# CHAPTER 9-2
## ARTHROPODS: MITE HABITATS AND MINOR ARACHNIDS

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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

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 lives among mosses and litter in pine forests in northern Latvia (Salmane 2011). Members of Epicrius (Figure 2) live among mosses (David E. Walter, pers. comm. 1 September 2011). Some members of the genus Epidamaeus (Figure 3) occur among leaf litter and mosses on soil. (Ermilov & Łochyska 2009). Labidostommatids 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 4). This soil/moss interface provides a moist environment where fungi and other micro-organisms can provide food sources.
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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 5) 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 6), Pleurozium schreberi (Figure 7), Ptilium crista-castrensis (Figure 8)], common boreal forest mosses, harbor a diversity of predatory Gamasina mites (Figure 5; 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 mite 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 (Huht et al. 1986; Pflug & Wolters 2001; Jučevića & Melecis 2002), and mites can easily follow them.
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Figure 8. *Ptilium crista-castrensis*, a feather moss known to harbor a number of predatory Gamasina mites. Photo by Janice Glime.

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*; 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 9).

Figure 9. *Acroseius*, new species from litter (including mosses), from Queensland, Australia. Photo by David E. Walter.

*Eremaeus stiktos* (see Figure 10-Figure 12) 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 11-Figure 12). Woolley (1968) reported *Li acarus bidentatus* on the forest floor among mosses in Washington state, USA, and in mosses in Wyoming. *Li acarus spiniger* also occurs among mosses. In Illinois, USA, *Platynothrus peltifer* (Figure 13; formerly *Hermannia bistriata*) lives among mosses and under logs (Ewing 1909).

*Minunthozetes pseudofusiger* 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, Cepheus tuberculatus, Nellacarus petrocoriensis, Liochthonius perfusorius,* and *Quadroppia pseudocircumita*. More than 100 species were living among the mosses at this location and nearby areas.

Figure 10. *Eremaeus* sp., member of a forest bryophyte-dwelling genus. Photo by Walter Pfiegl.

Figure 11. SEM of *Eueremaeus foveolatus* (formerly *Eremaeus foveolatus*), member of a moss-dwelling genus on logs and the forest floor. Photo by Valerie Behan-Pelletier and Barb Eamer.

Figure 12. SEM of *Eueremaeus tetrosus*, member of a forest bryophyte-dwelling genus. Photo by Valerie Behan-Pelletier and Barb Eamer.
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 14), recorded by Arroya et al. (2010) for the first time in Ireland, despite being known since 1841.

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).

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 bole 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. 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, Sphaerozetes, and Dendrozetes...
(Figure 16) 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.

Figure 16. SEM of *Dendrozetes* sp., member of a genus known from Sitka spruce canopy bryophytes. Photo by Valerie Behan-Pelletier and Barb Eamer.

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*) and huckleberry (*Vaccinium parvifolium*)] 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 trees species did not differ, but there seemed to be differences in communities that related to the location of the moss mats.

**Lobule Mites**

Leafy liverworts are common on the boles and canopy branches of forest trees. Among these, *Radula*, *Frullania*, *Porella*, and others have lobes. In *Frullania*, these lobes are modified into lobules (Figure 17-Figure 18) that trap and hold water through capillarity.

Andi Cairns, Tamas Pocs, Saci Pocs, Chris Cargill, and Elizabeth Brown discovered tiny oribatid mites moving about in the lobules of *Frullania ferdinandi-muelleri* (Figure 15-Figure 20) 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 20-Figure 23), the first record for the genus in Australia. Because of its association with liverwort lobes, Colloff and Cairns (2011) named this mite *Birobates hepaticolus* (Figure 21-Figure 23). The lobules of the *Frullania* (Figure 21) 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 environment. 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 17. 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.

Figure 18. *Frullania* sp., 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.

Figure 19. *Frullania ferdinandi-muelleri*, a leafy liverwort that serves as home to the newly described *Birobates hepaticolus*. Photo by Tamás Pócs.
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* 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.

**Semiaquatic Habitats**

Terrestrial members of *Parasitengonina* (parasitic mites) may be found among mosses in semiaquatic niches. In particular, members of *Johnstonianidae* can all be found in mosses (Wohltmann 2004). Among these, Wohltmann has specifically found *Johnstoniana* spp. (Figure 24), *Diplothrombium* spp., and *Centrotrombidium* (Figure 25; Wohltmann & Wendt 1996). Sevsay and Özkan (2005) reported the new species *Johnstoniana hakani* from mosses in Turkey.

