CHAPTER 9-1
ARTHROPODS: MITES (ACARI)

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Figure 1. SEM of *Lorryia formosa* (yellow mite; **Tydeidae**) on leaf. This citrus dweller (<250 μm) also lives on a variety of other plant species. Its habit of eating fungi actually reduces fungal infections on citrus crops (Mendel & Gerson 1982). Its commonness is at least partly due to the ability to produce young through unfertilized embryos. Some mites that infect crops use bryophytes during seasons when crop plants are unavailable. Photo Eric Erbè, through public domain.

Order Acari – Mites

Mites are similar to spiders, but differ in having no separation between the thorax and abdomen (

and   available   at <http://digitalcommons.mtu.edu/bryophyte-ecology2/>.). Like the spiders, the adults have eight legs, but the larval stage has only six.

I still remember my first experience with a mite among mosses. I was working late at night rehydrating and identifying mosses collected the previous summer for my M.S. research. No one else was around, and I was getting tired. Then I looked through my dissecting microscope and there was an apparition – a tiny, pink, roundish creature with six legs and red eyes! Despite its six legs, I knew by its shape it was no insect. A bit of exploring in my books revealed that this tiny creature was the larval stage of a mite (Figure 2). The extra pair of legs is a nymphal and adult characteristic. Mite life cycles include larval, several nymphal, and the adult stages.

Figure 2. Larval mite (chigger), showing its six legs. Photo by Hansell F. Cross, through Creative Commons.

Habitat Relations

Mites have been associated with bryophytes from their mutual beginnings. Fossil records from 470 million years ago (Ordovician period) provide evidence of fungi in fecal pellets of mites. McNamara and Selden (1993) suggest that these mites fed on the decomposing remains of bryophytes.

Although many mites traverse the cushions and mats of bryophytes at some time during their lives (Figure 3), a smaller number actually live there. And of those, we must ask how many require the bryophytes in any part of their life cycle. Temporary ponds, floodplains, and tidally influenced coastal regions are amphibious habitats that alternate between wet and dry conditions. Changes in these phases often open up new nutrient loads that are favorable to many of their inhabitants (Wiggins *et al*. 1980). In such amphibious habitats, an organism must be adapted for both very wet and quite dry conditions, or move elsewhere when conditions change. But being able to survive these changes in amphibious habitats can also make the organism suited for other habitats within that range of conditions. Wohltmann (2005) asked the question, "No place for generalists?" To answer the question, he compared members of the Parasitengonina, which seems an appropriate group for asking the question. Wohltmann found that the temporary pools of forests and the rocky shores of estuaries had a large percentage of habitat-specific mites, but that floodplains had mostly opportunistic colonizers. Can we use the literature to answer this question for any mossy habitats?

Figure 3. *Eutrombidium* sp., a mite that is parasitic on grasshoppers, sits here on a bed of mosses, most likely just travelling through. Photo by Jenilee, through Creative Commons.

Habitat is tied to food choice, locomotion, and respiration as a driver of evolution in many mites (Wohltmann 1991). For those mites that are able to swim in open water, respiration is greater, as one might expect. And for those in open water, catching swimming prey provides additional food choices, but a short survival period without food (about 2 weeks), and again requires a higher respiratory rate. For those mites that live in amphibious habitats such as temporary pools, being able to survive long periods without food is important, and the respiratory rate is lower. Mites survived up to 400 days with no food (*Thyas barbigera* and *Limnochares aquatica*), but these were species that ate only immobile food and **crawled** on their substrate to eat. Both of these species are able to use bryophytes as substrates (Smith in Smith *et al*. 2011; Andreas Wohltmann, pers. comm. 17 September 2011). Smith and Cook (2005) noted that the sclerotized plates on the backs of *Limnochares* species provided substrate for muscle attachment, hence facilitating their ability to crawl.

Lawrey (1987) cautioned that what may appear to be a preference of certain species may instead be a preference for the substrate of that species. Andre (1979) determined that what appeared to be an association with certain bark-inhabiting lichens was instead an association with the tree species where these lichens grew – *i.e.*, the mites and lichens preferred the same species of trees. Similar relationships are likely for mites inhabiting bryophytes.

