this source of oxygen, and submersed mosses are often so covered with bubbles that their own structure cannot be discerned (Figure 62).
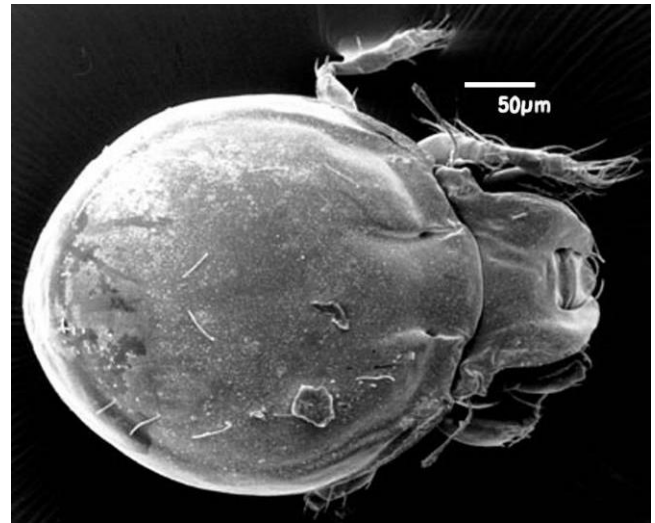
Figure 60. SEM of *Tegeocranellus muscorum*, an aquatic bryophyte-dwelling mite. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 61. SEM of ventral surface of aquatic bryophyte-dwelling *Tegeocranellus muscorum*, where air bubble is held for gas exchange. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.
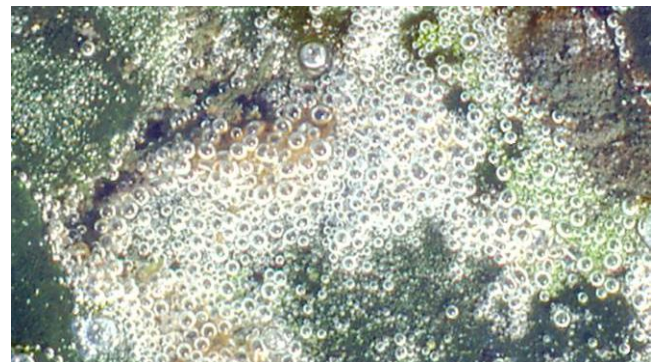

Figure 62. **Pearling** on submerged *Ceratodon purpureus* (Figure 141) from Casey Station, Antarctica, demonstrating complete coverage of the moss. Photo courtesy of Rod Seppelt.

Suren (1991) found that **Hydracarina** were poor indicators of bryophytes compared to gravel in two New Zealand alpine streams, but that they were moderate indicators of shaded conditions. They represented 3.3% of the fauna among gravels in unshaded streams, but only 1.1% among bryophytes there. In the shaded stream, they represented 11.4% of the gravel fauna, but only 5.9% among the bryophytes.

Hynes (1961) found somewhat higher percentages of **Hydracarina** (Figure 63) on bryophytes than on artificial silk mosses in a Welsh mountain stream. This might be the result of better places for these clumsy balls with legs to escape the current among the moss branches, but it could also be related to food availability.

Compared to other arthropods, the **Hydracarina** (Figure 63) on bryophytes are not very abundant. Stern and Stern (1969) found only 1-2 per 0.1 m^2 of moss/algae in a springbrook in Tennessee, USA. Similarly, Frost (1942) found only ca 1% of the fauna to be **Hydracarina** in her study of moss inhabitants in the River Liffey, Ireland. Nevertheless, these averaged 147 individuals per 200 g wet weight of bryophyte sample in the acid stream and 114 in the alkaline stream and comprised 29 species.

Figure 64. *Fontinalis antipyretica*, home for hydrachnid mites. Photo by Projecto Musgo through Creative Commons.

Figure 63. **Hydracarina**, a group of bryophytes that occasionally live among aquatic bryophytes. Photo by BioPix, through Creative Commons.

In a "rip-rapped" channel, Linhart *et al*. (2002) found a strong correlation between the size fractions and quantity of organic matter and mineral matter and the number of hydrachnid mites living within the sediments collected by the moss *Fontinalis* sp. (Figure 64). They contended that *Fontinalis* increased the biodiversity because of the number of organisms supported by that habitat. Needham and Christenson had already noted this phenomenon in 1927.

Cowie and Winterbourn (1979) compared the fauna of three mosses [*Achrophyllum quadrifarium* (=*Pterygophyllum quadrifarium*; Figure 67), *Fissidens rigidulus* (Figure 65), *Cratoneuropsis relaxa*] in the Southern Alps in New Zealand. They found the mites *Notopanisus* sp. (**Hydryphantidae**) on all three mosses and *Platymamersopsis* sp. (**Anisitsiellidae**) on *Achrophyllum quadrifarium* (=*Pterygophyllum quadrifarium*; Figure 67) and *Cratoneuropsis relaxa*. Nevertheless, knowledge of the bryophyte fauna is poor (Suren 1992). Suren found four new species of mites in his study of bryophyte communities in alpine streams of New Zealand.
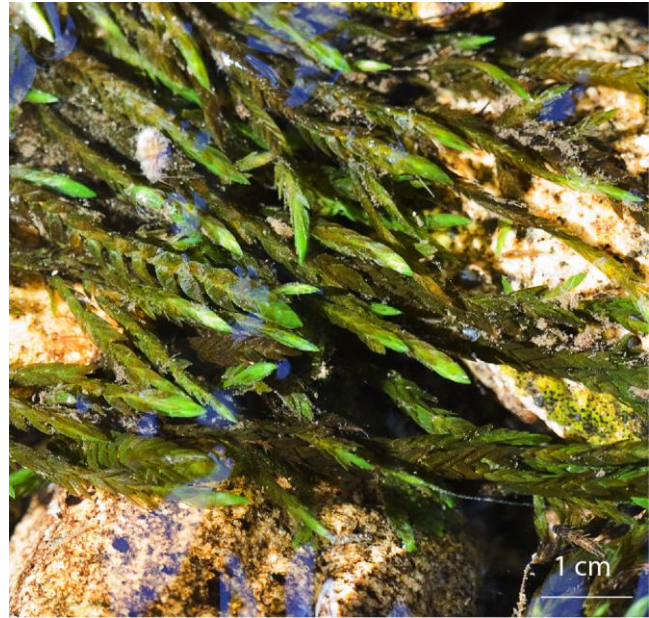

Figure 65. *Fissidens rigidulus*, home for mites in New Zealand. Photo from Museum of New Zealand, Te Papa Tongerewa, through Creative Commons.

Andreas Wohltmann (pers. comm. 17 September 2011) has found that in temporary pools, *Sphagnum* (Figure 66), and probably other mosses, can house species of **Hydryphantoidea** [*Euthyas* (Figure 68), *Parathyas* (syn. *Thyas*; Figure 69), *Hydryphantes* (Figure 70)]. During their terrestrial phase, these mites sit in the water film around the mosses. Unlike other water mites, **deutonymphs** and **adults** of this group can crawl in these terrestrial conditions and thus can move to more humid areas as the moisture conditions change. On the other hand, the superfamilies **Stygothrombioidea**, **Hydrovolzioidea**, **Hydryphantoidea**, and **Eylaoidea** all have terrestrial larvae, whereas only the **Hydryphantoidea** are able to crawl as deutonymphs and adults in that terrestrial environment. The eggs of all four of these superfamilies are deposited in the water, but larvae climb/crawl to the water surface and seek a host at the surface or in the surrounding terrestrial area. In at least some locations, the terrestrial surroundings as they emerge from the water are likely to be covered with bryophytes that help to conserve water.

Figure 66. *Sphagnum* pools, home for a variety of mites. Photo by Boréal, through Creative Commons.

Figure 67. *Achrophyllum quadrifarium*, a bryophyte habitat for mites in streams in the Southern Alps in New Zealand. Photo by Jan-Peter Frahm, with permission.

Figure 68. *Euthyas* sp. This is a preserved specimen that is normally red when alive. Photo CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Figure 69. *Parathyas barbigera* adult, a phase that sits in the water film of mosses near temporary pools. Photo by Andreas Wohltmann, with permission.

Figure 70. *Hydryphantes* sp., lacking normal color due to preservation. Photo courtesy of BOLD Systems Biodiversity Institute of Ontario.

On the other hand, the larvae of **Hydrachnoidea**, **Sperchontoidea**, **Arrenuroidea**, **Lebertioidea**, and **Hygrobatoidea** lack the musculature needed for crawling and must seek their larval hosts in the water column. Likewise, the adults of other water mite genera [*e.g.* *Arrenurus* (**Arrenuridae**; Figure 83-Figure 86), *Limnochares* (**Limnocharidae**; Figure 71), *Piona* (**Pionidae**; Figure 72), *Tiphys* (**Pionidae**; Figure 73)] lack this ability to crawl under terrestrial conditions. Most of them find hosts among the **Diptera**, especially the **Chironomidae** (midges; Figure 54), which are often abundant among aquatic mosses. The mite larvae locate larvae or pupae of these potential hosts and aggregate there, awaiting the emergence of the adult, which they will

parasitize. This method of finding a host (**preparasitic attendance**) is absent among those mites having terrestrial larvae and even among most of the terrestrial **Parasitengonina**.

Figure 71. *Limnochares appalachiana*, decolored due to preservation. The sclerotized plates on the back of this eastern North American species provide additional structure for muscle attachment to support its crawling ability (Smith & Cook 2005). Photo courtesy of BOLD Systems Biodiversity Institute of Ontario.

Figure 72. *Piona coccinea*, an aquatic moss that is unable to crawl on land. Photo by Roger S. Key, with permission.

Figure 73. *Tiphys cf. ornatus* swimming among moss leaves. Photo by Gerard Visser <www.microcosmos.nl>.

Larvae of *Panisellus thienemanni* (**Hydryphantoidea**; Figure 74) parasitize the springtail *Arthropleona* (**Collembola**; Figure 74) in the spring. Andreas Wohltmann (pers. comm. 17 September 2011) has found these mites exclusively in wet mosses of amphibious biotopes. Larvae are also known to parasitize both young and adults of the springtails *Pogonognathellus flavescens* (Figure 75) and *Tomocerus minor* (Figure 76) (Boehle 1996).

Figure 74. *Panisellus thienemanni* larva on the springtail *Arthropleona* sp. (Collembola). Photo by Andreas Wohltmann, with permission.

Figure 75. *Pogonognathellus flavescens*, a species whose larvae parasitize springtails. Photo by Ab H Baas, with permission.

Figure 76. *Tomocerus minor*, a species whose larvae parasitize springtails. Photo by Andy Murray, through Creative Commons.

Some species of **Eylaoidea** [*e.g.* *Eylais* (**Eylaidae**; Figure 77), *Piersigia* (**Piersigiidae**; Figure 78), but not *Limnochares* (**Limnocharidae**; Figure 81-Figure 82)], and of the so-called 'higher water mites' such as *Tiphys* (**Pionidae**; Figure 73) and some *Arrenurus* (**Arrenuridae**; Figure 83-Figure 86) and *Piona* (**Pionidae**; Figure 72) species inhabit temporary waters where they are likely to interact with bryophytes (Andreas Wohltmann, pers. comm. 17 September 2011). The larvae of the genus *Eylais* commonly parasitize **Coleoptera** (beetles), but Smith (1986) found six species that parasitize water boatmen (**Heteroptera**: **Corixidae**). This is a genus of large species, typically 5-6 mm (Halbert 1903). *Eylais hamata* (see also Figure 77) is heavily endowed with carotenoid pigments that can protect it from UV light and make it less conspicuous in its habitat (Czeczuga & Czerpak 1968). For most of these, data are needed to support just how the bryophytes are used.

Figure 77. *Eylais discreta*, an inhabitant of temporary ponds and pools where bryophytes most likely help them to maintain moisture as water levels decrease. Note the deep golden color due to carotenoid pigments. Photo by Andreas Wohltmann, with permission.
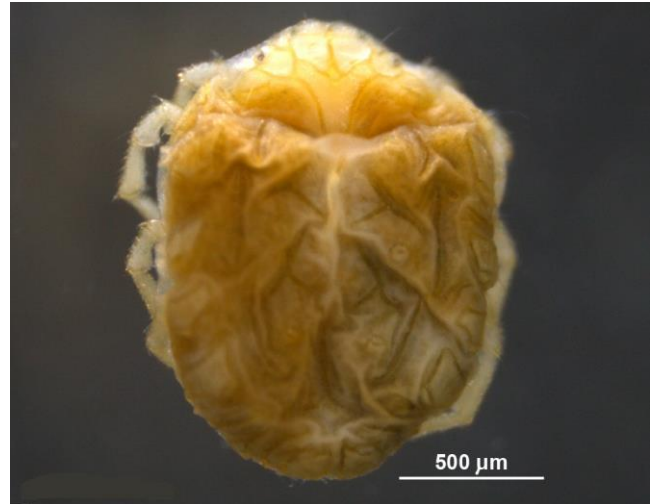
Figure 78. *Piersigia*, preserved – a genus that inhabits temporary waters where bryophytes occur. Photo by Centre for Biodiversity Genomics, through Creative Commons.

In the genus *Eylais* (**Eylaidae**; Figure 79), as many as twenty species may occur in the same area in central New York, USA, *i.e.*, they are **sympatric** (Lanciani 1970). Their larvae are parasitic on **Heteroptera** (true bugs) and **Coleoptera** (beetles) in shallow ponds. They venture to the surface of the water as larvae and await the host when it goes to the surface to renew its oxygen supply. At that time they are able to hitch a ride and attach to the host. According to the Gaussian principle, such species overlap of closely related mites should not occur unless they use their common resources differently. In this case, they partition the resources. Some separation occurs by having different host species, but for those that occupy the same host, separation can occur by season, location on the host, or **biotope** within the habitat. Once attached to the host, they begin feeding and become immobile (Lanciani 1971). Those that have the largest space available grow the most, and larger species tend to occupy larger hosts.

Figure 79. *Eylais* sp., member of a genus with moss-dwelling species. This decolorized preserved specimen reveals the red spots that are most likely internal eggs. Photo courtesy of BOLD Systems, Biodiversity Institute of Ontario.

In eastern Canada, there are at least ten species of the genus *Tiphys* (**Pionidae**; Figure 73) (Smith 1976, 1987). *Tiphys diversus* (**Pionidae**) lives in stream pools and lakes in the southeastern part of the country (Wiggins *et al.* 1980). Eight of the species live in vernal pools. These ten species of mites survive the drying of the temporary pools as

deutonymphs (non-feeding stage that moults into adult), embedding their mouthparts in the leaf axils of mosses. Here they remain at rest until the following spring when the pool again has water.