*Centrotrombidium schneideri* (Figure 25) larvae recognize the pupae of the biting midge *Culicoides* sp. (Figure 26) 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.

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
*Trombidiidae* (*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 *Trombidiidae* search among the mosses as well as
other locations for prey and for hosts for the next life stage.

![Figure 25. *Centrotrombidium schneideri*, a mite whose
larva is a parasite on the biting midge *Culicoides*. Photo by
Andreas Wohltmann.](image)

*Atractothrombium, Camerotrombidium* (Figure 39),
*Enemothrombium* (Figure 40), *Valgothrombium*,
*Echinothrombium rhodinum*, and *Platytrombidium*
(Figure 41) in the *Microtrombidiidae*.

![Figure 26. *Culicoides* (biting midges) adults, host (as a
larva) of the mite *Centrotrombidium schneideri*. Photo by A. J.
Cann through Creative Commons.](image)

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:
*Erythraeidae: Calyptostoma* (Figure 28-Figure 30) in the
*Calyptostomatidae*, *Leptus* (Figure 31-Figure 32),
*Erythraeus, Abrolopus* (Figure 33), and *Charletonia*
(Figure 34) in the *Erythraeidae*; *Trombidiidae: Trombidium* (Figure 35) and *Allothrombium* (Figure 36)
in the *Trombidiidae, Podothrombium* (Figure 37-Figure
38) in the *Podothrombidiidae, Microtrombidiun*,

![Figure 27. *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.](image)

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.

![Figure 28. 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.](image)

![Figure 29. 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.](image)
Figure 30. *Calyptostoma velutinus* adult, a free-living stage that can occur among mosses in semi-aquatic habitats. Photo by Andreas Wohltmann.

Figure 31. *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.

Figure 32. *Leptus beroni*, parasitic larva on the harvestman *Mitopus* sp. Both species can occur among bryophytes. Photo by Andreas Wohltmann.

Figure 33. *Abrolophus* larva, a mite that can occur frequently among mosses when it ventures into semi-aquatic habitats. Photo by Andreas Wohltmann.

Figure 34. *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.

Figure 35. *Trombidium holosericeum*, velvet mite on soil, where its bright red color makes it easy to see. Photo by Ruth Ahlburg.
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Figure 36. *Allothrombium* sp., a mite shown here on grass, but that can also inhabit bryophytes. Photo by Sankax on Flickr through Creative Commons.

Figure 37. *Podothrombium* sp., a mite of amphibious and other habitats and that can be frequent among bryophytes. Photo by Walter Pfliegler.

Figure 38. Female *Podothrombium filipes* with eggs visible in her body. It is likely that the eggs are sometimes deposited among mosses in various habitats. 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.

Figure 39. *Camerotrombidium pexatum* adult, a free-living stage that can occur among bryophytes in a variety of habitats. Photo by Andreas Wohltmann.

Figure 40. *Enemothrombium bifoliosum* adult, a free-living stage that can occur among bryophytes in a variety of habitats. Photo by Andreas Wohltmann.

Figure 41. *Platytrombidium fasciatum* adult, a free-living stage that occurs among bryophytes in a variety of habitats, including semi-aquatic ones. Photo by Andreas Wohltmann.

Hosts of parasitic stages of these mites are typically arthropods, where new ones are still being discovered. Stur *et al.* (2005) suggested that the moss-dwelling habit of the midge *Chaetocladius perennis* (Figure 42) 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* and *T. bavarica* 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 42. *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.

**Aquatic Habitats**

Aquatic mosses have their own mite fauna, the most common being *Hydrachnidia* (Vlěková 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* (Figure 44) in eastern North America as having special structures above the middle two pairs of legs for holding an air bubble when submerging (Figure 45). These bubbles, a condition known as *pearling* (Figure 43) when they come from underwater plants (Benito Tan, pers. comm. 6 June 2011), work like a diving bell into which the mite can exchange CO₂ for O₂ gases. When the bubble gets too small, the mite must return to the surface for another bubble. Oxygen bubbles produced during plant photosynthesis can provide this source of oxygen, and submerged mosses are often so covered with bubbles that their own structure cannot be discerned (Figure 46).

Figure 43. Pearling (air bubbles) on the brook moss *Fontinalis* sp. Photo by Loh Kwek Leong.