Mite Adaptations to Bryophyte-Dwelling

Many of the mites are brilliant red or orange (Hingley 1993; Figure 4). This coloration is due to carotenoids and is thought to protect the mites from UV light (David E. Walter, pers. comm. 6 June 2011). However, David Walter finds that even in *Sphagnum*, most of the mites are duller colors, with brown to beige predominating (Figure 5). This cryptic coloration makes them less conspicuous against the soil and among the bryophytes. Oribatid (moss mites), usually the most abundant mites in mosses, are almost uniformly dull. These are slow-moving creatures (Kinchin 1990) and some feed on contents of moss leaf cells or on capsules (Figure 6; Gerson 1969). The prostigmatids, on the other hand, are often bright red (Figure 4) and may be very fast-moving (Kinchin 1990). It is likely that the bright red color serves as a warning coloration against some predators.
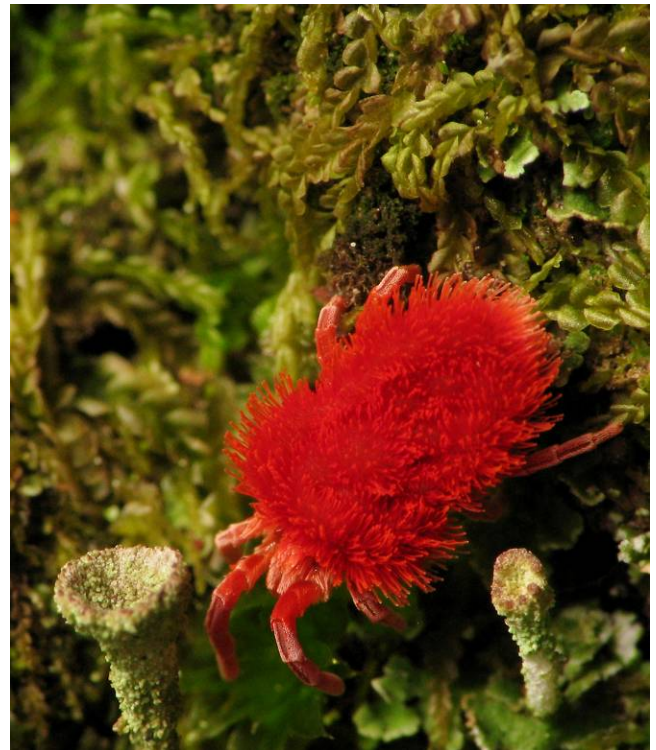

Figure 4. Velvet mite, probably *Austrothrombium* (**Parasitengonina**: **Trombidiidae**), among liverworts and lichens on a tree trunk. This mite has a parasitic larval stage. Photo by Michael Whitehead, through Creative Commons.

Figure 5. *Atropacarus* sp. mite, showing the subdued colors typical of many peatland-dwelling and moss mites. Photo by Scott Justis, with permission.

Figure 6. **Erythraeidae** mite on a moss capsule. Lipid sources in the spores may serve as a rich food source, but these spores are still young and the capsule most likely presents an impenetrable barrier to the mite. Photo by Aniruddha Dhamorikar, through Creative Commons.

Figure 7. *Leptus beroni* larva on the harvestman *Mitopus*. Both are moss dwellers. Photo by Andreas Wohltmann, with permission.

Mites are tiny creatures, mostly less than 1 mm in length (Wikipedia: Acari 2011), sometimes appearing as specks on the legs and other body parts of insects and other arachnids (Figure 8-Figure 9). This small size makes it easy for them to maneuver among the stems and leaves of bryophytes. And their sucking mouth parts permit some of them to use the bryophytes as a food source.

Figure 8. *Mitopus morio* (harvestman) with a red mite larva in the genus *Leptus* (**Parasitengonina**: **Erythraeidae**) attached to its leg. Photo by Ed Nieuwenhuys, with permission.

Figure 9. *Leptus trimaculatus* adult, a known moss dweller. Photo by Andreas Wohltmann, with permission.

Since many of the moss mites are bright colored, camouflage is not going to work for them. This seems to be the case for some of the bright red moss mites such as *Trombidium*. Instead of hiding or running (many mites are not very good at this), they roll onto their backs and play dead (**thanatosis**). Figure 10 shows one of these moss mites doing just that. Aside from being motionless, and thus attracting less attention, I have never figured out how that helps, but opossums seem to think so, and so do some salamanders, snakes, and insects, and so do humans facing grizzly bears!