Moss crawling seems to be common for moss-inhabiting mites, perhaps as a means to maintain moisture. *Chelomideopsis besselingi* (**Athienemanniidae**; Figure 80) is one northeastern North American mite that is common crawling in moss mats and in detritus in springs in the mixed wood plains (Smith 1991, 1992). In *Sphagnum* mats of bog pools (Figure 66), one can find the crawling species *Limnochares aquatica* (**Limnocharidae**; Figure 81; Smith in Smith *et al*. 2011), whose larvae may be attached to the bodies of other arthropods (Figure 82).

The mite *Trichothyas muscicola* (**Hydryphantidae**) in the eastern USA lives in mats of mosses and algae kept moist by seepage areas and splash (Smith 1991). Its northern limit is the Niagara Gorge of the Lake Erie Lowland Ecoregion.

Another Canadian species is *Arrenurus dinotoformis* (**Arrenuridae**; see Figure 83-Figure 86)*, a taxon known exclusively from moss mats at margins of boggy pools where the mites are in and out of the water (Smith in Smith *et al*. 2011). *Arrenurus siegasianus*, a predaceous species (Smith *et al*. 2004) with a boreal distribution, is common in sluggish streams from Newfoundland to Alberta, thus occupying a different niche.

Figure 82. *Limnochares aquatica* **larvae** attached to the legs of a water strider (Heteroptera). Adults can live among mosses in bog pools. Photo by Walter Pfliegler, with permission.

Figure 83. *Arrenurus* sp.; some species of this genus live exclusively among *Sphagnum*. Photo by Ian M. Smith, Val Behan-Pelletier, and Barb Eamer, with permission.

Figure 80. *Chelomideopsis besselingi*, a dweller of moss mats in springs. Photo by Ian M. Smith, Evert E. Lindquist, and Valerie Behan-Pelletier, with permission.

Figure 81. *Limnochares aquatica*, a mite that lives in moss mats of *Sphagnum* pools, shown here in front view displaying two red eyes. Photo by Andreas Wohltmann.

Figure 84. *Arrenurus* (*Megaluracarus*) *globator* female; some members of this genus live exclusively among *Sphagnum*. Photo by Walter Pfliegler, with permission.

Figure 85. *Arrenurus* (*Megaluracarus*) *globator* female; some members of this genus live exclusively among *Sphagnum*. Photo by Walter Pfliegler, with permission.

Figure 86. *Arrenurus* sp. larva; some members of this genus live exclusively among *Sphagnum*. Photo by Walter Pfliegler, with permission.

Some mites, such as *Malaconothrus* (**Malaconothridae**; Figure 87), can appear in large numbers among the aquatic mosses (Krantz & Lindquist 1979). Behan-Pelletier (1993) reports that deutonymphs and adults of aquatic mites are often specialized for their habit of crawling among mosses and detritus. Most of them are also cold-adapted. Others, such as *Laversia berulophila* (**Laversiidae**), are more generalized and are able to live in the **profundal** zone (deep zone of inland body of free-standing water, located below range of effective light penetration) of **oligotrophic lakes** (lake relatively low in plant nutrients, containing abundant oxygen in deeper parts) as well (Smith in Smith *et al.* 2011). In bog/fen pools there are nearly 50 species in Canada in the mixed forest plains. These are adapted for clinging to *Sphagnum* (Figure 95) and other mosses (Figure 88), but also for swimming. They are adapted for cool water in the northeastern and boreal peatland pools, mostly in relict habitats.

Figure 87. *Malaconothrus* sp., member of a genus that can be found among aquatic mosses. Photo courtesy of BOLD Systems, Biodiversity Institute of Ontario.

Figure 88. These water mites (probably **Hydryphantoidea)** are inhabiting the moss *Palustriella falcata*, a species common in moderate to highly mineral-rich pools and ponds. Photo by Dan Spitale, with permission.

In **streams**, Badcock (1949) found that mites were most abundant where moss or other substrate provided shelter. In my own collections of stream mosses, I did occasionally find tiny red mites. However, these were never abundant and were infrequent. Stream edge and streamside habitats, on the other hand, provide a moist habitat where these non-streamlined mites are out of the danger of current. Red seems to be a common color for water mites, possibly serving as warning coloration – or not (Figure 1, Figure 88).

In an attempt to determine the role of bryophytes that had been lost from a stream suffering from sewage effluents, Dewez and Wauthy (1981) used sponges to simulate the bryophyte habitat and capture water mites. These sponge colonizations suggested that loss of bryophytes had impacted both numbers and diversity of mites negatively. They also found that the mite *Hygrobates fluviatilis* (**Hygrobatidae**; Figure 89) played a major role in determining the numbers and organization of the communities. Since sponges served as a suitable habitat, one might conclude that the bryophyte served primarily as a substrate and safe site, not as a direct source of food.

Angelier *et al.* (1985) found that both the presence and type of moss, compared to gravel, were important in determining the mite community. One factor that seemed to play a role in this relationship was stability of the rock substrate. Mosses only developed colonies on rocks that stayed put.

The species *Hydrovolzia mitchelli* (**Hydrovolziidae**; Figure 90), a species from the mixed wood plains, prefers cold **springs** and seepage areas (below 10°C) (Smith in Smith *et al.* 2011). The deutonymphs and adults spend

time crawling through detritus and moss mats, a slow feat for them. The larvae are parasites on adult **Empididae** (Figure 91), a small dipteran whose larvae sometimes live among mosses. Members of the **Unionicolidae** (Figure 92) can be found in streams, where they inhabit mosses like *Hygroamblystegium* (Figure 93) (Paul Davison, pers. comm. 27 September 2011). *Fissidens fontanus* (Figure 94) also serves as a suitable habitat for water mites. These mites avoid open water and seem to need to be in contact with a substrate.

Figure 91. *Empis bistortae*, host of larval mites (*Hydrovolzia mitchelli*) that crawl among mosses as adults. Photo by James K. Lindsey, with permission.

Figure 89. *Hygrobates fluviatilis*, a species that depends on aquatic mosses. Note the brown patches – they are body parts visible through the transparent soft body integument. Photo by Nigrico, through Creative Commons.

Figure 92. Water mite (probably **Unionicolidae**), a common group among aquatic mosses. This one was in a spring-fed stream on mosses like *Hygroamblystegium*. Photo by Paul Davison, with permission.

Figure 90. *Hydrovolzia mitchelli*, a mite of cold springs where it crawls among detritus and moss mats. Photo by Ian M. Smith, Evert E. Lindquist, and Valerie Behan-Pelletier, with permission.

Figure 93. *Hygroamblystegium fluviatile*, home for members of **Unionicolidae**. Photo by Michael Lüth, with permission.

Figure 94. *Fissidens fontanus*, home for aquatic mites that avoid open water. Photo by Michael Lüth, with permission.

Sphagnum Peatlands

Peatlands present unique challenges to their inhabitants (Behan-Pelletier & Bissett 1994). Not only do they experience highly fluctuating temperatures at the surface, seasonal water-logging, and low nutrients, but they also have a low *p*H resulting from the activities of the *Sphagnum* (Figure 95) itself (see below). Furthermore, the low conductivity of the moss results in a shorter frost-free season than that of the surrounding habitats. Relative humidity among the moss stalks generally remains at 100%, but at the surface it may drop to 40% during the day. For those mites able to migrate up and down (see below), finding a suitable temperature and humidity combination should not be difficult.

Figure 95. *Sphagnum capillifolium* lawn. Photo by Bernd Haynold, through Creative Commons.

Among the microarthropods, the mites are the most abundant and diverse group of organisms on the peatland bryophytes (Behan-Pelletier & Bissett 1994), but not in the open water. These peatland mites include water mites, oribatids, and **Mesostigmata** (Hingley 1993). The **Oribatida** (moss mites) are predominant among these (Behan-Pelletier & Bissett 1994). Behan-Pelletier and Bissett (1994) reported 71 species of oribatids in the peatlands of Canada. These are species of widespread distributions, either Holarctic or worldwide. The aquatic

species, on the other hand, seem to be restricted to the Nearctic.

Peatland mosses typically offer a compact cover that is generally moist, hence providing both protection from predators and from desiccation. For mites, this habitat is therefore often an inviting one (Seyd 1988). This habitat is, nevertheless, quite variable in water availability. Silvan *et al.* (2000) demonstrated that "soil" mites increased in numbers with drainage and draw-down of peat soils, suggesting that in many areas the peatlands are simply too wet for many species. In fact, older drained sites typically had mite populations ten times as large as those on undrained sites. Re-wetting caused an abrupt drop in numbers. Among those invertebrates found, the oribatid mites were the most frequent, comprising nearly 60% of the fauna on undrained sites.

Many mite families found elsewhere in the general area, including those on mosses (*e.g.* some **Eremaeidae**, **Oppiidae**, **Galumnidae**), are absent or poorly represented in peatlands. Both wet and dry extremes in peatlands have few mite species but a high number of individuals. Thus, it is the intermediate levels of moisture that provide the best locations for most of the oribatid mite species (Tarras-Wahlberg 1961; Belanger 1976; Borcard 1988, 1991c, e; Behan-Pelletier & Bissett 1994).

Within the peatlands, one can find multiple niches with considerable differences in microclimate. Belanger (1976) found 44 species of oribatids in a North American poor fen peatland, 26 of which were also known from European peatlands. Among the microarthropods there, oribatids comprised 84% of the species within the peat, 70% of that on *Sphagnum* (Figure 95) stalks, and 39% of that on *Sphagnum* tops. But from the perspective of the mites, the *Sphagnum* stalks seemed to be the "optimum microhabitat" in the *Sphagnum* because of its species richness and density. This was the habitat where the oribatid assemblage was the most stable.

In Europe, the mite fauna of *Sphagnum* (Figure 95) peatlands is well known (*e.g.* Scandinavia: Tarras-Wahlberg 1954, 1961; Dalenius 1960, 1962; Solhøy 1979; Markkula 1986a, 1986b; Russia: Laskova 1980; Druk 1982; Lithuania: Eitminavichyute *et al.* 1972; Germany: Beier 1928; Willmann 1928, 1931a, b, 1933; Peus 1932; Sellnick 1929; Popp 1962; Switzerland: Borcard 1988, 1991a, b, c, d, e). These studies indicate that the peatland oribatid species are seldom restricted to peatlands. North American studies seem to have lagged behind, with notable ones scattered broadly in time (Banks 1895; Jacot 1930; Belanger 1976; Behan-Pelletier 1989; Larson & House 1990; Palmer 1990; Hingley 1993; Behan-Pelletier & Bissett 1994).

The Fauna

Peatlands generally have low numbers of mite species. Smith (in Smith *et al.* 2011) reported that *Hydrozetes* (**Hydrozetidae**; Figure 96) are the most numerous of the oribatids in peatland pools, where they move about by clinging to the surface film of the water. In eastern Canada, the most species-rich genus within the moss mat is *Limnozetes* (**Limnozetidae**; Figure 97), often being the only genus in the dripping *Sphagnum* (Figure 95) and layers of peat (Behan-Pelletier & Bissett 1994; Smith in

Smith *et al*. 2011). Borcard (1991c) reported up to 100,000 specimens of oribatid mites from just one cubic meter of wet *Sphagnum* in Canada. Popp (1962) reported *Limnozetes ciliata* and *L. rugosus* (see Figure 107-Figure 112) in the *Sphagnum fuscum* (Figure 98) association in Germany; in the same bog, *Pilogalumna tenuiclavus* (**Galumnidae**) occurred in the *Sphagnum magellanicum* association (Figure 99).

Figure 96.   *Hydrozetes* sp., member of a genus that is common in peatland mills. Photo by Walter Pfliegler, with permission.
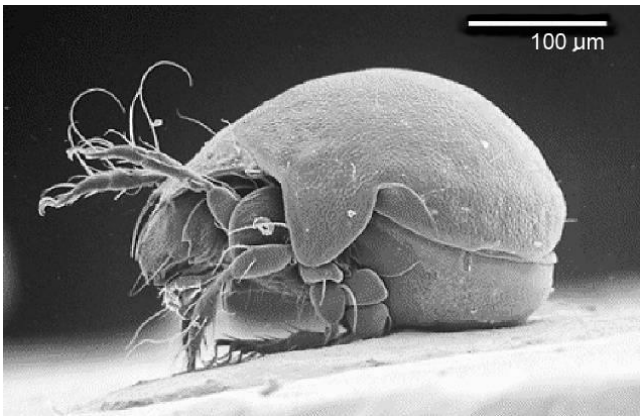

Figure 97.   *Limnozetes*, a common genus in dripping *Sphagnum* and peat layers. Photo by Valerie Behan-Pelletier & Barb Eamer, with permission.

Figure 98.   *Sphagnum fuscum* in Alaska. Photo by Andres Baron Lopez, with permission.

Figure 99.   *Sphagnum magellanicum* (red) mixed with other species of *Sphagnum* at Cape Hope. Photo from NY Botanical Garden, through public domain.

Donaldson (1996) demonstrated the richness of oribatid mites in a moat bog in New Hampshire, USA. Among the 220 adult oribatids collected, 44 species were represented from three *Sphagnum* species. These three species formed a moisture gradient with increasing height above the water surface, from *S. cuspidatum* (Figure 100) in the water, to *S. recurvum* (Figure 101), to *S. magellanicum* (Figure 99) on top. This same gradient also represented increasing light levels. The oribatid mite species diversity increased from water level to hummock top. The genus *Limnozetes* (**Limnozetidae**; Figure 107-Figure 112) was well represented by four species associated with *Sphagnum* in this bog.

Figure 100. *Sphagnum cuspidatum*, a moss that is typically mostly submersed. Photo by Jutta Kapfer, with permission.

Figure 101. *Sphagnum recurvum* var *mucronatum*, a moss that is typically mostly submersed. Photo by Jan-Peter Frahm, with permission.

This study was surpassed in breadth by that of Mumladze *et al.* (2013). They reviewed studies on the oribatid mites throughout the Holarctic region by examining data from 46 peat bog localities and found reports of 410 species. They found a non-random metacommunity structure for all the ecological guilds studied. Although they found no latitudinal gradients in species composition, they did find a non-linear decay with distance between communities. They found that at the community level, structure of the species is determined primarily by interspecific interactions and common biogeographical history. At the metacommunity level, on the other hand, the postglacial colonization processes are the most important factors in determining patterns.