Figure 44. SEM of *Tegeocranellus muscorum*, an aquatic bryophyte-dwelling mite. Photo by Valerie Behan-Pelletier and Barb Eamer.

Figure 45. 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.
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Figure 46. Pearling on submerged Ceratodon purpureus from Casey Station, Antarctica, demonstrating complete coverage of the moss. Photo by 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 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.

Compared to other arthropods, the Hydracarina on bryophytes are not very abundant. Stern and Stern (1969) found only 1-2 per 0.1 m² 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.

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. 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 47), Fissidens rigidulus, Cratoneuropsis relaxa] in the Southern Alps in New Zealand. They found the mites Notopanisus sp. on all three mosses and Platymamersopsis sp. on Pterygophyllum quadrifarium 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.

Andreas Wohltmann (pers. comm. 17 September 2011) has found that in temporary pools, Sphagnum, and probably other mosses, can house species of Hydryphantoidea [Euthyas (Figure 48), Parathyas (syn. Thyas) (Figure 49), Hydryphantes (Figure 50)]. These mites sit in the water film around the mosses during their terrestrial phase. 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 47. Achrophyllum quadrifarium, a bryophyte habitat for mites in streams in the Southern Alps in New Zealand. Photo by Jan-Peter Frahm.

Figure 48. Euthyas sp. This is a preserved specimen that is normally red when alive. Photo courtesy of BOLD Systems, Biodiversity Institute of Ontario.

Figure 49. Parathyas barbigera adult, a phase that sits in the water film of mosses near temporary pools. Photo by Andreas Wohltmann.
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Figure 50. *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 *Hygrobatoida* 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* (Figure 58-Figure 60), *Limnocharis* (Figure 51), *Piona*, *Thiphys*] lack this ability to crawl under terrestrial conditions. Most of them find hosts among the *Diptera*, especially the *Chironomidae* (midges), 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 51. *Limnocharis 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.

Larvae of *Panisellus thienemanni* (*Hydryphantoidea*; Figure 52) parasitize the springtail *Arthropleona* (Collembola) in the spring. Andreas Wohltmann (pers. comm. 17 September 2011) has found these exclusively in wet mosses of amphibious biotopes.

Figure 52. *Panisellus thienemanni* larva on the springtail *Arthropleona* sp. (Collembola). Photo by Andreas Wohltmann.

Larvae are also known to parasitize both young and adults of the springtails *Pogonognathellus flavescens* and *Tomocerus minor* (Boehle 1996).

Figure 53. *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.

Some species of *Eylaoidea* [e.g. *Eylais* (Figure 53), *Piersgia*, but not *Limnocharis* (Figure 56-Figure 57)] and of the so-called 'higher water mites' such as *Thiphys* and some *Arrenurus* (Figure 58-Figure 60) and *Piona* 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, 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 53) 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.
In the genus *Eylais* (Figure 54), 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 water 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.

In eastern Canada, there are at least ten species of the genus *Tiphys* (Smith 1976, 1987). *Tiphys diversus* 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 molts 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* (Figure 55) 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, one can find the crawling species *Limnochares aquatica* (Figure 56; Smith in Smith *et al.* 2011), whose larvae may be attached to the bodies of other arthropods (Figure 57).

The mite *Trichothyas muscicola* 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* (see Figure 58-Figure 60), a taxon known exclusively from moss mats at margins of boggy pools where the mites are in and out of the water. *Arrenurus siegasianus*, a species with a boreal distribution, is common in sluggish streams from Newfoundland to Alberta (Smith in Smith *et al.* 2011).
Figure 58. *Arrenurus* sp.; some species of this genus live exclusively among *Sphagnum*. Photo by Ian M. Smith, Val Behan-Pelletier, and Barb Eamer.

Some mites, such as *Malaconothrus* (Figure 61), 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*, are more generalized and are able to live in the profundal zone of oligotrophic lakes 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* and other mosses (Figure 62), but also for swimming. They are adapted for cool water in the northeastern and boreal peatland pools, mostly in relict habitats.

Figure 59. *Arrenurus (Megaluracarus) globator* female; some members of this genus live exclusively among *Sphagnum*. Photos by Walter Pfliegler.

Figure 60. *Arrenurus* sp. larva; some members of this genus live exclusively among *Sphagnum*. Photo by Walter Pfliegler.