Miyatake *et al.* (2004) asked that same question about potential advantage. And to our good fortune, they asked it using an arthropod, the beetle *Tribolium castaneum*. First, they showed that there was heritable variability in the duration of the death-feigning behavior.   Using ten

generations of this species, they showed that the strain that had the greatest inheritance of the behavior (longest duration of death feigning) had the greatest frequency of thanatosis. Next they showed that there was greater fitness (greater survival) of those with the long-duration thanatosis trait when they were presented with a predator, a female Adanson jumper spider (**Hasarius adansoni**, Salticidae). Finally, they showed that the frequency of predation was lower on those mites in the strain with long-duration death feigning than from those with short-duration feigning. These experiments met the three criteria proposed by Endler (1986) to demonstrate the evolution of an adaptive trait by natural selection: variation of the trait among individuals; differences in fitness as related to the trait; inheritance of the trait.

Figure 10. **Trombidium holosericeum** in a state of **thanatosis** (playing dead). In this case, the mite was touched with a brush. Photo by Andreas Wohltmann, with permission.

The behavior of the spider, when encountering her prey, may help us to understand how this trait is adaptive. The Adanson's jumper spider had rather different behavior when provided with a live fly, *Drosophila hydei*. She never set the fly free and immediately ate it. But when the spider was presented with the *Tribolium castaneum*, she always let go again. The researchers suggested that this was due to the hard cuticle and/or a chemical released as anti-predator defense (Happ 1968). Only if the beetle moved after the attack did the spider once again attack, and in several cases, eat the beetle.

There might be a nutritional reason as well. If the fly has evolved along with its prey organisms, dead organisms, at least arthropods, could mean a waste of energy when attempting to eat them. Enzymes released from the cells of the insect quickly digest the interior of the insect, leaving mostly chitin, which presumably supplies little energy and may take more energy to penetrate than will be obtained. It is likely that some of the same powerful enzymes that help the mites digest their food are also released when they die, potentially digesting the interior of the mite as well.

Having a number of species with the same adaptive defense behavior of playing dead is considered a form of **aggressive mimicry**. According to the World of Darkness Wiki (2010), the appearance of death is supposed to conjure up the sense of rot and decay and all that goes along with death. But I would think that would require the attendant odors as well. Could it be that these beasts elicit the odor of rotting bodies that we humans have not yet detected, but that these animals have? In fact, that may be the case for the beetle *Tribolium costatum* and others (Miyatake *et al.* 2004).

Symbioribates papuensis has an unusual adaptations to mosses. It lives on mosses that grow in the backs of Papuan weevils, hence getting a free ride that provides dispersal (Aoki 1966).

The Inhabitants

Mites are abundant in bryophytic habitats (Sellnick 1908; Willmann 1931, 1932; Rajski 1958; Aoki 1959; Higgins & Woollery 1963; Wood 1966; Popp 1970; Seniczak 1974; Bonnet *et al*. 1975; von der Dunk & von der Dunk 1979; Harada 1980; Seyd 1988; Seyd & Colloff 1991; Smith & Cook 1991; Hoffmann & Riverón 1992; Kinchin 1992; Seniczak *et al*. 1995; Seyd *et al*. 1996; Winchester *et al*. 1999; Fischer 2005; Bettis 2008), so much so that oribatid mites have been termed moss mites. Aoki (2000) reported on oribatid mites in moss cushions on Japanese city constructions. Their abundance is illustrated by a study by Yanoviak *et al.* (2006), who reported that 65% of the arthropod fauna among epiphytes in a Costa Rica cloud forest were mites.

Weiss (1916) reported **Bdella cardinalis** in mosses as well as under leaves and rotten wood in New Jersey, USA. Jacot (1938) later concluded that this species was a synonym of **Bdella oblonga**, which is common on decayed fallen trunks and among their mosses. Members of the family **Bdellidae** (snout mites; Figure 11-Figure 13) occupy mosses in Mexico (Baker & Balock 1944) where they feed on other arthropods, including mites. These include **Biscirus lapidarius** (only a single specimen) and **Bdella oblonga** from mosses at Deseirto de los Leones. The type specimen of **Bdella rio-lermensis** was collected from mosses in Rio Lerma. **Bdella mexicana** is known from mosses in Valle del Bravo. Likewise, the type specimen for both the genus and the species of **Opserythraeus hoffmannae** were collected as larvae from mosses in Rugege Forest, Rwanda (Fain 1996).