Among the oribatids, the community composition varies among peatlands, with many of the species also found in other types of wetlands. Nevertheless, two genera have a high fidelity to Canadian peatlands: *Malaconothrus* (**Malaconothridae**; Figure 87) and *Limnozetes* (**Limnozetidae**; Figure 107-Figure 112) (Behan-Pelletier & Bissett 1994). But even these may be absent in some dry, oligotrophic bogs (Solhøy 1979). *Limnozetes*, a fungal grazer on the surface of the *Sphagnum* (Figure 95) plants, is so important in describing the community that Behan-Pelletier and Bissett (1994) suggested that the species composition could be useful to characterize peatlands. The adults of *Limnozetes* species graze all surfaces of the moss, whereas the immatures graze only the inner, cupped surfaces. *Ceratozetes parvulus* (**Ceratozetidae**; see Figure 102), a "constant component" of the peatland fauna, seems to have some subtle restrictions; in one virgin bog in Finland it was restricted to the hollows (Markkula 1986a).
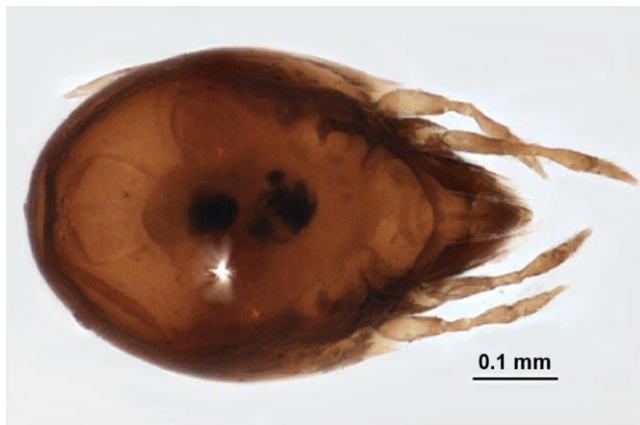

Figure 102. *Ceratozetes* sp. *Ceratozetes parvulus* is a predictable bog dweller. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

In some areas of Europe, the bog mite fauna seems to lack study. The family **Cunaxidae** (Figure 103) lives in saturated mosses such at those at the edge of bog pools (Hughes 1959). Krogerus (1960) found records of three species of **Erythraeoidea** from Finnish bogs, but there were no preserved specimens available for species verification (Gabryś *et al.* 2009).

In Great Britain, over 60 species have been recorded in peatlands (Hingley 1993). Many species of oribatids (seed mites) occur. In addition, there are several species of **Hydracarina** (water mites) and **Mesostigmata**. The characteristic genera include *Malaconothrus*

(*Trimalaconothrus*; **Malaconothridae**; Figure 87), *Hydrozetes* (**Hydrozetidae**; Figure 104-Figure 106), and *Limnozetes* (**Limnozetidae**; Figure 107-Figure 112). *Hydrozetes lacustris*, and probably also *Limnozetes ciliatus* (see Figure 107-Figure 112), live among the stems and leaves. *Trimalaconothrus maior* (**Malaconothridae**) lives in the leaf axils. Seeming to defy the Gaussian principle, up to five species of *Limnozetes* (see Figure 107-Figure 112) can occur on a single *Sphagnum* (Figure 98-Figure 99) sample, but perhaps no resource, especially space, is limiting. None of these species is limited to *Sphagnum*. Fewer species but more individuals occur in the drier parts of the peatlands.

Figure 103. Member of **Cunaxidae**, a peatland family. Photo by Scott Justis, with permission.

Figure 104. *Hydrozetes* sp. on the leaf of an aquatic plant. This genus is common in peatlands. Photo by Walter Pfliegler, with permission.
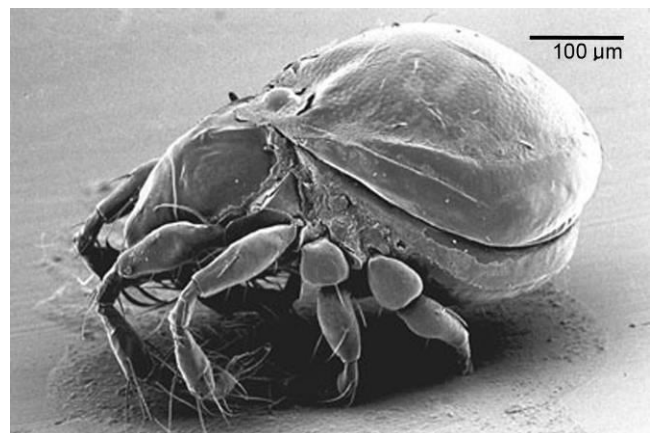

Figure 105. SEM of *Hydrozetes*, a genus common in peatlands. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.
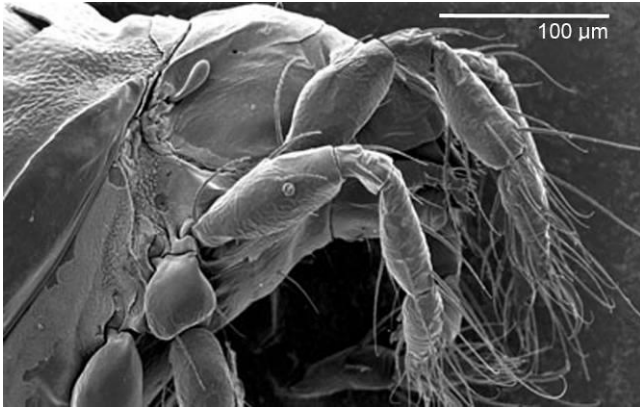
Figure 106. SEM of head region of **Hydrozetes**, a genus common in peatlands. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 107. SEM of **Limnozetes borealis**. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 108. SEM of **Limnozetes guyi**. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 109. SEM of dorsal view of **Limnozetes palmerae**, member of a genus that is common on peatland mosses. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 110.   SEM of head region of **Limnozetes latilamellatus**, member of a genus that can have high diversity on peatland mosses. Photos by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 111. SEM of **Limnozetes latilamellatus**, member of a genus that can have high diversity on peatland mosses. Photos by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 112. SEM of side view of **Limnozetes palmerae**, member of a genus that is common on peatland mosses. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

In Canada, the genera are somewhat different from those in Europe, with mites such as **Parhypochthonius** (**Parhypochthoniidae**; Figure 113) and **Nanhermannia** (**Nanhermanniidae**; Figure 114) occurring in peatlands (Smith *et al*. 2011). The latter is one of the most common and most abundant of the oribatid mites in northeastern North American peatlands (Behan-Pelletier & Bissett 1994). By contrast, the poorly represented families **Oppiidae** and **Suctobelbidae** in Canada are dominant in some bogs in Europe (Sweden: Tarras-Wahlberg 1961; Finland: Markkula 1986a; Switzerland: Borcard 1992), with

Oppiella nova (**Oppiidae**; Figure 115) being among the most abundant (Behan-Pelletier & Bissett 1994).

Figure 113.   SEM of *Parhypochthonius* sp., member of a Canadian peatland mite genus.   Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 114.   *Nanhermannia* from peatlands in Canada. Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 115. *Oppiella nova*, an abundant mite in bogs. Photo from SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

Trampling

I know of no other study on the effects of trampling in bogs and poor fens, but the study by Borcard and Matthey (1995) is quite interesting. Not only does it demonstrate differences between species of *Sphagnum* (Figure 95, Figure 98-Figure 99) in their response to this abuse, but its primary objective was to determine the effects on the oribatid mite community.

During cranberry season, and in some bogs and poor fens, during blueberry season, the mosses can be subjected to considerable trampling by berry pickers. I have been to these habitats just after picking season and could see the destruction. I have also seen it following a class field trip, causing me to keep the students off the mat in later trips. But I had given little thought to the effects on the organisms within the mat.

In experiments involving 1 m^2 plots, Borcard and Matthey (1995) compared mite communities associated with hollow (wet) species *Sphagnum recurvum* (Figure 101) with that of hummock (drier) species *Sphagnum fuscum* (Figure 98) in a raised bog in Switzerland. Two plots of each species were trampled for ten minutes each, three times per year for four years, and compared with control plots. The plot with *S. recurvum* became a "muddy depression." The oribatid mites fared no better, dropping from 20 species to 4. *Limnozetes ciliatus* (**Limnozetidae**; see Figure 97), a common peatland mite, had a 96% relative frequency and was the overwhelming dominant following trampling.

The *Sphagnum fuscum* (Figure 98) hummock had a quite different response. The moss died, but the hummock retained its shape. The mite community, as in *S. recurvum* (Figure 101), had a reduction in species, but in this case was only reduced to 10 compared to its former 23. The surprise was that one species, *Ceratozetes parvulus* (**Ceratozetidae**; see Figure 102), that had been nearly absent before the trampling actually benefitted from the trampling.

Several factors account for the decrease in mite diversity and abundance. In both cases, the mosses were strongly compacted.   The density of the top 3.5 cm increased more than 2-fold in both species.   The entire vertical expanse became very homogeneous, lacking the vertical stratification of space and moisture available in the controls. Water content increased on a per volume basis. This compaction and increased water content made a habitat unsuitable for the original moss mite inhabitants.

The sampling itself made changes to both control and experimental plots. Removal of three cores (5 cm diameter, 13 cm deep) created a less dense habitat that permitted greater drying.   This resulted in species shifts, even in control plots. In *Sphagnum recurvum* (Figure 101) control plots, *Oppiella nova* (**Oppiidae**; Figure 115) increased in numbers, possibly benefitting from drying around sampler holes.   More hygrophilous species [*Limnozetes ciliatus* (**Limnozetidae**; see Figure 97), *Hoplophthiracarus pavidus* (**Phthiracaridae**)] tended to decrease for the same reasons. On the other hand, fungi invaded sample holes, providing a potential food source for fungivorous mites.

Loss of abundance followed different patterns in the two moss species (Figure 116).   Those in *Sphagnum recurvum* (Figure 101) exhibited a "saw-tooth" pattern that indicates partial recovery between autumn and spring or summer sampling/trampling dates.   Furthermore, the evenness dropped precipitously, with the semi-aquatic *Limnozetes ciliatus* (**Limnozetidae**) see Figure 97) having extreme dominance. By contrast, the decrease in number of species in *S. fuscum* (Figure 98) was less dramatic, and evenness did not change significantly. The latter greater constancy is attributable to a greater retention of non-inundated spaces within the hummock.
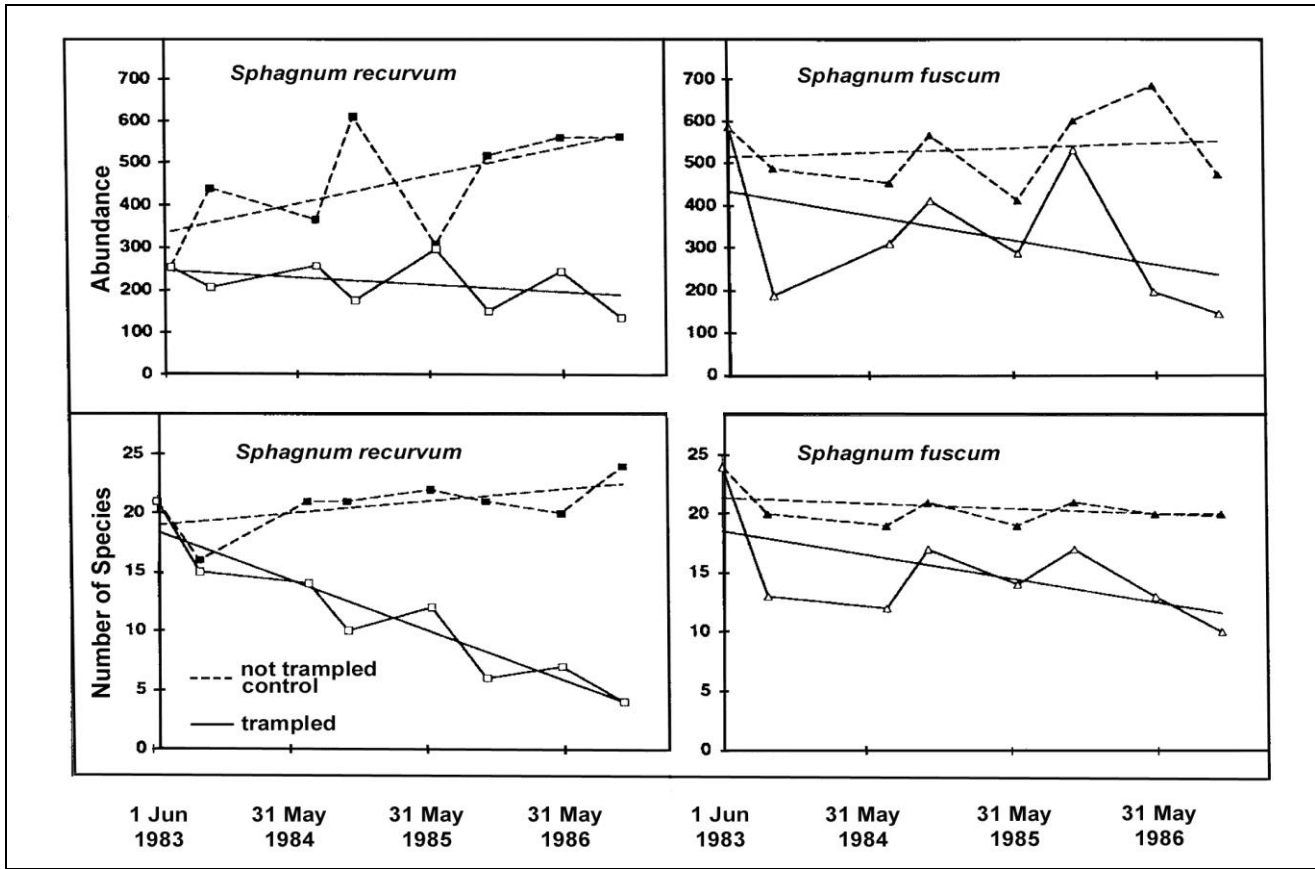
Figure 116. Changes in number of oribatid mite species and abundance in sample *Sphagnum* cores (5 cm diameter, 13 cm deep) through four successive years of trampling. Redrawn from Borcard & Matthey 1995.
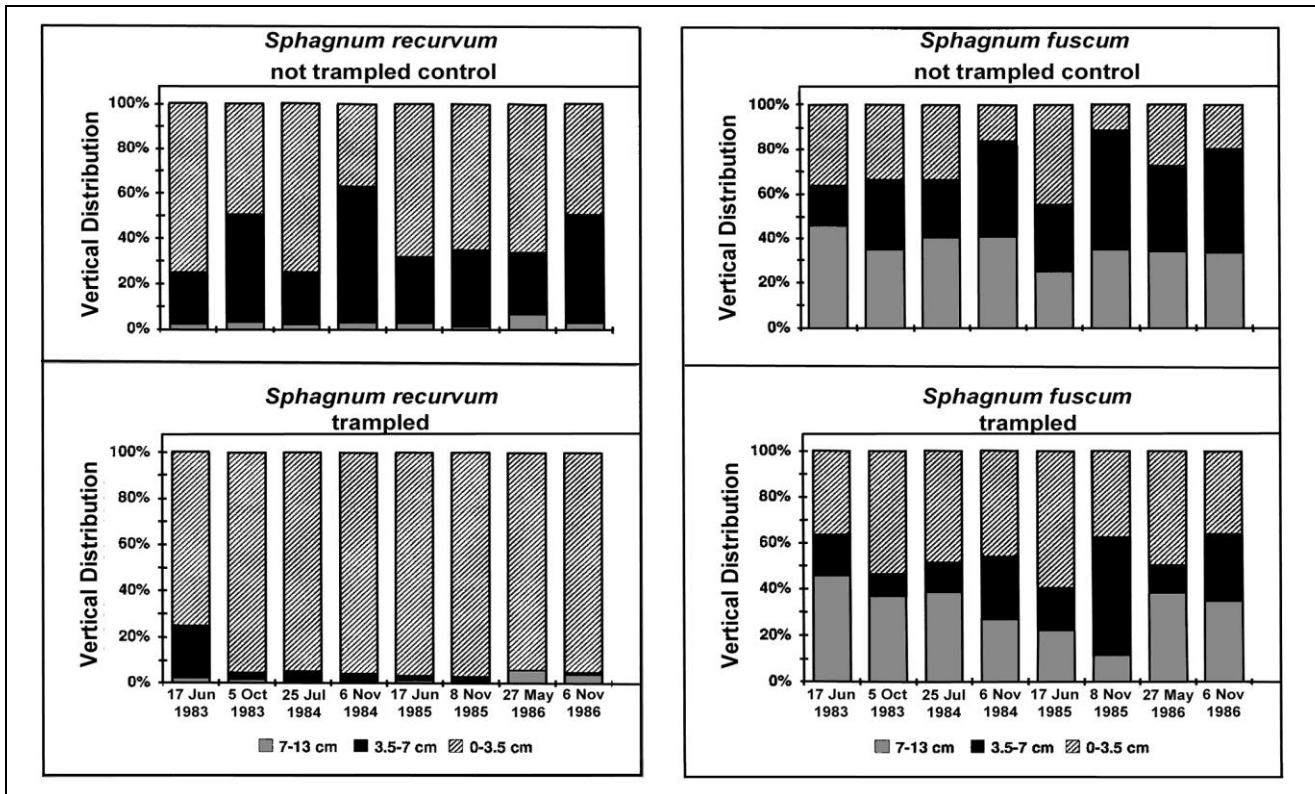

Figure 117. Vertical distribution of oribatid mites in two *Sphagnum* species in trampled and non-trampled control plots in a bog in Switzerland. Redrawn from Borcard & Matthey 1995.