Figure 61. *Malaconothrus* sp., member of a genus that can be found among aquatic mosses. Photo courtesy of BOLD Systems, Biodiversity Institute of Ontario.

Figure 62. 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.
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).

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* (Figure 63) 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* (Figure 64), 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 65), a small dipteran whose larvae sometimes live among mosses. Members of the *Unionicolidae* (Figure 66) can be found in streams, where they inhabit mosses like *Hygroamblystegium* (Paul Davison, pers. comm. 27 September 2011). *Fissidens fontanus* 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.

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**Figure 63.** *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 64.** *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.

**Figure 65.** *Empis bistorta*, host of larval mites (*Hydrovolzia mitchelli*) that crawl among mosses as adults. Photo by James K. Lindsey.

**Figure 66.** 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.
**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 pH resulting from the activities of the *Sphagnum* 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.

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, 1991e, 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* 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* 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: Eitminavichyte 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* (Figure 67) 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* (Figure 68), often being the only genus in the dripping *Sphagnum* 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* in the *Sphagnum fuscum* association (Figure 69) in Germany; *Pitogalumna tenuiclavus* occurred in the *Sphagnum magellanicum* association (Figure 70).

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**Figure 67.** *Hydrozetes* sp., member of a genus that is common in peatland mills. Photo by Walter Pfliegler.

**Figure 68.** *Limnozetes*, a common genus in dripping *Sphagnum* and peat layers. Photo by Valerie Behan-Pelletier & Barb Eamer.
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* (Figure 61) and *Limnozetes* (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* 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*, 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).

The family *Cunaxidae* (Figure 71) lives in saturated mosses such as 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 water mites (*Hydracarina*) and *Mesostigmata*. The characteristic genera include *Malaconothrus* (*Trimalaconothrus*) (Figure 61), *Hydrozetes* (Figure 72-Figure 74), and *Limnozetes* (Figure 75-Figure 80). *Hydrozetes lacustris*, and probably also *Limnozetes ciliatus*, live among the stems and leaves. *Trimalaconothrus maior* lives in the leaf axils. Seeming to defy the Gaussian principle, up to five species of *Limnozetes* (see Figure 75-Figure 80) can occur on a single *Sphagnum* (Figure 69-Figure 70) 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.
In Canada, the genera are somewhat different from those in Europe, with mites such as *Parhypochthonius* (Figure 81) and *Nanhermannia* (Figure 82) 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* being among the most abundant (Behan-Pelletier & Bissett 1994).
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- **Figure 81.** SEM of *Parhypochthonius* sp., member of a Canadian peatland mite genus. Valerie Behan-Pelletier and Barb Eamer.

- **Figure 82.** *Nanhermannia* from peatlands in Canada. Valerie Behan-Pelletier and Barb Eamer.

**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* 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 m² plots, Borcard and Matthey compared mite communities associated with hollow (wet) species *Sphagnum recurvum* with that of hummock (drier) species *Sphagnum fuscum* 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*, a common peatland mite, had a 96% relative frequency and was the overwhelming dominant following trampling.

The *Sphagnum fuscum* hummock had a quite different response. The moss died, but the hummock retained its shape. The mite community, as in *S. recurvum*, 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*, 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* control plots, *Oppiella nova* increased in numbers, possibly benefitting from drying around sampler holes. More hygrophilous species (*Limnozetes ciliatus*, *Hoplophthiracarus pavidus*) 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 83). Those in *S. recurvum* 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* having extreme dominance. By contrast, the decrease in number of species in *S. fuscus* 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.

As one might expect, the vertical distribution of the mites changed as the structure of the moss strata changed (Figure 84). In *Sphagnum recurvum*, 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*, where original structure changed little following trampling, despite death of the moss.

One interesting result is a dramatic increase of the tiny *Ceratozetes parvulus* in the *Sphagnum fuscum* 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?
Figure 83. 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 84. 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.
Predation

Hiding oneself deep in the Sphagnum 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, 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 on the inner surfaces of the leaves where they were much more protected. The Odonata guts also contained predators of the mites, suggesting that these insect naiads were both friend and foe.

Acidity Problems

One problem that organisms always face in Sphagnum peatlands is the low pH. Although Sphagnum is usually too acid for most mites, Hydrovolzia placophora (see Figure 64) seems to be tolerant of the low pH and occurs in the axils of leaves that protect it from open water. This mite is not able to swim (Gledhill 1960).