Figure 11. **Bdellidae**, a family that inhabits mosses on rotten logs and elsewhere.   Photo by S. E. Thorpe, through Wikimedia Commons.

Even in habitats where numbers of mites are few, greater numbers are likely to be found among bryophytes (Covarrubias & Mellado 1998).   Oribatid mites were recorded from mosses and lichens in the Krkonose Mts. (Czech Republic) along an altitudinal gradient reaching from submontane to the alpine belt (Materna 2000). In 197 stands, 104 oribatid species were present. On the other hand, Materna found rather poor oribatid mite communities

among saxicolous mosses in the Krkonose Mountains, Czech Republic. Among these the predominant taxa were *Oribatula* *cf*. *pallida* (see Figure 14), *Mycobates tridactylus* (see Figure 15), and *Trichoribates monticola* (see Figure 16). Despite the poor representation in some rock communities, Shure and Ragsdale (1977) found that mites contribute to the fauna during primary succession on granite outcrops.

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Figure 12. **Bdellidae** species, a moss-dweller family. Photo by Walter Pfliegler, with permission.

Figure 13. **Bdellidae** species on rotting wood with mosses. Photo by John Davis, with permission.

Figure 15. SEM of *Mycobates dryas*, a member of a genus with moss-dwellers on rocks. Photo by Valerie Behan-Pelletier & Barb Eamer, with permission.
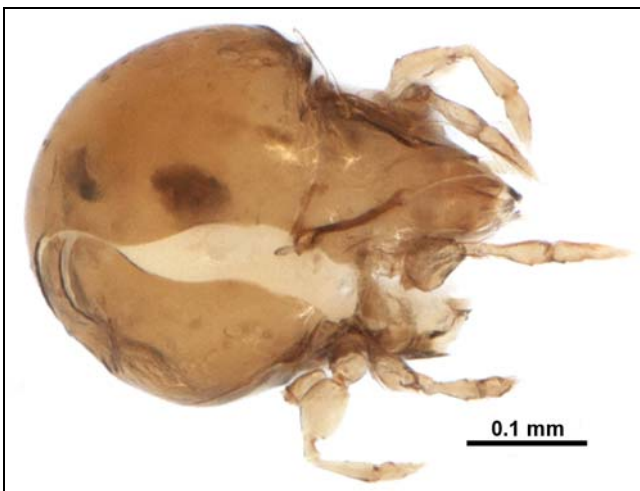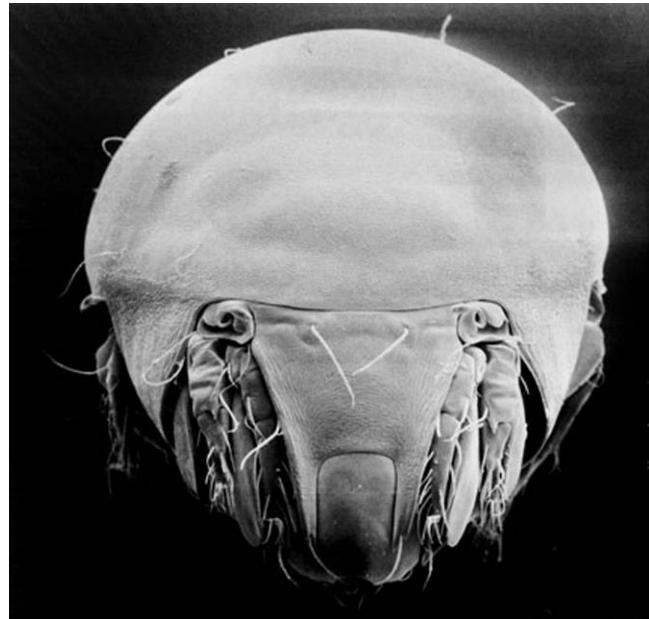