As one might expect, the vertical distribution of the mites changed as the structure of the moss strata changed (Figure 117). In *Sphagnum recurvum* (Figure 101), there was a severe loss of mites from lower strata, with remaining individuals located predominately in the upper 3.5 cm. Such dramatic change was not evident in *Sphagnum fuscum* (Figure 98), where original structure changed little following trampling, despite death of the moss.

One interesting result is a dramatic increase of the tiny *Ceratozetes parvulus* (see Figure 102) in the *Sphagnum fuscum* (Figure 98) hummock. This species is rare throughout the bog, so its increase to 13-30% under disturbance is a surprise. Could this flattened species have benefitted from compaction that permitted it to maneuver out of reach of larger predators?

Predation

Hiding oneself deep in the *Sphagnum* (Figure 98) peat may prevent at least some predation on the mite fauna. This would seem to be likely for those known to be prey of the newt *Notophthalmus viridescens* (Figure 118), also a peatland dweller. At least 45 species of oribatids are known food items for this species (Norton & MacNamara 1976). The compact peat is often impenetrable for this newt. But known oribatid predators such as the smaller beetles and ants (Riha 1951; Schuster 1966; Schmid 1988; Norton & Behan-Pelletier 1991) that co-inhabit the mosses should be able to penetrate many of the same small spaces as the mites. For those living in the pools and channels of the peatlands, the naiads of dragon- and damselflies (**Odonata**) can be major predators. Behan-Pelletier and Bissett (1994) found that 63% of the 60 *Aeshna sitchensis* guts they examined had oribatid mites in them, with a mean of 7 per gut. Presence in the other four species examined ranged from 10% frequency upward. Adult mites were more common than immatures, a phenomenon that Behan-Pelletier and Bissett suggested might relate to the habit of the immatures to graze only on the inner surfaces of the leaves where they were much more protected. The **Odonata** were apparently better collectors than the researchers – several species in the gut had not been located previously in the bog pools! The **Odonata** guts also contained predators of the mites, suggesting that these insect naiads were both friend and foe.

Figure 118. *Notophthalmus viridescens* adult, a predator on mites. Photo © Gary Nafis at <CaliforniaHerps.com>, with permission.

Acidity Problems

One problem that organisms always face in *Sphagnum* peatlands (Figure 66) is the low *p*H. Although *Sphagnum* is usually too acid for most mites, *Hydrovolzia placophora* (**Hydrovolziidae**; see Figure 90) seems to be tolerant of the low *p*H and occurs in the axils of leaves that protect it from open water (Gledhill 1960). This mite is not able to swim.

For mites, the acidity could present itself as difficulty in hardening of the cuticle due to the need for calcium. Although a common form of calcium is calcium carbonate, it appears that calcium oxalate (whewellite) can also serve this purpose, at least for the mites *Eniochthonius minutissimus* (**Eniochthoniidae**; Figure 119), *Archoplophora rostralis* (**Mesoplophoridae**), and *Prototritia major* (**Protoplophoridae**), and is deposited even in *Sphagnum* peatlands (Figure 66) (Norton & Behan-Pelletier 1991). Norton and Behan-Pelletier (1991) suggested that the calcium oxalate is probably obtained from crystals precipitated by fungi and used as food by the mites. This discovery was the first to demonstrate the role of minerals in hardening of the cuticle of arachnids.

Figure 119. *Eniochthonius minutissimus* ventral composite. Photo by Matthew Shepherd, through Creative Commons.

Jarmo Holopainen (pers. comm. 16 September 2011) considers the biochemistry of peatlands to have a negative impact on mites. Volatile organic compounds are released from the *Sphagnum* (Figure 95) and many of the compounds produced by this genus have antibiotic effects against microbes – important food organisms for many mites. The peat has a high content of **Actinobacteria** (=**Actinomycetes** – formerly thought to be fungi; Figure 120), a group that produces antibiotics that might also have an effect on mite abundance. On the other hand, oribatid mites are known to have **Actinobacteria** in their digestive systems (Cromack *et al*. 1977), suggesting that at least some might benefit from the fungi.
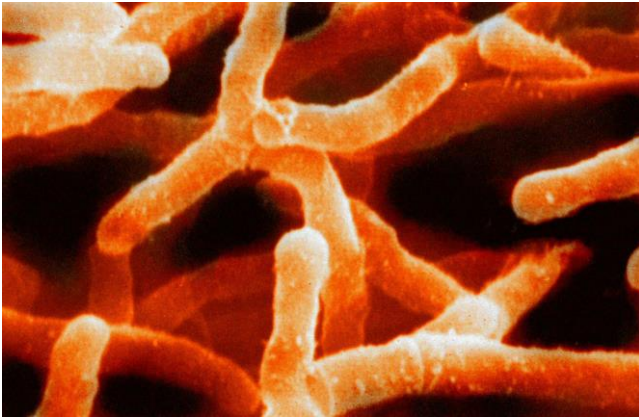
Figure 120. *Actinomyces israelii* with false color, a member of **Actinobacteria**. Photo by Graham Colm through Creative Commons.

Mites have a role in this scenario in another way. Spores of the Actinomycetes, and other **propagules** (dispersal units), are transported by the mites (Ruddick & Williams 1972) and in some cases undoubtedly introduce them to peatlands and other bryophytic habitats.

Historical Indicators

Like the testate amoebae, mites have been used to reconstruct the long-term history of peatlands and lakes (Erickson 1988; Markkula 1986a; Behan-Pelletier & Bissett 1994; Luoto 2009). Birks *et al*. (2000) used community structure of subfossil vegetation including mosses and invertebrates including mites to reconstruct past history (late-glacial and early-Holocene) of Kraekenes Lake, western Norway. *Hydrozetes oryktosis* (**Hydrozetidae**; see Figure 104-Figure 106) and *Limnozetes cf. rugosis* (**Limnozetidae**; see Figure 107-Figure 112) can be used to infer lake levels (Erickson 1988; Solhøy 2001). In the Antarctic, Hodgson and Convey (2007) found *Alaskozetes antarcticus* (**Ameronothridae;** Figure 130) and *Halozetes belgicae* (**Ameronothridae**), both known moss dwellers, in a sediment core. The expansion of their numbers indicated a temperate period. In Finland, Markkula (1986a) found that *Limnozetes ciliatis* (see Figure 97) indicated presence of hollows, being absent in the hummocks. For the genus *Limnozetes*, acidity is important in defining which species occur (Behan-Pelletier & Bissett 1994).

Antarctic and Arctic

The Antarctic usually provides a good source of information on moss-dwelling invertebrates, and mites are no exception (Goddard 1979; West 1984; Schenker & Block 1986; Mitra 1999). In the Antarctic, bryophytes are an especially important habitat for mites (Booth & Usher 1986). Barendse *et al*. (2002) suggest that bryophytes and lichens may have served as glacial refugia during the Neogene (23.03 ± 0.05 million years ago), had their own fauna, and still provide a source from which tracheophytes can be colonized.

Ino (1992) found that moss colonies at Langhovde, East Antarctica, housed mites, among other invertebrates. Barman (2000) examined the mites inhabiting mosses on the Schirmacher Oasis in East Antarctica. He found the family **Haplochthoniidae** (Figure 121), the first report

from the Antarctic, and reported three new species [*Haplochthonius antarcticus* (**Haplochthoniidae**), *H. maitri*, and *H. longisetosus*]. *Tyrophagus antarcticus* (**Acaridae**; see) was likewise recorded for the first time in the Antarctic. He considered the prostigmatid mites to be some of the toughest terrestrial animals in the world, occupying nunataks on the Antarctic continent. The Antarctic *Nanorchestes antarcticus* (see Figure 123) is only 0.3 mm long.

Figure 121. **Hypochthoniidae** mite, probably *Eohypochthonius*. Photo by David E. Walter, with permission.
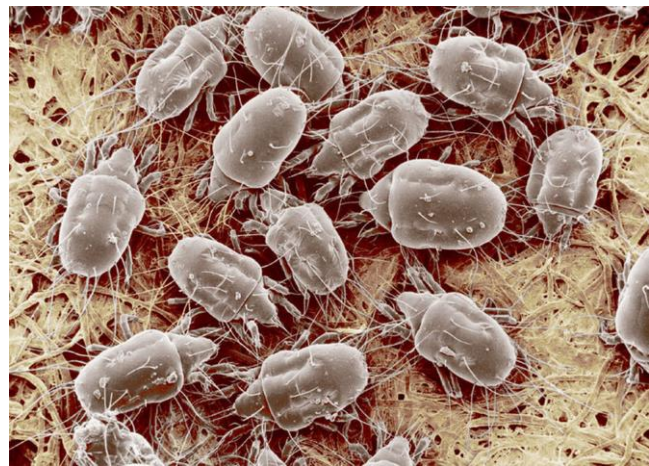

Figure 122. *Tyrophagus putrescentiae*. Some members of this genus are present in Antarctic mosses. Photo from USDA, through public domain.

Figure 123. *Nanorchestes* sp., member of an Antarctic bryophyte-dwelling genus. Photo by David E Walter, with permission.

One might expect bryophytes to be a safe site in the Antarctic, with edible moss tissue and cover to protect from larger predators. But not all bryophytes are equally protective. Usher and Booth (1986) found that the predatory *Cyrtolaelaps* (*Gamasellus*; **Ologamasidae**) lacked any pattern of distribution related to scale of sampling, exhibiting random distribution, whereas the prostigmatic *Ereynetes* (**Ereynetidae**), *Eupodes* (**Eupodidae**; Figure 124), and *Nanorchestes* (**Nanorchestidae**; Figure 123) had distinct patterns at a scale less than 30-40 cm. A small scale pattern was present at 10-20 cm in *Polytrichum* (Figure 125), with slightly larger scales (up to 30 cm) in *Chorisodontium* (Figure 126) as well as in lichens. For other species, large scale (40-50 cm or more) differences were related to environmental variables. By contrast, relationships between species were more important at smaller scales (5-10 cm). Perhaps the *Cyrtolaelaps* (*Gamasellus*) lacks a pattern of scale because it goes where the food is, crossing "zones."

Figure 124. *Eupodes longisetatus*. The genus *Eupodes* is a moss dweller in the Antarctic. Photo from Museum of New Zealand, Te Papa Tongarewa, with online permission.

Among these same mosses, Davis (1981) found the turf communities [*Polytrichum strictum* (formerly *P. alpestre*; Figure 125) and *Chorisodontium aciphyllum* (Figure 126)] and the carpet communities [*Calliergidium austrostramineum* (Figure 126), *Warnstorfia sarmentosa* (Figure 127), and *Sanionia uncinata* (Figure 128)] had similar levels of productivity, trophic structure, and organic matter transfer efficiency, but the standing crops of Collembola and mites differed. Concurrent with these standing crop differences were differences in moss turnover and accumulation of dead organic matter. There was no bryophyte consumption in these two communities.

Figure 125. *Polytrichum strictum*, a mite habitat in the Antarctic. Photo by Michael Lüth, with permission.

Figure 126. *Chorisodontium aciphyllum*, a common Antarctic moss that serves as habitat for mites. This picture was taken in Tierra del Fuego with *Nothofagus* in the background. Photo by Juan Larraín, with permission.

Figure 127. *Warnstorfia sarmentosa*, a common mite habitat in the Antarctic. Photo by Michael Lüth, with permission.

Figure 128. *Sanionia uncinata*, a common Antarctic moss with mite inhabitants. Photo by Michael Lüth, with permission.

But in the Stillwell Hills region of Kemp Land, East Antarctica, Kennedy (1999) found that microalgae supported more of the microarthropods than did the sites with a mix of mosses, lichens, and macroalgae. Kennedy suggested that the mites were able to avoid the extremes of temperature, but that they were limited by heat stress and desiccation. Furthermore, they found only three taxa, all under rocks.

Schwarz *et al*. (1993) found the greatest abundance of mites and other invertebrate groups in the top 5 cm of mosses in post-melt conditions. Usher and Booth (1984; Booth & Usher 1986) found a distinct vertical distribution among the mites and **Collembola** living among mosses in an Antarctic turf. The distribution of a species varied with its developmental stage. The populations were aggregated, but again, that aggregation within the mite species depended on the developmental stage. A major factor in the vertical distribution was the state of the moss tissue. The green moss community (living; 0-1.5 cm layer at surface) differed from the dead moss community (below 3 cm). The same six species of mites and Collembola occurred in both communities, but the relative proportions differed considerably. An interesting aside to this story is the fact that Booth and Usher (1984) found that the chemical characteristics (sodium, potassium, calcium, phosphorus) of the environment most influenced the distribution of the arthropods in the green moss communities, with physical characteristics being of less importance. The percentage of the various mite species in the green moss zone ranged from 24% (**Ereynetidae**: *Ereynetes macquariensis*) to 63% (**Ologamasidae**: *Gamasellus racovitzai*). In the *Polytrichum* (Figure 125) cover, only a weak relationship existed between moss cover and arthropods, including mites, in the green moss zone, whereas none existed in the dead moss zone.