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 serve this purpose and is deposited even in Sphagnum peatlands, at least for the mites Eniochthonius minutissimus, Archophlophora rostralis, and Prototritia major (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.

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 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), 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.

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 mussels and invertebrates including mites to reconstruct past history (late-glacial and early-Holocene) of Kraekenes Lake, western Norway. Hydrozetes oryktosis (see Figure 72-Figure 74) and Limnozetes cf. rugosus (see Figure 75-Figure 80) can be used to infer lake levels (Erickson 1988; Solhøj 2001). In the Antarctic, Hodgson and Convey (2007) found Alaskozetes antarcticus (Figure 92) and Halozetes belgicae, both known moss dwellers, in a sediment core. The expansion of their numbers indicated a temperate period. In Finland, Markkula (1986a) found that Limnozetes ciliatus 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 85), the first report from the Antarctic, and reported three new species (Haplochthonius antarcticus, H. maitri, and H. longisetosus). Tyrophagus antarcticus 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 86) is only 0.3 mm long.

Figure 85. Haplochthoniidae mite, probably Eohypochthonius. Photo by David E. Walter.
Figure 86. *Nanorchestes* sp., member of an Antarctic bryophyte-dwelling genus. Photo by David E. Walter.

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 *Cyrtoladaps* (*Gamasellus*) lacked any pattern of distribution related to scale of sampling, exhibiting random distribution, whereas the prostigmatic *Ereynetes, Eupodes,* and *Nanorchestes* (Figure 86) had distinct patterns at a scale less than 30-40 cm. A small scale pattern was present at 10-20 cm in *Polytrichum,* with slightly larger scales (up to 30 cm) in *Chorisodontium* 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 *Cyrtoladaps* (*Gamasellus*) lacks a pattern of scale because it goes where the food is, crossing "zones."

Among these same mosses, Davis (1981) found the turf communities [*Polytrichum strictum* (formerly *P. alpestre*) (Figure 87) and *Chorisodontium aciphyllum* (Figure 88)] and the carpet communities [*Calliergidium austrostramineum* (Figure 88), *Warnstorfia sarmentosa* (Figure 89), and *Sanionia uncinata* (Figure 90)] 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 86. Nanorchestes sp., member of an Antarctic bryophyte-dwelling genus. Photo by David E. Walter.](image1)

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.
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% (*Ereynetes macquariensis*) to 63% (*Gamasellus racovitzai*).

At the Canada Glacier, mites were less abundant than protozoa, rotifers, nematodes, and tardigrades (Schwarz *et al.* 1993). 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.

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 protection from temperature 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 87) could reach January temperatures up to 13°C above atmospheric temperature, but *Drepanoclados* (*sensu lato*; Figure 89-Figure 90) 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 (Somme 1981). This seems to involve both use of such cryoprotective compounds as glycerol and the elimination of nucleating proteins from the gut.

The moss-dwelling *Ameronothrus lineatus* (Figure 91) lives in the high Arctic heath of the Svalbard, West Spitsbergen. Collections of soil demonstrated that at least some individuals can survive temperatures of -22°C (Coulson & Birkenme 2000).

Block *et al.* (1978) noted that the mite *Alaskozetes antarcticus* (Figure 92) 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 91. *Ameronothrus lineatus*, a moss-dweller from the high Arctic of Svalbard. Photo by Steve J. Coulson.

Figure 92. *Alaskozetes antarcticus*, an Antarctic moss-dweller that is capable of supercooling. Photo by Richard E. Lee, Jr.

Cannon (1986a) experimented with the humidity relations of *Alaskozetes antarcticus* (Figure 92) 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 (Somme 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* (Figure 92) 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 bryophyte in maintaining survival of this species. Since the bryophyte is likely to be frozen during a large portion of the year in the Antarctic, it is possible that ice crystals on its surface could contribute to desiccation of the mite by drawing the nearby water to the ice crystals of the bryophyte. Removal of water in this way from the mite would reduce the danger of crystal formation within the mite. Evacuation of the gut would further support the inability to form internal ice crystals. This could potentially protect the mite within the mat 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 its great variability. Not only does it have extremes through time, but it experiences 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* 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, 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.

**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 and primary forest 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 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. Some 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 sieving 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*, that is epizoic on backs of Papuan weevils (Aoki 1966). The beetle genus *Gymnopholus* (subfamily *Leptopiinae*) 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 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).