Figure 14. Ventral side of *Oribatula tibialis*, member of a genus in which some members are among the few moss-dwelling mites on rocks. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.
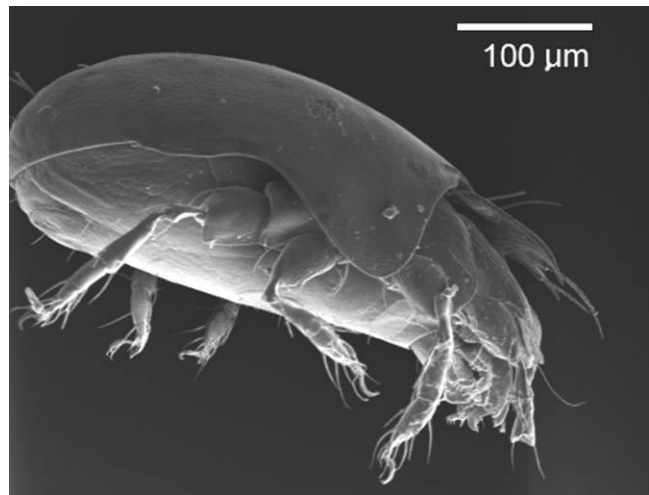

Figure 16. SEM image of *Trichoribates*, a contributor to primary succession of mosses on rocks. Photo courtesy of Birgit Balkenhol, Samantha Kühnel, and the Senckenberg Museum of Natural History, Görlitz.

In wet litter and mosses near bodies of water in the mixed forest plains of Canada, one can find adults of the **Trombellidae** and **Johnstonianidae** (Figure 17; Smith *et al.* 2011). The mite *Rostrozetes ovulum* (Figure 22) occurs in bogs. *Johnstoniana errans* (Figure 18-Figure 20) lives in forests and at the edge of ponds where its **deutonymph** stage and adult, the two active stages in the life cycle, live primarily in damp mosses on rotting wood (Wohltmann 1996). These mites are nocturnal and use the mosses as hunting grounds for larvae and pupae of the cranefly *Tipula* **spp.** (Diptera; Figure 18). The mite larvae search for the pupae (Figure 19) of the craneflies, where they aggregate and await the transformation from the *Tipula* pupa into the emergence of the adult. The larval mites are parasites on *Tipula* adults, beginning just after emergence, once the larvae have moved onto the adult body from the surface of the pupa (Figure 18).

Figure 19. Pupa of the cranefly *Tipula*, a moss dweller that is often host to mite larvae. Photo by Ted Kropiewnicki through Creative Commons.

Figure 17. *Johnstoniana parva* (Parasitengonina) mite larvae parasitic on the mite *Microtrombidium pusillum* (**Parasitengonina**); both can live among mosses near water. Photo by Andreas Wohltmann, with permission.

Figure 20. *Johnstonaina errans* adult on moss litter. Photo by Andreas Wohltmann, with permission.

Figure 18. *Johnstoniana errans* larva on the cranefly *Tipula* sp. Both are known moss dwellers. Photo by Andreas Wohltmann, with permission.

Figure 21. *Johnstoniana errans* deutonymph on moss. Photo by Andreas Wohltmann, with permission.

Some genera seem to show up on mosses fairly often, as indicated by the number of pictures with a mossy substrate. For example, George (1908) found *Trombidium bicolor* (Figure 23) in damp mosses, especially in ditches.

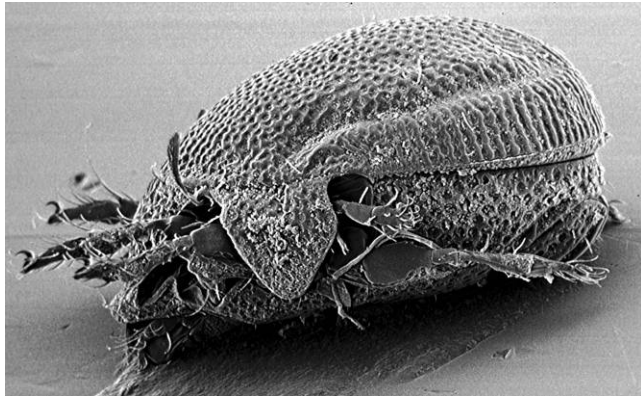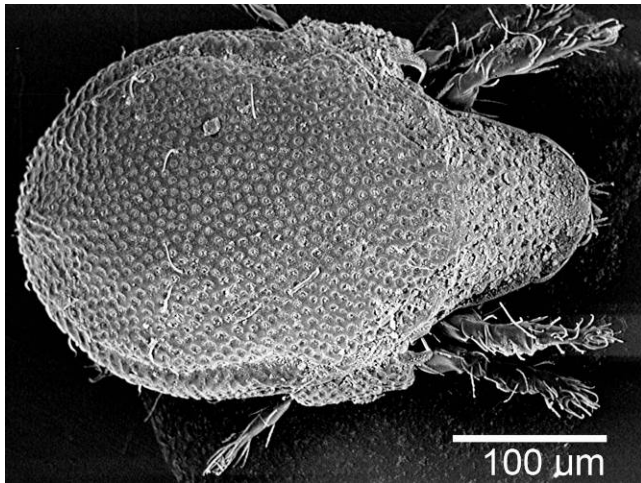Michael Whitehead shared his picture of a species of *Austrothrombium* (Figure 24) on a leafy liverwort.