At the Canada Glacier, mites were less abundant than protozoa, rotifers, nematodes, and tardigrades (Schwarz *et al*. 1993). On the other hand, Strong (1967) found mites to have the greatest species richness at Palmer Station, with at least 11 species representing the suborders **Prostigmata**, **Mesostigmata**, and **Cryptostigmata**. The **Collembola** comprised 4 species and **Diptera** 1. The two predatory mites feed mostly on the **Collembola**. Three of the oribatid species form aggregations to survive the winter. The others spend the winter in the same locations as their summer homes.

Antarctic Lakes likewise have an important mite fauna. In Priyadarshani, an oligotrophic lake, mosses and algae cover the bottom sediments. There one can find a microfauna that includes mites (Ingole & Parulekar 1990).

Temperature and Humidity Protection

Bryophytes may afford a protection from the Antarctic temperature that is not present elsewhere. Gressitt (1967) measured temperatures among mosses and found that some could create thermal conditions quite different from those in the atmosphere. *Polytrichum* (Figure 125) could reach January temperatures up to 13°C above atmospheric temperature, but *Drepanocladus* (*sensu lato*; Figure 127-Figure 128) maintained temperatures that differed little from ambient. (Note that the actual bryophyte species of these two genera may now be in different genera.)

As suggested for the two lycosid spiders earlier in this volume, other arthropods may also benefit from the ameliorating effects that bryophytes have on temperature. For example, the mites and **Collembola** have no known tolerance to freezing and survive winter by supercooling (Sømme 1981). This seems to involve both use of such cryoprotective compounds as glycerol and the elimination of nucleating proteins from the gut.

Block *et al*. (1978) noted that the mite *Alaskozetes antarcticus* (**Ameronothridae**; Figure 130) in the Antarctic has the ability to supercool to -30°C, but to realize this ability it depends on starvation, and possibly desiccation. They reported that about 1% of its fresh weight is glycerol. Cannon (1986b) found that for this species, those cold-hardy mites provided with distilled water and glucose lost about 20-25°C in supercooling ability. When no liquid was provided, they lost only about 4°C. In both cases, the glycerol concentrations in the mites decreased. In the Antarctic, even the summer temperatures can be quite cool. Block (1985) found that these could reach -8.4°C within the moss mats.
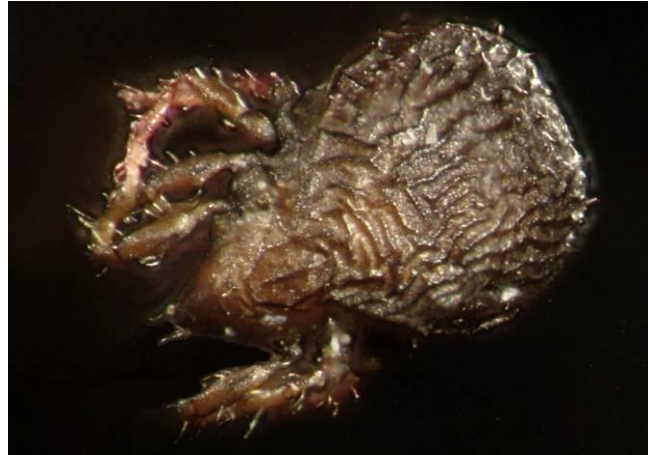

Figure 129. *Ameronothrus lineatus*, a moss-dweller from the high Arctic of Svalbard. Photo by Steve J. Coulson, with permission.

Figure 130. *Alaskozetes antarcticus*, an Antarctic moss-dweller that is capable of supercooling. Photo by Richard E. Lee, Jr., permission unknown.

Cannon (1986a) experimented with the humidity relations of *Alaskozetes antarcticus* (**Ameronothridae**; Figure 130) at 0, 26, 42, 55, 86, and 100% relative humidity at 4°C. He found that under saturated conditions the winter mites gradually lost cold hardiness while losing glycerol and increasing the temperature to which they could supercool. When they were maintained in dry conditions (r.h. <55%), their glycerol levels were relatively high (accumulation of glycerol was directly related to rate of water loss) and their supercooling temperature remained relatively constant. Even in summer conditions, the loss of water stimulated the accumulation of glycerol and the depression of the supercooling temperature.

Ice nucleation is always a danger at sub-freezing temperatures. Most invertebrates evacuate the gut in preparation for low temperatures (Sømme 1982), and this may relate to the problems seen when glucose was made available.

On the other hand, **tritonymphs** (third developmental stage) and adults of the mite *Alaskozetes antarcticus* (**Ameronothridae**; Figure 130) collected from mosses (or soil) in the Antarctic summer exhibited poor supercooling ability (-3 to -4°C) compared to those collected from beneath rocks (-20 to -30.8°C for tritonymphs, -2 to -29°C for adults) (Shimada *et al*. 1993). They were able to survive at temperatures below 0°C until they were frozen. This supports the notion that desiccation may be important to their cryoprotection mechanisms. Active mites survived lower temperatures than did the resting mites, and Shimada and coworkers suggested that items in their diet might contribute ice nucleating proteins that permit them to survive. It also appears that these mites are able to make antifreeze proteins that protect them from freezing in the fluctuating temperatures of summer (Block & Duman 1989). They are aided in their survival of low temperatures by having a very dark color that makes them into a "black body" that absorbs heat from the sun. Their slow development (5-7 years) is most likely a result of the low temperatures, but it could also mean they require less resources to continue their development.

Like most things, not all cryoprotection depends on the same conditions. Block (1979) found that the cryptostigmatid mites of the Alaskan taiga had supercooling ability that increased with the cold of autumn and early winter. But for these mites, there was no correlation with water content. Freezing was generally lethal, but supercooling prevented death until a frozen condition was reached.

One can only speculate on the role of the bryophytes in maintaining survival of *Alaskozetes antarcticus* (**Ameronothridae**; Figure 130). Since the bryophytes are likely to be frozen during a large portion of the year in the Antarctic, it is possible that ice crystals on their surfaces could contribute to desiccation of the mites by drawing the nearby water to the ice crystals of the bryophytes. Removal of water in this way from the mites would reduce the danger of crystal formation within the mites. Evacuation of the gut would further support the inability to form internal ice crystals. This could potentially protect the mites within the mats from episodes of fog and other moisture sources during cold weather, wherein small objects tend to collect the moisture and hold it, be they mites or mosses. Certainly research is needed to support my hypothesis on the role of the bryophytes.

A major problem for such small organisms in the Antarctic climate is the great variability in climatic conditions. Not only does the mite experience extremes through time, but it has great variability among its niches at the same time. Hence, having plasticity in one's response to this environmental heterogeneity is an asset for organisms such as mites. *Halozetes belgicae* (**Ameronothridae**) has **superplasticity** in its acclimation potential, as shown by the cold acclimation of an Antarctic population (Hawes *et al*. 2007). This species can cold harden very rapidly in the range of 0 to -10°C. In just two hours at 0°C, mites that had been acclimated at 10°C adjusted their supercooling points by 15°C. This is the most efficient ability to lower the lethal temperature known for any terrestrial arthropod. They seem to achieve this supercooling ability by evacuation of the gut, thus ridding themselves of potential nucleation sites in the gut. This could be a difference in physiological races or microspecies because the ability varies latitudinally, but it also varies with seasons.

Nielsen and Wall (2013) predicted that climate change responses will differ between Arctic and Antarctic invertebrate communities. They consider the changes in the Arctic to be driven by changes in the vegetation, whereas the Antarctic will respond to changes in the microbial community as well as changes in the plant communities. Both areas will most likely have a greater arrival of non-native species. In the species-rich Arctic, this may have a locally negative impact, with invaders reducing the diversity of native species by competition. These changes could cause the Arctic to become a carbon source, whereas the Antarctic could become a carbon sink.

The moss-dwelling *Ameronothrus lineatus* (**Ameronothridae**; Figure 129) lives in the high Arctic heath of the Svalbard, West Spitsbergen (Coulson & Birkemoe 2000). Collections of soil demonstrated that at least some individuals can survive temperatures of -22°C. But how tolerant will these high Arctic species be to greater maximum temperatures? Deep *Sphagnum* may be a refuge, but dark colors in the sun, including red *Sphagnum* species, will actually become warmer than the atmosphere on sunny days.

On the other hand, warming alone might not harm the mites. In the Arctic, Coulson *et al*. (1996) found no change in mite populations and species composition between controls and soil heated by having small polythene tents covering them. At the same time, numbers of **Collembola** declined significantly. The number of juveniles of mites increased significantly in the polar semi-desert regions of the Arctic, suggesting that this life stage might survive better at warmer temperatures, ultimately increasing the population size overall.

Tropics

In the cloud forest of Costa Rica, Yanoviak *et al*. (2006) found abundant arthropods among the epiphytes (including but not limited to bryophytes). There seemed to be little difference in faunal frequency and abundance between the **secondary forest** (forests regenerating largely through natural processes after significant human and/or natural disturbance) and **primary forest** (forest with native

species and no indication of human intervention) except for the significantly greater abundance of ants (11.4% with more than 10 per sample) in the secondary forest compared to 1.7% in the primary forest. Wet versus dry season seemed to make little difference in abundance. There was a slight tendency toward more morphospecies (10%) of arthropods in the wet season compared to the dry season. Yanoviak and coworkers warned that arthropods might be undercollected during the dry season because they become dormant and therefore do not fall into the Tullgren funnel due to lack of movement.

Nadkarni and Longino (1990) found in montane forests of Costa Rica that relative abundances of the major arthropod taxa were "the same" in the canopy and on the forest floor. They interpreted this to mean that the organic matter was similar in these two habitats, resulting in similar invertebrate communities. On the other hand, densities were 2.6 times as high on the ground as in the canopy. The highly mobile ants seemed to have equal densities in both places. Mites were among the dominant taxa in both canopy and ground detritus, but were less abundant in the canopy. They considered more wind, more frequent mist, higher maximum air temperatures, and more frequent wetting/drying cycles as contributing to a high biomass (4730 kg ha^{-1}) of organic matter in the canopy. These same factors seemed to contribute to reduced densities of arthropods. Tree species seem to make little difference in contributions by the thick epiphytic mats (Lawton & Dryer 1980).

These invertebrates are major fragmenters of the organic matter in tropical montane forests, although in most sites oligochaetes (worms such as earthworms) are also major contributors (Collins 1980, Pearson & Derr 1986, Leakey & Proctor 1987). Reported differences in abundance of oligochaetes in other studies, accompanied by lower relative abundances of arthropods, may reflect the different sampling techniques, where this study used sifting methods and others used hand sorting (Nadkarni & Longino 1990).

Epizootic

Even in the miniature community of bryophytes, there are animals that get a free ride on other animals. Among these is the oribatid mite, *Symbioribates papuensis* (**Symbioribatidae**; Figure 133), that is epizoic on backs of Papuan weevils (Aoki 1966). The beetle genus *Gymnopholus* (subfamily **Leptopiinae**; Figure 131) is inhabited by both lichens and liverworts, and liverworts in turn house the oribatid mite (Gressitt & Sedlacek 1967). Gressitt and Sedlacek (1967) reported a new species of weevil from New Guinea (*Gymnopholus carolynae*) that had abundant algae, fungi, and mosses growing on its back.

Vertical Distribution

Various types of gradients exist in habitats, and the responses of mites is to have different communities in

different areas of these gradients (Popp 1970; Behan-Pelletier & Winchester 1998; Proctor *et al.* 2002; Smrž 2006). Bryophytes can provide amelioration of some of the critical differences among habitats due to their ability to absorb water rapidly, reduce substrate evaporation, and reduce extremes of both moisture and temperature (Gerson 1982; Smrž 1992). Oribatid mites commonly are abundant where there is decaying plant material and high moisture, both of which are present in bryophyte communities (Bonnet *et al.* 1975; Seyd & Seward 1984).

Figure 131. *Gymnopholus reticulatus* with the moss *Daltonia angustifolia* living epizootically on the weevil. Mites are known to live in this association. Photo courtesy of Rob Gradstein.

Lindo *et al.* (2008) found that within one year, 90 artificial canopy habitats of soil and mosses attached to planks were colonized by 59 oribatid mite species. These artificial habitats were distributed at three heights on 10 western red cedar (*Thuja plicata*; Figure 132) trees and represented three patch sizes. The established communities exhibited a typical species-area relationship. Richness increased with moisture content and size of habitat patch. Hence, species richness and abundance decreased with increased height in the canopy. The community composition and species richness patterns exhibited a non-random distribution and were significantly nested. Non-randomness could be explained in part by individual species tolerances and dispersal abilities. Previously known canopy-specific species [*Eupterotegaeus rhamphosus* (**Cepheidae**), *Epidamaeus* nr *floccosus* (**Damaeidae**; see Figure 11), *Scheloribates* (**Scheloribatidae**; Figure 133)] from the area were all present on the artificial substrata. These species were even found in the small, desiccated patches located highest in the canopy and exhibited drought tolerance and adaptations to living in a patchy environment. The earliest colonists were generally strongly desiccation tolerant. These canopy specialists seemed to lack dispersal limitation.

Figure 132. *Thuja plicata* showing vertical structure where mite communities differ by height in canopy. Photo by Abdallahh, through Creative Commons.

Figure 133. *Scheloribates clavilanceolatus*. Some members of the genus are high-canopy bryophyte dwellers. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Forest Habitat Strata

Vertical differences exist within the forest. In the canopy, bryophytes are often a primary habitat (Winchester

et al. 1999). Proctor *et al*. (2002) found distinct communities among the base, trunk, and canopy habitats in Australia. Bonnet *et al*. (1975) examined the vertical gradient of mites at Tarn, France, from soil to arboreal mosses. There were 63 species of mites, although only 58 could be identified. The importance of temperature and humidity were clear, with invertebrate communities following the same transitions as the habitat. These communities can differ in both abundance and species composition. In the tropical montane forest of Costa Rica, where mites represented one of the numerically dominant groups, Nadkarni and Longino (1990) found that the forest floor fauna had a mean density 2.6 X that of the canopy.

In attempts to determine the impact of moss harvesting on invertebrate faunas, Peck and Moldenke (1999) compared the fauna at the stem base and at the tips of shrubs in the Eugene District, Oregon, USA. They found that presence of hardwood trees and greater abundance of mosses increased the mite fauna. At the bases of the shrubs, typical moss fauna were *Ceratoppia* sp. (**Ceratoppiidae**; Figure 134), *Hermannia* spp. (**Hermanniidae**; Figure 135), and *Phthiracarus* sp. (**Hermanniidae**; Figure 136) (all turtle mites). Samples at the tips were characterized by **microspiders** and **springtails**. Based on these community structures, they recommended that moss harvesting be prohibited in mixed or hardwood-dominated stands and from the lower 0.5 m of any shrubs.

Figure 134. *Ceratoppia* sp. Photo by Walter Pfliegler, with permission.

Figure 135. *Hermannia reticulata*. Photo by Bold Systems Biodiversity Institute of Ontario, with permission.