**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. (Figure 93), *Hermannia* spp. (Figure 94), and *Phthiracarus* sp. (Figure 95) (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.

**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* 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 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 and Hypochthonius rufulus in response to hummock temperature changes.

Ceratozetes and Eremaeus 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 Mixonomatidæ and the families Oribatellidæ, Galumnidæ, Oppiidæ, Microzetidæ, Cepheidæ, Adelphacaridæ, Mycobatidæ, Phthiracaridæ, Carabodidæ (Figure 96-Figure 97), and Cymbaeremaeidæ. All but Adelphacaridæ and Cymbaeremaeidæ were collected in more than one location. On Mt. Otira, New Zealand, the researchers found Oribatulidæ, Eutieidæ, Epilohmanniidæ (only at higher elevations of 1000-1500 m), Oribotritiidæ, Nanhermanniidæ (Figure 82), Pedrocortesellidæ (the latter three only from lower elevations of 250 m), Microzetidæ (1 location at 750 m), and Tectocephidæ (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. 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.

<table>
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<tr>
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<th>500</th>
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<th>1000</th>
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Mt Otira only

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Table 2. 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.

<table>
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<tr>
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<td>3</td>
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</tbody>
</table>

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, Ceratozetes parvulus, and Trimalaconothrus novus migrate to the deeper layers of the peat hummocks to spend the winter.

Gerson (1969) dug the mosses Ceratodon purpureus and *Bryum* out from 1.6 m of snow on Montreal Island, Quebec, Canada, and found many live *Eustigmaeus* (Figure 98) 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.

Salmane (2000) investigated the seasonal activity of Gamasina mites (Figure 5) 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 (*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 *Polytrichum* and *Bryum* spp. 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 99) were already known from studies by Smrž (1994). The oribatid microarthropods may reach 200 or more morphospecies in less than 20 m² (Starzomski & Srivastava 2007). In their BC study, 163 species were found, comprising 26,274 individuals.
Connectedness between patches was 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* (Figure 100) increases with industrial effluent additions (Bolle et al. 1977).

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* 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 in the morphology of the *Sphagnum* capitulum.

![Figure 100. *Hygrobates fluviatilis*, a pollution-tolerant moss mite. Photo by Nigrico through Creative Commons](https://example.com/hygrobates-fluviatilis.jpg)
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 101-Figure 104) 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.

Zhang and coworkers (2002) provide further evidence of possible transport of gemmae in the moss *Octoblepharum albidum* (Figure 105-Figure 106). 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!

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 106. Gemmae of *Octoblepharum albidum*, potentially distributed by mites that also eat some of them. Photo by Li Zhang.

**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* (Figure 107) was more common on moss-covered oak trees than on trees without mosses. They found that the moss reduced the surface temperature by ~1.9°C 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).

![Image of Ixodes pacificus](https://via.placeholder.com/150)

**Figure 107.** *Ixodes pacificus*, an inhabitant of moss-covered oak trees. Photo by CDC/ Amanda Loftis, William Nicholson, Will Reeves, Chris Paddock/ James Gathany - Creative Commons.
In the Antarctic, the tick *Ixodes uriae* likewise makes use of mosses. It lays its eggs under mosses or grasses (Gressitt 1967).

**SUBPHYLUM MYRIAPODA**

The myriapods represent a much smaller subphylum (~13,000) than that of the Arachnida (Wikipedia: Myriapoda 2010). The name myriaid 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. It is likely this dependence on water that makes mosses such as *Sphagnum* suitable habitat for some species. *Lithobius curtipes* (Figure 108) lives among the mosses [*Polytrichum commune* (Figure 110), *Sphagnum girgensohnii* (Figure 111), *S. squarrosum* (Figure 109)] 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* (see Figure 112) also occurs on *Polytrichum commune* (Biström & Pajunen 1989).

**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 113). They are not common among mosses, or at least there are few reports. Biström and Pajunen (1989) found *Polyzonium germanicum* (Figure 114), *Proteroiulus fuscus* (Figure 115), *Polydesmus complanatus* (Figure 116), and *Leptotius proximus* (Figure 118), on the *Polytrichum*
commune (Figure 110) in Finnish forests. Polydesmus complanatus occurred not only on Polytrichum commune, but also on Sphagnum girgensohnii (Figure 111) and S. squarrosum (Figure 109).