minuta in parts of eastern central USA, less than 0.5 mm in length, occurs among mosses, although it occurs mostly on animal substances (Banks 1895).

Figure 22.　SEM of *Rostrozetes ovulum*, a bog dweller. Photos by Barb Eamer, with permission.

Figure 24.　Trombidioid mite, probably *Austrothrombium*, on a bed of leafy liverworts.　Photo by Michael Whitehead, through Creative Commons.

Figure 23.　*Trombidium holosericeum*.　Photo by Ruth Ahlburg, with permission.

Some of the moss dwellers seem to be somewhat specialized.　The genera *Damaeus* (Figure 25), *Belba*, and *Metabelba* (Figure 28) are fungal eaters and live in habitats that make close contact with the soil, such as mosses (Smrž 2010).　They rarely occur among mosses on trees.　*Belba*

Figure 25.　*Damaeus onustus*.　Photo by Mick E Talbot, through Creative Commons.

Figure 26.　*Belba* sp.　Photo by Barbara Thaler-Knoflach, with permission.

Figure 27. *Metabelba* sp., a fungal eater that can find its food sources among mosses. Photo by Walter Pfliegler, with permission.

Figure 28. *Metabelba* sp., a moss-dwelling fungal eater. Photo by Walter Pfliegler, with permission.

Armed with names like **Bryobiinae** (Figure 29) and *Bryobia* (Figure 30), I searched with anticipation for information on their habits. My first find was that the common name was **clover mite**, somewhat dashing my hopes for a bryophyte dweller. But when I keyed in moss with its name, I found it did legitimately use *bryo* in its name, using mosses as habitat.

Figure 29. Member of **Bryobiinae**, a family with moss-dwellers. This green one suggests that it is a plant eater, but do they eat bryophytes? Photo by Walter Pfliegler, with permission.
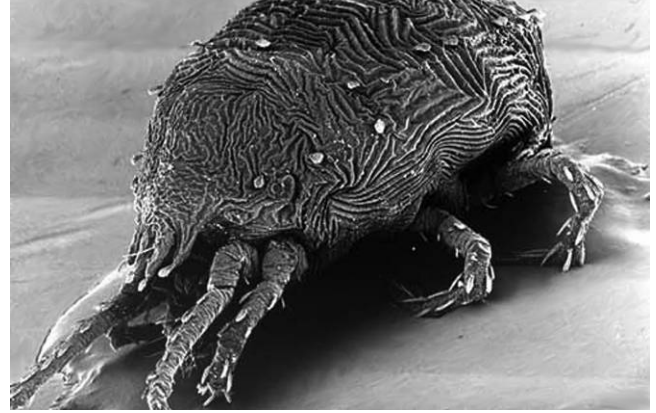

Figure 30. *Bryobia* sp., member of a genus that uses mosses when larger hosts are not available. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Bryobia praetiosa (as *B. humeralis*; Figure 31) was first described by Halbert (1923) from mosses and a wall. Later, Flechtmann and Baker (1970) listed bryophytes among its hosts, and Tuttle and Baker (1976) reported it from mosses in Utah. Nevertheless, it seems to live predominantly on tracheophyte hosts. From there, the records seemed scarce until Hatzinikolis and Panou (1996) discovered *Bryobia emmanoueli* and *B. meteoritica* as new species among mosses in Greece. I suspect that more moss dwellers have been described in the older literature that has not yet found its way to the internet. As you will see, mosses can act as alternate "hosts" when tracheophytes are seasonally absent.