Figure 136. *Phthiracarus* sp. Photo by Walter Pfliegler, with permission.

Wagner *et al*. (2007) examined the distribution of epiphytes and invertebrates on the bole of red maple trees (*Acer rubrum*; Figure 137) in Maine, USA. They found that mites were among the predominant fauna at the base and **Diptera** (flies) above 2 m. Gap harvesting reduced the cover of epiphytes and the arthropod fauna, suggesting that the epiphytic bryophytes could play a role in the distribution of these invertebrates.

Figure 137. *Acer rubrum* bark with epiphytes, home for mites and diptera. Photo by Wanda Rice, with permission.

Within Bryophyte Clumps

Because of moisture differences, and possible UV damage, vertical differences exist among mite communities within bryophyte clones (Dalenius 1962; Harada 1980). The importance of humidity differences (Smrž 1994) is reflected in the vertical positioning of the mites within the moss clone.

In Canada, nearly 50% of the 100 moss samples collected by Richardson (1981) had mites living among them. The distribution of mite species can differ within the vertical strata of the mosses, indicating differences in conditions at these depths (Harada & Aoki 1984; Usher & Booth 1984). Borcard (1993) found that the 38 species of oribatid mites in *Sphagnum* (Figure 95) differed between two vertical layers of moss. Evidence for these differences is further supported by the daily migrations of mites that have been observed in some mosses (Rajski 1958).

In a cloud forest in Costa Rica, Yanoviak *et al*. (2004) found a vertical distribution of mites within epiphytic mats of bryophytes, with a greater mass of oribatid mites occurring in the brown portions than in the upper green portions. The brown tissue was more dense and its grain was finer than that of the green portion. On the other hand, the green portions had a greater density and richness of arthropods than did the brown parts. Mites were the most abundant arthropod group in this habitat. As expected, Booth and Usher (1984) found an increase in arthropod abundance with an increase in moss dry mass.

Vertical Migration

Vertical migration permits some species to escape the heat and desiccating events of the day by escaping to deeper layers of the mosses. Among the moss habitats, this may be most prevalent in *Sphagnum* (Figure 95) habitats, where the surface is exposed to full sun and can become quite hot and dry while lower depths remain cool and moist. Popp (1962) observed such vertical migration behavior for *Limnozetes ciliatus* (see Figure 107-Figure 112) and *Hypochthonius rufulus* (Figure 138) in response to hummock temperature changes.

Figure 138. *Hypochthonius rufulus* on *Sphagnum*. Photo by Walter Pfliegler, with permission.

Ceratozetes (**Ceratozetidae**; Figure 102) and *Eremaeus* (**Eremaeidae**; Figure 5-Figure 4) species migrate in the soil to optimize moisture and temperature conditions (Mitchell 1978). They also segregate by ages, with younger members occupying lower depths that have a more ameliorated climate. These migrate upward as adults. These two genera are also known among bryophytes, so it is likely that at least some of these bryophyte dwellers also exhibit vertical migrations.

Magalhães *et al*. (2002) showed that some mites respond to species-specific predator odors that stimulate their migration upward or downward in response. In tracheophytes, this behavior combination can actually benefit the plants. Mite predators sit in the rapidly growing

tender tips, causing the herbivorous mites to migrate downward, thus protecting these sensitive plant areas (Magalhães *et al*. 2002; Onzo *et al.* 2003) from mite herbivory. I can find no study to indicate whether bryophyte-dwelling mites respond to similar chemical stimuli of predators among the bryophytes. If they do, would this likewise protect growing tips from mite damage, or is their often fungivorous diet sufficient protection for the bryophytes? Might the chemical odors of the bryophytes override predator odors, or nullify them, or in some other manner ameliorate their effectiveness?

Elevational Differences

Elevational differences exist as well. Andrew *et al.* (2003) examined the elevational relationships of mites among bryophytes in New Zealand (Table 1-Table 2). Taxa on Mt. Field and Mt. Rufus represented the **Mixonomatides** and the families **Oribatellidae**, **Galumnidae**, **Oppiidae**, **Microzetidae**, **Cepheidae**, **Adelphacaridae**, **Mycobatidae**, **Phthiracaridae**, **Carabodidae** (Figure 139-Figure 140), and **Cymbaeremaeidae**. All but **Adelphacaridae** and **Cymbaeremaeidae** were collected in more than one location. On Mt. Otira, New Zealand, the researchers found **Oribatulidae**, **Eutieidae**, **Epilohmanniidae** (only at higher elevations of 1000-1500 m), **Oribotritiidae**, **Nanhermanniidae** (Figure 114), **Pedrocortesellidae** (the latter three only from lower elevations of 250 m), **Microzetidae** (1 location at 750 m), and **Tectocepheidae** (in 10 out of 12 locations at 1500 m only).

Elevational patterns for mite species richness were not in evidence in this study (Andrew *et al.* 2003), and those that did exist differed widely between mountains. Nevertheless, for some families, as mentioned above, distinct elevational ranges are suggested. Evidence is needed to tie these elevational differences to differences in bryophyte species. Nigel Andrew (Bryonet) suggested that moss species and growth form were important factors in determining arthropod abundance and diversity in the New Zealand mountains; these are likely to differ with elevation.

Table 1. Elevational distribution of mite families living among bryophytes on Kaikoura, New Zealand. Each location is represented by six samples. Elevations are in meters. Data are presence out of six locations at that elevation. From Andrew *et al.* 2003.

	m asl					
	1130	1225	1325	1425	1520	2000
Oribatellidae	4	5	1		6	1
Oribatulidae		4	1			5
Oppiidae			1	1		
Crotonidae						

Table 2. Family presence of mites among bryophytes at 250-m elevation intervals on three mountains in Tasmania and New Zealand. For Mt. Field and Mt. Rufus in Tasmania, two locations were included at each elevation; the numbers represent the number of locations. For Mt. Otira in New Zealand, 12 samples were included at each elevation. Locations are **Mt Field first line, Mt. Rufus second line, Mt. Otira third line.** From Andrew *et al.* 2003.

	m asl					
	250	500	750	1000	1250	1500
Mixonomatides	2	2	1	1	1	
	1					
Oribatellidae	1	2	2			
	2	2	1		1	
	7	1		5	3	
Galumnidae	1	1		1		
			1	1		
Oppiidae	1	1	2		2	
	2					
	7	1	1		2	10
Microzetidae	1		1	1	2	
	2	1		2	1	
			1			
Cephidae		1	1			
				1	1	
Adelphacaridae	1			1		
Mycobatidae	1	1	1	1		
Phthiracaridae		1	1		1	
	3	1		1	3	
Carabodidae		2	2	1		
Cymbaeremaeidae						
			1			
Mt Otira only						
Oribatulidae	5	3		2	2	
Euieidae	3	4			1	
Epilohmanniidae				1	2	6
Oribotritiidae	1					
Nanhermanniidae	3					
Pedrocortesellidae		2				
Tectocepheidae						10

Figure 139. Mite species in the family **Carabodidae**, sitting on a moss. Photo by Walter Pfliegler, with permission.

Figure 140. Mite species in the family **Carabodidae**, sitting on a moss. Photo by Walter Pfliegler, with permission.

Seasons

Sampling season will influence the abundance of mites in the soil (Popp (1970), and presumably among the bryophytes. Merrifield and Ingham (1998) found that the abundance of aquatic mites (and tardigrades) among mosses varied significantly between sampling dates in the Oregon Coastal Range, USA. Gerson (1969) reported oribatids that live on mosses under the snow. Block (1966) found that mites were most abundant in May and December, and least abundant in August in Westmorland, UK, but this can be modified by the weather.

Just as vertical differences exist within the moss mat on any given day, they likewise exist seasonally. Moss depths provide a safe overwintering habitat for mites, protecting them from extreme temperatures and desiccation. Popp (1962) found that the peatland oribatids *Limnozetes ciliatus* (**Limnozetidae**; see Figure 107-Figure 112), *Ceratozetes parvulus* (**Ceratozetidae**; see Figure 102), and *Trimalaconothrus novus* (**Malaconothridae**; see Figure 87) migrate to the deeper layers of the peat hummocks to spend the winter.

Gerson (1969) dug the mosses *Ceratodon purpureus* (Figure 141) and *Bryum* (Figure 142) out from 1.6 m of snow on Montreal Island, Quebec, Canada, and found

many live *Eustigmaeus* (**Stigmaeidae**; Figure 143) present. These began to oviposit when warmed on a suitable substrate in the lab. It is likely that bryophytes are important overwintering sites for a number of mites. The ability of at least some members of this genus to eat mosses (Walter & Latonas 2011) may help them to survive there.

Figure 141. *Ceratodon purpureus*, home for *Eustigmaeus*. Photo by Bob Klips, with permission.

Figure 142. *Bryum caespiticium*. *Bryum* serves as home for *Eustigmaeus*. Photo by Bob Klips, with permission.

Figure 143. *Eustigmaeus* sp., a mite that can overwinter on mosses in Canada. Photo by David E. Walter and A. O'Toole, with permission.

Salmane (2000) investigated the seasonal activity of **Gamasina** (an infraorder of the **Mesostigmata**) mites (Figure 13) in soil under mosses in a pine forest in Latvia. She determined that the abundance and diversity of this predatory mite group was seasonally dynamic. These

changes in abundance and diversity related first to relative humidity and secondarily to temperature. The greatest diversity was in August (17 species), but some species (**Rhodacaridae**: *Rhodacarus reconditus*) did not appear until October. In her April to October study, the greatest numbers of **oribatid** and **Gamasina** mites were in April and August.

Disturbance Effects

Starzomski and Srivastava (2007) conducted one of the few experimental studies on terrestrial arthropod communities, where mites (**Acari**) and springtails (**Collembola**) comprised part of the fauna. These were tiny animals, mostly less than 1 mm in length, that inhabited patches of the mosses *Polytrichum* (Figure 125) and *Bryum* spp. (Figure 142) on granitic outcrops in Vancouver, British Columbia, Canada. In their experiments, they simulated drought frequencies as a form of disturbance. Effects of humidity on *Scutovertex minutus* (**Oribatida**; see Figure 144) were already known from studies by Smrž (1994). The oribatid microarthropods may reach 200 or more morphospecies in an area of less than 20 m^2 (Starzomski & Srivastava 2007). In their BC study, 163 species were found, comprising 26,274 individuals.
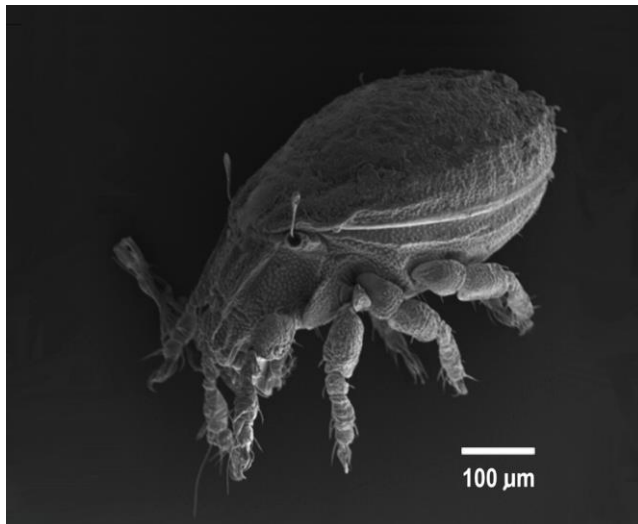

Figure 144. SEM of *Scutovertex sculptus*, members of a genus that lives on *Polytrichum* and *Bryum.* Photo by Jürgen Schulz, with permission.

Connectedness between patches is important in determining number of species, although microarthropods may migrate across bare rock to other moss patches (Starzomski & Srivastava 2007). Increases in drought disturbances decreased the number of species, but not the number of individuals. On the other hand, fragmentation caused an increase in species abundance. In unconnected plots with no disturbance, the mean number of individuals was 620, whereas in the undisturbed connected patches, mean abundance was only 372. However, disturbance in the fragmented sites caused a drop in abundance below that of the other treatments. The smallest regions experienced the greatest rate of drop in both species richness and abundance (2.5X faster for species richness, 4X faster for number of individuals). In connected regions, oribatid

mites exhibited a dampened response to disturbance compared to other species, perhaps due to protection from desiccation by their hard exoskeleton. For all the other taxa, abundance, body size, and trophic position had no effect on their responses to disturbance.

Although corridors are undoubtedly important in providing safe sites for migration between patches of bryophytes, they do not always provide the same benefits. Starzomski and Srivastava (2007) found that the microarthropods offer increased community resilience to disturbance and enhanced species richness in small patches. Corridors facilitate movement (Schmiegelow *et al.* 1997), maintain ecosystem processes (Gonzalez & Chaneton 2002; Levey *et al.* 2005), and prevent local extinctions (Gonzalez *et al.* 1998). However, Hoyle and Gilbert (2004) found that different connectivity treatments did not contribute to species richness, a finding supported by Starzomski and Srivastava (2007). Both of these studies did suggest that corridors are important under disturbance (in this case drought) conditions, supporting the contention of Honnay *et al.* (2002) that they may be very important in the presence of climate change.

Cryptogamic crusts are subject to disturbance by grazing animals. Within these crusts of lichens, mosses, and algae/Cyanobacteria, many invertebrate types dwell, including mites (Brantley & Shepherd 2004). In a piñon-juniper woodland in central New Mexico, 29 of 38 taxa of invertebrates occurred on mossy patches and 27 on mixed lichen and moss patches. Mosses had the highest abundance, suggesting that their ability to hold moisture might benefit these organisms. Furthermore, abundance was greater in winter than in summer.

Pollution Indicators

Watermites (**Prostigmata**) can serve as bioindicators of pollution in streams, in part because they are affected by the changes in moss growth caused by the pollution (Bolle *et al.* 1977). Most moss mites (Oribatida) decline in numbers when exposed to industrial pollution. On the other hand, the pollution-tolerant mite *Hygrobates fluviatilis* (**Hygrobatidae**Figure 145) increases with industrial effluent additions (Bolle *et al.* 1977).

Figure 145. *Hygrobates fluviatilis,* a pollution-tolerant moss mite. Photo by Nigrico through Creative Commons

Terrestrial mites can be used as well; in a Scots pine forest in Poland, bryophyte mite fauna responded to nitrogen fertilizer pollution (Seniczak *et al.* 1995).

Recent evidence of increasing levels of UV-B suggest that bryophytes could provide refugia for invertebrates such as mites, blocking the dangerous radiation from reaching their inhabitants (Robson *et al.* 2001). To my surprise, Robson and coworkers found that biodiversity of **microfauna** among *Sphagnum* (Figure 95) species increased in plots exposed to higher UV-B levels. Nevertheless, mites responded negatively to the increase in near UV-B by having reduced numbers (Robson *et al.* 2005). Robson and coworkers suggested that under UV-B radiation at near-ambient levels, leaching of nutrients from the mosses may result and possibly changes occur in the morphology of the *Sphagnum* capitulum.