Polydesmus angustus commonly had nests on moss cushions in London, UK, especially during April to July (Banerjee 1973). The nests were constructed from "worked-up" soil from the gut of the female. As the millipedes developed, different instars constructed their own moulting chambers using bits of soil and humus.

Figure 113. Millipede on moss. Photo by Josh Jones.

Figure 114. Polyzonium germanicum, a millipede that lives among bryophytes, shown here on leaf litter. Photo by Ruth Ahlburg.

Figure 115. Proteroiulus fuscus, one of the few millipedes that lives among bryophytes, shown here on a bed of leafy liverworts. Photo from the Public Domain at EOL.com.

Figure 116. Polydesmus complanatus, a millipede known from both Sphagnum and Polytrichum, shown here on a mat of mosses. Photo by Dana Sipkova.

In the UK, Stenhouse (2007) reported Ommatoiulus sabulosus (striped millipede; Figure 119) in moss and Nemostoma bimaculatum under moss.

Figure 117. Polydesmus angustus at Crowle Moors, UK. Photo by Brian Eversham.

Figure 118. Leptoiulus proximus, a millipede known from Polytrichum commune. Photo by Stefan Schmidt through Creative Commons.

Figure 119. Ommatoiulus sabulosus on mosses. Photo by Roger S Key.
**Tachypodoiulus niger** (black snake millipede; Figure 120), 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 (Bannerjee 1967). When disturbed, it will coil itself into a spiral with its legs on the inside and its head in the center (Figure 121; Wikipedia 2012), but it also has the option to flee with sidewinding movements like some snakes. These millipedes feed on algae, detritus, and some fruits such as raspberries (Wikipedia 2012).

![Figure 120](image1.png)

*Figure 120. Tachypodoiulus niger* on a mat of moss. Photo from Wikimedia Commons.

![Figure 121](image2.png)

*Figure 121. 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** on a species of the moss *Thuidium* (Figure 122). 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 (Bannerjee 1967).

![Figure 122](image3.png)

*Figure 122. The moss Thuidium sp. with the millipede Cylindroiulus punctatus.* Photo by 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**, differing somewhat from the European *P. lagurus* (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 123](image4.png)

*Figure 123. Ventral view of Polyxenus lagurus or P. fasciculatus from Ceratodon purpureus.* Photo by Erin Shortlidge.

![Figure 124](image5.png)

*Figure 124. Dorsal view of Polyxenus lagurus or P. fasciculatus from Ceratodon purpureus.* Photo by Erin Shortlidge.

![Figure 125](image6.png)

*Figure 125. Polyxenus lagurus.* Photo by Mick E. Talbot.
Epizootic Bryophytes

Rob Gradstein recently (14 November 2011) sent me a note that I might be interested in a Colombian millipede with ten bryophyte species (Figure 126) 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* (Figure 127), from a transitional Andean-Pacific montane rainforest in Colombia (Hoffmann et al. 2011).

Out of 18 individuals, 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*, *Lejeunea* sp. 1, and *Fissidens weirii*. All species were epiphylls except for the two *Fissidentaceae* species, which are typical of soil. The bryophytes were especially located on the keels (Figure 128-Figure 130).

**Figure 126.** Percentage of bryophyte species on the exoskeletons of *Psammodesmus bryophorus*. Redrawn from Martínez-Torres et al. 2011.

**Figure 127.** *Psammodesmus bryophorus* male with bryophytes in numerous positions on the dorsal exoskeleton. Photo by Shirley Daniella Martínez-Torres.

**Figure 128.** The moss *Fissidens* sp. on *Psammodesmus bryophorus*. Photo by Shirley Daniella Martínez-Torres.

**Figure 129.** A leafy liverwort in the family *Lejeuneaceae* on *Psammodesmus bryophorus*. Photo by Shirley Daniella Martínez-Torres.

**Figure 130.** *Pilotrichaceae* on the exoskeleton of *Psammodesmus bryophorus*. Photo by Shirley Daniella Martínez-Torres.

**Class Symphylla**

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. In the Finnish forests, Biström and Pajunen (1989) found an unidentified member of the *Scutigerellidae* (Figure 131) in two samples of *Polytrichum*. 
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 eggs 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.


Banerjee, B. 1967. Diurnal and seasonal variations in the activity of the millipedes Cylindrolus punctatus (Leach), Tachopodoiulus niger (Leach) and Polyesmus angustus Latzel. Oikos 18: 141-144.