Figure 31. *Bryobia praetosa*. Photo by Jarmo Holopainen, with permission.

Figure 32. *Erythraeus* (**Parasitengonina**) on bark with a moss branch nearby. Photo by James K. Lindsey, through Creative Commons.

Some mites that live on bark and other substrates traverse mosses and obtain moisture from them. Such is likely the case for some members of the **Erythraeoidea** (Figure 32).

Wood (1967) documented the presence among mosses of the mite *Eustigmaeus* (as *Ledermuelleria*; Figure 33), a genus of red species. In 1972 Wood described new species of *Eustigmaeus*, from mosses in Canada. With publication in the same year, Gerson (1972) sampled 160 mosses in eastern Canada and the USA and found that nearly half of them housed mites. Of these, eleven species were in the genus *Eustigmaeus*. Furthermore, among the 55 species of mosses, 38 housed *Eustigmaeus* species. The species *E. arcticus*, *E. gersoni*, and *E. rhodomela* occurred primarily on mosses that colonize open soil. On the other hand, *E. frigida* preferred mosses in shaded, humid places.

Figure 33. *Eustigmaeus* sp., a genus that is common on mosses and uses some of them for food. Photo by David E. Walter and Anthony O'Toole, with permission.

The Role of Bryophytes

Bryophytes can offer an important physical component that provides a habitat for mites. Dewez and Wauthy (1981) used sponges as artificial substrata and found that mites did colonize the sponges in areas where bryophytes had been removed.

This suggests that the ability to provide a moist environment permits mosses to provide suitable mite habitat even on rocks (Materna 2000). In the Krkonose Mountains of The Czech Republic, mosses in areas approaching the treeline and protected by tracheophytes housed a rich community of ubiquitous mite species with high moisture requirements. Where the rocks lacked tracheophytes, the soil was less developed and few soil mites occurred. The moss mite community had few frequent species. The most common mite was *Oribatula cf. pallida* (Figure 14). Two of the species [*Mycobates tridactylus* (see Figure 15) & *Trichoribates monticola* (see Figure 34)] were specialists that lived only on mosses and lichens.

Leafy liverworts such as species of *Frullania* with lobules (Figure 37) provide a protected habitat that maintains moisture when most other places are dry and house such mites as *Birobates hepaticolus* (Figure 37), as both immature and adult individuals (Colloff & Cairns 2011). And for food? It eats liverwort tissue!
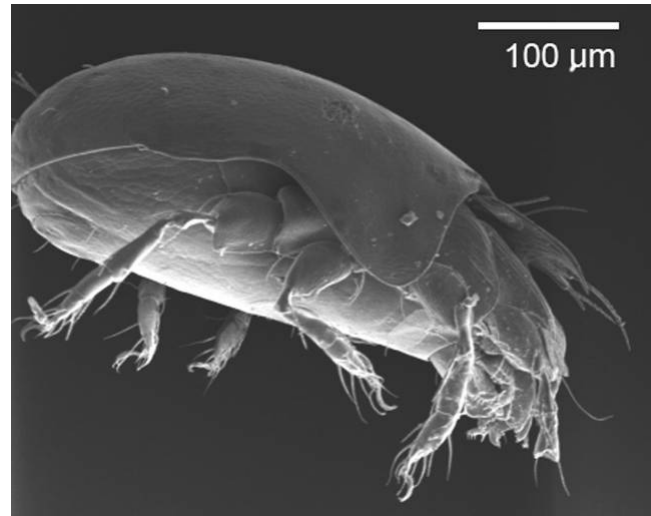

Figure 34. SEM of *Trichoribates* sp., member of a genus where some members specialize on moss and lichen habitats. Photo by Birgit Balkenhol and Samantha Kühnel, the Senckenberg Museum of Natural History, Görlitz, with permission.

Experimental work with moss mites can provide us with information to help explain their presence in a given habitat. Smrž (2006) studied the saprophagous mites living among mosses on a roof to determine their biology. Two species of oribatid mites [*Scutovertex minutus* (see Figure 35-Figure 36), *Trichoribates trimaculatus* (see Figure 34)] comprised the moss mite community. They used these mites in laboratory experiments to determine their nutritional needs, moisture relations, mobility, and food selection. Such factors as digestive processes, vertical and horizontal distribution, and ability to disperse defined different niches within the moss community for these two species.