Steiner (1995a) found that air pollution can alter the species composition and abundance of the mites among mosses. Richness decreases and the mite communities become more uniform. The species *Zygoribatula exilis* (**Oribatulidae**; see Figure 20) proved to be the most useful as an air quality indicator. Not only does air pollution have direct effects on the mites, but it also can alter relative humidity, substrate availability, and *p*H of the mosses, which in turn influence the mite species able to live there. Even so, the mites are less sensitive to pollution than nematodes and tardigrades (Steiner 1995b). Exceeding tolerance demonstrated by tardigrades is quite a feat.

Dispersal of Mites and Bryophytes

It is likely that dispersal works both ways in the moss-mite relationship. Several studies have indicated the role of mites in bryophyte dispersal. Both mites and bryophytes can be dispersed aerially (Mandrioli & Ariatti 2001).

Risse (1987) pointed to studies that indicate the bryophyte gemmae do not develop below the ground surface, and this includes rhizoidal gemmae and tubers. But the attachment of gemmae of *Schistostega pennata* (Figure 146-Figure 149) to the legs of mites indicates that these bryophytes have a means of dispersal that is likely to drop off at least some of the propagules at the surface (Ignatov & Ignatova 2001). Such a form of dispersal is likely to remove them from the territory of the parent, where the gemmae may be inhibited, presumably by chemicals from the parent.

Figure 146. *Schistostega pennata* mature leafy gametophyte plants. This species has gemmae that are dispersed by attaching to the legs of mites. Photo courtesy of Martine Lapointe.

Figure 147. *Schistostega pennata*. Reflective protonemata with a few leafy plants. The protonemata produce gemmae that can be dispersed by mites. Photo courtesy of Martine Lapointe.

Figure 148. *Schistostega pennata*. Young leafy plants developing from the protonemata. Photo courtesy of Misha Ignatov.
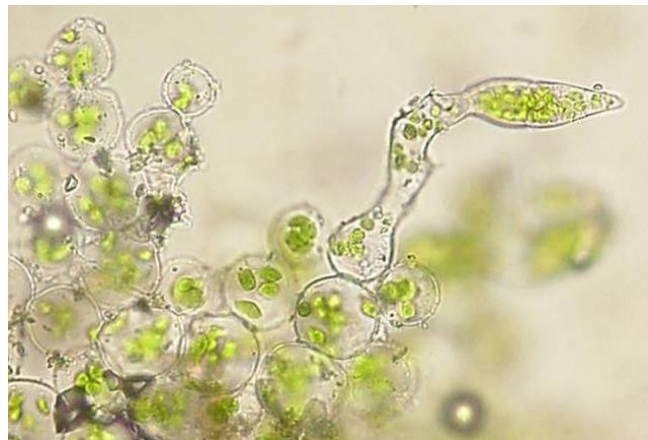

Figure 149. *Schistostega pennata*. Microscopic view of the protonemata, showing the loosely connected cells that can develop into new leafy plants. The long, fusiform branch is a protonemal gemma that can be carried to the surface by mites. Photo courtesy of Misha Ignatov.

Zhang and coworkers (2002) provide further evidence of possible transport of gemmae in the moss *Octoblepharum albidum* (Figure 150-Figure 151). In this species, mites consume the gemmae, and in the process could manage to transport some of those gemmae to new locations. At the very least, they are likely to dislodge some gemmae that drop before they get eaten. One must wonder if gemmae cells survive the digestive system, providing yet another mechanism for transport. More experiments waiting to be done!

Figure 150. *Octoblepharum albidum*, a moss whose gemmae are dispersed by mites. Photo by Janice Glime.

But mites themselves can have some difficulties getting dispersed. Sudzuki (1972) did wind tunnel experiments with mosses, using various wind speeds. During the two months of experiments, mites were apparently never dispersed, and the Crustacea and Arachnomorpha were rarely dispersed at wind velocities under 2 m s^{-1}. They concluded that mites are not transported by wind. On the other hand, this does not preclude the passive dispersal of mites along with mosses that are moved by the wind, especially in such vulnerable locations as the canopy or among the terrestrial moss balls.

Lindo (2011) suggested mosses might serve as "magic carpets" for the mites. She reported 57 species of oribatid mites among litterfall, including mosses, in her study of canopy and ground level litter. She found a high species richness in litterfall in canopy habitats and suggested that the mosses not only served as transportation vessels, but that they also increased survivorship during the journey.

Figure 151. Gemmae of *Octoblepharum albidum*, potentially distributed by mites that also eat some of them. Photo by Li Zhang, with permission.

No Place for Generalists?

At the beginning of the first subchapter on mites, I introduced the question "Can we use the literature to answer this question for [mites in] any mossy habitats?" My first response to this is that I would have to change my professional path from bryology to acarology to attempt to answer it. My second response is almost as wishy-washy.

Certainly many examples in this chapter have included mites that go to bryophytes to replenish moisture, and probably to hide. These might be called generalists because they use a variety of habitats. But we know that many mites that are plant pests seem to be specialists. The mosses, on the other hand, often seem to be only a refuge habitat when the primary habitat becomes unavailable or unsuitable. But the bryophytes where they seek refuge may in some cases be the only suitably moist habitat. It's a good thing that some of these plant specialists can go for a long time without eating.

I am inclined to think that those mites that live on bacteria and fungi are generalists, able to live wherever there is sufficient moisture and a fungal or bacterial food source. For many, this means soil, leaf litter, and mosses.

At the other end of the spectrum are those mites that eat mosses and lay their eggs there, but how many of these can survive as well in other locations? To answer that question we must await more research, experimentation, and publication of older literature on the web. And before that can provide us with definitive answers, DNA-based identification of species will be necessary to separate the cryptic species that may indeed represent specialists.

Limitations of Methods

The high abundance of mites among bryophytes often requires special extraction techniques (Borcard 1986; see discussion in Chapter 6-1 of this volume). When general surveys are done, they typically have a bias against some groups of organisms and favor others. Furthermore, most require that the organisms are mobile, so dormant organisms are missed. Yanoviak *et al*. (2003) reminded us of the limitations of fogging, a common canopy method, for invertebrates such as mites because they would typically remain within the moss mat.

Likewise, information on bryophyte-dwelling mites requires special and extensive searching techniques. Most of the information is hiding in species descriptions, or not mentioned at all. As I am finishing this chapter, I have the feeling I have only scratched the surface on the available information of bryophyte-dwelling mites.

Nelson and Hauser (2012), students at Lewis and Clark College working on an undergraduate report, tested two methods of surveying invertebrate communities of epiphytic bryophytes in the Tryon Creek State Natural Area, Oregon, USA. They compared arthropod extraction using a Berlese funnel to a simple water technique. In the latter, they examined ten drops of water from each wet bryophyte sample. Acari were the most abundant and most frequent. They could find no differences in communities between mosses and liverworts. But a comparison of the two extraction techniques demonstrated almost no overlap in taxa! Rather, the two techniques complemented each other. The Berlese funnel sampling provided the greatest numbers of different species of Acari.

Order Acari – Ticks

Ticks are not organisms we normally think of as moss fauna, but Slowik and Lane (2001) showed that the western black-legged tick *Ixodes pacificus* (**Ixodidae**; Figure 152) was more common on moss-covered oak trees than on trees without mosses. They found that the moss reduced the

surface temperature by ~1.9ºC and increased the relative humidity 2.5%, perhaps contributing to the greater abundance of these ticks as bryophyte associates. Slowik and Lane suggested that the bark provided refugia and that the western fence lizard could be responsible for presence of these ticks on the bark. Mites, on the other hand, are quite common as bryophyte fauna (Kinchin 1990; Seyd & Colloff 1991; Seyd *et al.* 1996).

Figure 152. *Ixodes pacificus*, an inhabitant of moss-covered oak trees. Photo by CDC/ Amanda Loftis, William Nicholson, Will Reeves, Chris Paddock/ James Gathany, through Creative Commons.

In the Antarctic, the tick *Ixodes uriae* (**Ixodidae**; Figure 153) likewise makes use of mosses. It lays its eggs under mosses or grasses (Gressitt 1967).

Figure 153. *Ixodes uriae*, an Antarctic that lays its eggs under mosses. Photo from Tromso University Museum, through Creative Commons.

SUBPHYLUM MYRIAPODA

The myriapods represent a much smaller subphylum (~13,000) than that of the **Arachnida** (Wikipedia: Myriapoda 2010). The name myriad literally refers to 10,000 (legs). Although this is not literally true, these arthropods can have from fewer than 10 up to 750 legs. Three classes are represented among bryophytes: **Chilopoda** (centipedes), **Diplopoda** (millipedes), and **Symphyla** (garden centipedes). The eggs hatch into miniature myriapods with fewer segments and legs. Secretions from many of the members can cause one's skin to blister.

Class Chilopoda (Centipedes)

Centipedes are mostly carnivorous and are distinguished by one pair of legs per segment (Wikipedia: Chilopoda 2010). They lack a waxy covering and lose water easily, hence preferring high humidity and low light (Mitić & Tomić 2002). It is likely this dependence on water that makes mosses such as *Sphagnum* suitable habitat for some species. *Lithobius curtipes* (**Lithobiidae**; Figure 154) lives among the mosses [*Polytrichum commune* (Figure 156)*, Sphagnum girgensohnii* (Figure 157), *S. squarrosum* (Figure 155)] on the forest floor in Finland (Biström & Pajunen 1989). In Great Britain, Eason (2009) found it in great numbers in moss, under stones, and on bark. In the Ural Mountains, this is the only centipede species that extends into the tundra (Farzalieva & Esyunin 2008). *Geophilus proximus* (**Geophilidae**; see Figure 158) also occurs on *Polytrichum commune* (Biström & Pajunen 1989).

Figure 154. *Lithobius curtipes*, a centipede inhabitant of *Sphagnum girgensohnii*, *S. squarrosum*, and *Polytrichum commune*. Photo by Stefan Schmidt through Creative Commons.

Figure 155. *Sphagnum squarrosum*, a forest floor species that is home to some species of centipedes. Photo by Michael Lüth, with permission.

Figure 156. *Polytrichum commune*, home to some centipedes, but unfit for many other bryophyte dwellers. Photo by Michael Lüth, with permission.

Figure 157. *Sphagnum girgensohnii*, a forest floor moss that is home to some species of centipedes. Photo by Michael Lüth, with permission.

Figure 158. *Geophilus carpophagus*, a centipede member of a genus that is present among bryophytes, shown here on leaf litter. Photo by Walter Pfliegler, with permission.

In their study of invertebrate communities among bryophytes [predominantly *Atrichum undulatum* (Figure 159), *Brachythecium rutabulum* (Figure 160), and *Hypnum cupressiforme* (Figure 161-Figure 162)] in the Czech Republic, Božanić *et al.* (2013) found that the **Chilopoda** chose habitats on the ground or close to it. They, like the **Diplopoda** and **Isopoda**, were numerous in small cushions, whereas the **Enchytraeidae** (**Annelida**) were abundant in larger moss carpets. The larger centipedes, including adults of somewhat smaller species,

feed on smaller chilopods such as *Lithobius* (**Lithobiidae**; Figure 154) species that inhabit the soil surface (Rawcliffe 1988). This causes some of the *Lithobius* species to escape into the mosses at the lower parts of living trees (Biström & Pajunen 1989). Others such as *Lithobius mutabilis* (Figure 163) and juveniles of other species of *Lithobius* occur among mosses on larger trees (Božanić *et al*. 2013).

Figure 159. *Atrichum undulatum*, home for ground-dwelling **Chilopoda**. Photo by Michael Lüth, with permission.

Figure 160. *Brachythecium rutabulum*, one of the ground mosses chosen by **Chilopoda** as a home. Photo by Michael Lüth.
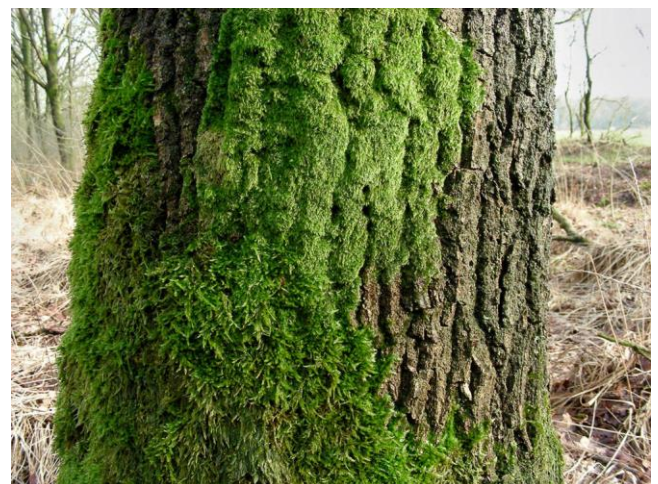

Figure 161. *Hypnum cupressiforme* habitat, housing species of **Chilopoda** that live near the ground. Photo by Dick Haaksma, with permission.

Figure 162. *Hypnum cupressiforme* var *cupressiforme*, home for centipedes near the ground. Photo by David T. Holyoak.

Figure 164. Millipede on moss. Photo courtesy of Josh Jones.

Figure 165. *Polyzonium germanicum*, a millipede that lives among bryophytes, shown here on leaf litter. Photo by Ruth Ahlburg, with permission.

Figure 163. *Lithobius mutabilis* female, a species that lives among mosses on larger trees. Photo by Walter Pfliegler, with permission.

Figure 166. *Proteroiulus fuscus*, one of the few millipedes that lives among bryophytes, shown here on a bed of leafy liverworts. Photo by E. C. Schou, with permission.

Figure 167. *Polydesmus complanatus*, a millipede known from both *Sphagnum* and *Polytrichum*, shown here on a mat of mosses. Photo by Joerg Spelda, SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

Class Diplopoda (Millipedes)

The millipedes are unusual in having each pair of segments fused, hence having two pairs of legs per fused segment (Wikipedia: Diplopoda 2010; Figure 164). They are not common among mosses, or at least there are few reports. Biström and Pajunen (1989) found *Polyzonium germanicum* (**Polyzoniidae**; Figure 165), *Proteroiulus fuscus* (**Figure** 166), *Polydesmus complanatus* (**Polydesmidae**; Figure 167), and *Leptoiulus proximus* (**Julidae**; Figure 170), on the *Polytrichum commune* (Figure 156) in Finnish forests. *Polydesmus complanatus* occurred not only on *Polytrichum commune*, but also on *Sphagnum girgensohnii* (Figure 157) and *S. squarrosum* (Figure 155).

Božanić *et al*. (2013) found that type of substrate and height above ground are often the most important factors in determining the invertebrate fauna of the bryophytes in the Litovelské luhy National Nature Reserve, Czech Republic. The mosses here are mostly *Atrichum undulatum* (Figure 159), *Brachythecium oedipodium* (Figure 168), *B.*

rutabulum (Figure 160, and *Hypnum cupressiforme* (Figure 161-Figure 162). As a whole, these house the highest numbers of invertebrate species. In contrast to the **Chilopoda**, the **Diplopoda** live among mosses high in the trees, sometimes as high as 160 cm above the ground. They prefer small cushions to larger carpets.

Figure 168. *Brachythecium oedipodium*, a moss that houses **Chilopoda**. Photo by Michael Lüth, with permission.

Polydesmus angustus (**Polydesmidae**; Figure 169) commonly make nests on moss cushions in London, UK, especially during April to July (Banerjee 1973). The nests are constructed from "worked-up" soil from the gut of the female. As the millipedes develop, different instars construct their own molting chambers using bits of soil and humus.

Figure 169. *Polydesmus angustus* at Crowle Moors, UK. Photo by Brian Eversham, with permission.

Figure 170. *Leptoiulus proximus*, a millipede known from *Polytrichum commune*. Photo by Stefan Schmidt through Creative Commons.

In the UK, Stenhouse (2007) reported *Ommatoiulus sabulosus* (striped millipede; **Julidae**; Figure 171) in moss and the daddy-long-legs *Nemastoma bimaculatum* (**Nemastomatidae**; Figure 172) under moss.

Figure 171. *Ommatoiulus sabulosus* on mosses. Photo by Roger S. Key, with permission.

Figure 172. *Nemastoma bimaculatum*, a daddy-long-legs that lives under mosses. Photo by Tom Murray, through Creative Commons.

Tachypodoiulus niger (black snake millipede; **Julidae**; Figure 173), a millipede of chalky and limestone soils, is very common in the UK and occurs among mosses and similar habitats (Stenhouse 2007). Haacker (1968) considers it to be a dry-resistant or xerophilous species that prefers cool temperatures, but has only limited freezing tolerance (David & Vannier 1997). *Tachypodoiulus niger* is active mostly from one hour after sunset to one hour before sunrise, but can become active in the afternoon during summer (Banerjee 1967). When disturbed, it will coil itself into a spiral with its legs on the inside and its head in the center (Figure 174; Wikipedia 2012), but it also has the option to flee with side-winding movements like some snakes. These millipedes feed on algae, detritus, and some fruits such as raspberries (Wikipedia 2012).

Figure 173. *Tachypodoiulus niger* on a mat of moss. Photo from Wikimedia Commons.

Figure 174. *Tachypodoiulus niger* curled in its defensive position. Note legs on inner side of spiral and head in the middle. Photo from Wikimedia Commons.

Josh Jones (pers. comm.) found *Cylindroiulus punctatus* (**Julidae**; Figure 175) on a species of the moss *Thuidium* (Figure 175). It has a diurnal cycle with a major activity period from one hour before sunrise to one hour after in April, May, and July, but also one hour before sunset to one hour after throughout March-August except July (Banerjee 1967).

Figure 175. The moss *Thuidium* sp. with the millipede *Cylindroiulus punctatus.* Photo courtesy of Josh Jones.

In January 2012, Erin Shortlidge queried Bryonet about an unusual invertebrate she found among the bryophytes. This, Bryonetters identified as the millipede *Polyxenus* (**Polyxenidae**; Figure 176-Figure 177), differing somewhat from the European *P. lagurus* (Figure 178) (Edi Urmi, Bryonet 8 January 2012). The bristles serve as defense against ants (Paul G. Davison, Bryonet 8 January 2012). Jean Faubert offered the identification of *P. fasciculatus* (Figure 176-Figure 177).

Figure 176. Ventral view of *Polyxenus lagurus* or *P. fasciculatus* from *Ceratodon purpureus* (Figure 141). Photo courtesy of Erin Shortlidge.

Figure 177. Dorsal view of *Polyxenus lagurus* or *P. fasciculatus* from *Ceratodon purpureus*. Photo courtesy of Erin Shortlidge.

Figure 178. *Polyxenus lagurus*. Photo by Mick E. Talbot, through Creative Commons.

Božanić (2008) found that the most abundant taxa of invertebrates among mosses were **Isopoda** (439 individuals among 66 moss samples) and **Diplopoda** (240 individuals). The most important factors in determining taxa were type of substrate, height above ground, and size of moss sample. For epiphytic bryophyte dwellers, the tree diameter was important. One should exercise some caution in interpreting these results because researchers used a Tullgren funnel with heat extraction, a method that works against less-mobile organisms that are unable to escape the moss clump before dying from heat or desiccation.

Epizootic Bryophytes

Rob Gradstein (14 November 2011) sent me a note that I might be interested in a Colombian millipede with ten bryophyte species (Figure 179) growing on it! Of course I was interested. These ten species represented five families (**Fissidentaceae**, **Lejeuneaceae**, **Metzgeriaceae**, **Leucomiaceae**, **Pilotrichaceae**) that comprised both mosses and liverworts (Martínez-Torres *et al.* 2011), a record Gradstein suggested might be suitable for the Guinness Book of World Records. The millipede of interest is *Psammodesmus*, ultimately named *Psammodesmus bryophorus* (**Platyrhacidae**; Figure 180), from a transitional Andean-Pacific montane rainforest in Colombia (Hoffmann *et al*. 2011).
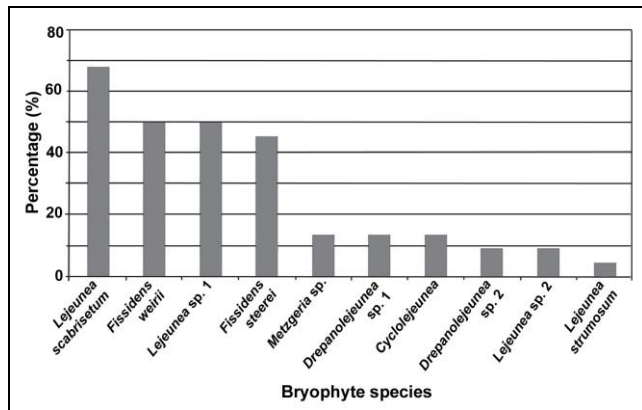
Figure 179. Percentage of bryophyte species on the exoskeletons of *Psammodesmus bryophorus*. Redrawn from Martínez-Torres *et al.* 2011.

Figure 180. *Psammodesmus bryophorus* male with bryophytes in numerous positions on the dorsal exoskeleton. Photo by Shirley Daniella Martínez-Torres, with permission.
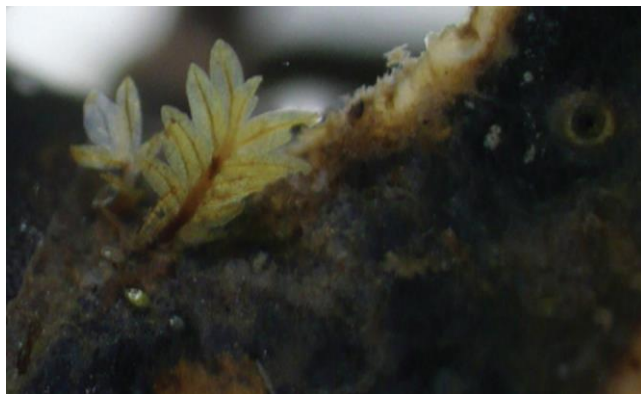

Figure 181. The moss *Fissidens* sp. on *Psammodesmus bryophorus.* Photo by Shirley Daniella Martínez-Torres, with permission.

Out of 18 individuals of *Psammodesmus bryophorus* (**Platyrhacidae**; Figure 180), 11 had more than 400 individuals of bryophytes, mostly on the dorsal side. In all, 22 individuals were inspected, and 15 of these had a species mosaic, primarily of *Lepidopilum scabrisetum* (Figure 182), *Lejeunea* sp. 1 (Figure 183-Figure 184), and *Fissidens weirii* (Figure 181) (Martínez-Torres *et al.* 2011). All species were epiphylls except for the two **Fissidentaceae** species, which are typical of soil. The bryophytes were especially located on the keels (Figure 181-Figure 185).

Figure 182. *Lepidopilum scabrisetum*, a species that can live on the millipede *Psammodesmus bryophorus*. Photo by Claudio Delgadillo, with permission.
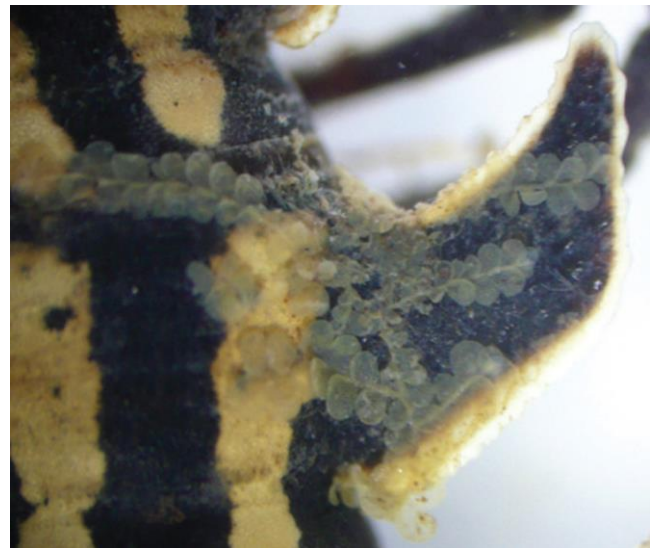

Figure 183. A leafy liverwort in the family **Lejeuneaceae** on *Psammodesmus bryophorus.* Photo by Shirley Daniella Martínez-Torres, with permission.

Figure 184. *Lejeunea cf aphanella*, member of a genus that inhabits the millipede *Psammodesmus bryophorus*. Photo by Michaela Sonnleitner.
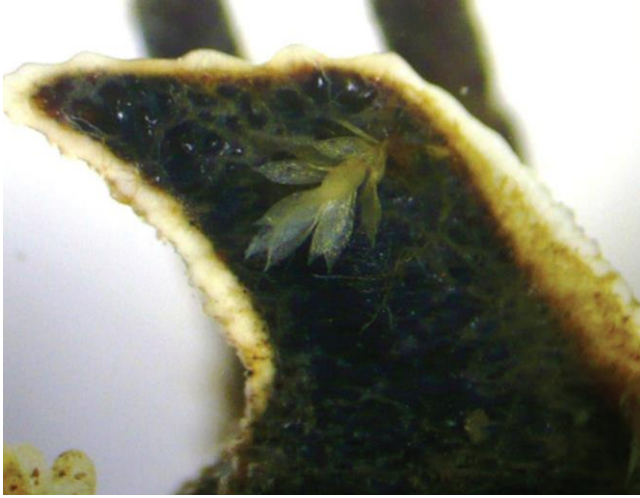
Figure 185. **Pilotrichaceae** on the exoskeleton of *Psammodesmus bryophorus*. Photo by Shirley Daniella Martínez-Torres, with permission.

Class Pauropoda

Pauropods (Figure 186) are small, light-colored arthropods that resemble centipedes but are more closely related to millipedes. They live mostly in the soil and leaf litter, but some find mosses to be a suitable habitat (Greenslade 2008). In the temperate rainforests of Tasmania the mosses typically have a higher moisture content than their usual habitats elsewhere, and here one can find numerous **Pauropoda**. Greenslade found fifteen species among mosses in 79 collection records. These species were not common in other habitats of the collections areas, attesting to the importance of the mosses as a habitat.

Figure 186. Typical member of Pauropoda. Photo by David R. Maddison through Tree of Life Creative Commons.

Class Symphyla

This small class includes the common house-hold centipede with the long legs. Symphylans lack eyes, so their long antennae serve as sensory organs. The female lays her eggs and attaches them in crevices or to moss or lichen with her mouth (Barnes 1982). In the Finnish forests, Biström and Pajunen (1989) found an unidentified member of the **Scutigerellidae** (Figure 187) in two samples of *Polytrichum* (Figure 125).

Figure 187. *Scutigerella* sp., member of a family of symphytans know to inhabit bryophytes. Photo by Walter Pfliegler, with permission.

Summary

Bryophytes on the forest floor can provide unique habitats that have moss mite faunas different from that of the leaf litter. However, it is often the interface between the bryophytes and the soil where mites find food and suitable moisture environments.

Epiphytic leafy liverworts with lobules seem to be especially good at providing both a safe site and moisture, and fecal pellet volatile compounds suggest they are also a food source. This lobule niche is especially important in the tropical canopy.

Aquatic bryophytes provide safe sites not only against some predators, but against the rapid current in streams. In peatlands, the need for calcium carbonate, unavailable in the low pH, can be avoided by using calcium oxalate in the hardening of the cuticle.

Peatland genera differ between Europe and North America, with *Limnozetes* and *Malaconothrus* dominating in Canadian peatlands. *Limnozetes* is also the most species-rich and its communities may be useful in characterizing peatlands. Oribatids are the predominant mite group in both European and North American peatlands.

Peatland pools may have *Hydrozetes*. Predation by **Odonata** causes some mites to hide in the concavity of the upper surfaces of *Sphagnum* leaves.

In the Antarctic, bryophytes can have temperatures up to 13°C above the ambient air temperature; some mites are able to supercool. Tropical bryophytes, especially epiphytes, are often rich habitats for invertebrates, including mites. The mites can contribute to the breakdown of canopy litter and thus have a role in nutrient cycling.

Vertical zonations exist among both the bryophytes and the mites, with the canopy increasing stresses due to UV-B light and desiccation. Within a bryophyte mat, zonation can separate communities of the older, brown portions and the young growing tips. The lower brown

portion of these two habitats differs in providing more decaying material, greater moisture, and less exposure to UV-B radiation. The temperature at that depth may be greater or lower than near the surface and is usually buffered compared to apical portions. The apical green portions (growing tips) provide greater ease of movement and fresh moss material for those able to use it as food.

Vertical migrations permit mites to seek suitable combinations of moisture and temperature within the moss mat. Some may migrate in response to predators, and some may migrate as a response to entering a new life cycle stage.

Communities of bryophyte-dwelling mites differ as elevation increases, with both numbers and kinds of species changing. Seasons affect numbers, with most mites becoming dormant during cold seasons. Some mites will migrate lower into the ground or lower portions of the moss to escape cold of winter or heat of summer.

When bryophyte patches are disturbed, corridors help mites to reach other patches, although some will traverse bare rocks and soil to reach a new patch. Dispersal is passive in most cases and does not seem to be facilitated by wind, but mites can be dispersed with their mossy shelter. On the other hand, mobile mites can carry sperm and gemmae to new locations.

Mites can serve as pollution indicators and monitors. Most will decline in numbers under stress of industrial pollution. However, **Hygrobates fluviatilis** will actually increase in numbers. Most species are sensitive to UV-B light and will respond negatively.

It is likely that moss mites provide a significant role in recycling nutrients from moss communities back to the ecosystem. This miniature ecosystem and the role of its fauna is poorly known and may yield fascinating relationships as we explore the interrelationships.

Ticks, centipedes, and millipedes occur among bryophytes, but both diversity and numbers are low.

Acknowledgments

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