Figure 35. *Scutovertex sculptus*, in a genus where some members live among mosses. Photo by Matthew Shepherd, through Creative Commons.

Figure 36.   SEM of *Scutovertex sculptus*, a species in a moss-dwelling genus. Photo by Jürgen Schulz, Birgit Balkenhol, and Samantha Kühnel, the Senckenberg Museum of Natural History Görlitz, with permission.
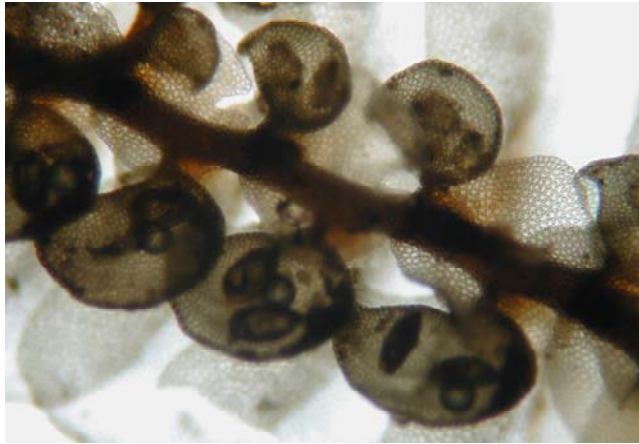

Figure 37.   *Frullania ferdinandi-muelleri* with *Birobates hepaticolus* in its lobules. Photo courtesy of Andi Cairns.

Bryophytes as Food

The oribatid mites eat fungi, algae, and dead organic matter (Bhaduri & Raychaudhuri 1981).   With about 10,000 described species (David E. Walter, pers. comm. 15 September 2011), their habitats are varied, including leaf litter, lichens, bryophytes, humus, and compost heaps. Ponge (1991) found all these foods in feces of the phthiracarid mites living among Scots pine litter. Within the bryophyte communities, mites can often find all of their favorite food sources.

Lawrey (1987) contends that "there is only the scantest evidence that mosses are actually eaten" by mites. Nevertheless, Gerson (1969) states that mites are among the few animals known to eat bryophytes regularly. Woodring (1963) reported that he had been able to rear several mites [*Euphthiracarus flavum* (see Figure 38), *Galumna nervosa* (see Figure 39-Figure 41), *Oribotria* spp., *Pseudotrita* spp.] on mosses as food, indicating that at least some mosses are nutritionally adequate for at least some mites.

Gerson (1969) provided us with his personal observation of oribatid mites "gnawing" on various moss capsules and eating the spores. The fact that mites can be sustained on mosses under laboratory conditions suggests that either the mosses or the microflora and fauna of the mosses provide sustenance (Sengbusch 1954; Woodring 1963; Lawrey 1987). Schuster (1956) found moss remains in the guts of four out of 40 oribatid species. In Brazil, Flechtmann (1984) described the species *Eustigmaeus bryonemus* (see Figure 33) for the first time, noting that it feeds on mosses. When the mite is cleared of its red color, the green moss in the gut becomes visible. But is it the moss that serves the nutritional needs, or micro-organisms and detritus on and among the leaves?
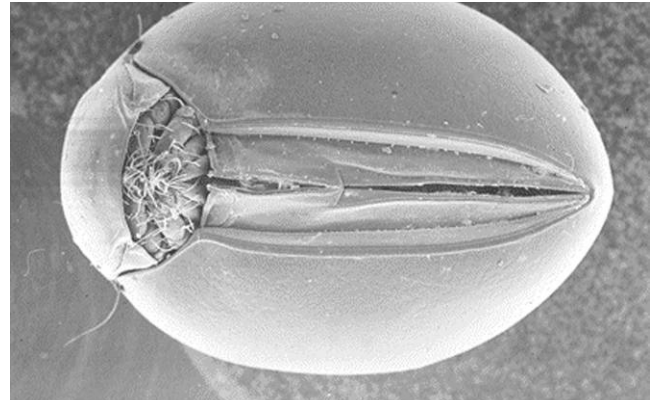
Figure 38.   SEM of **Euphthiracaroid** mite from peatlands. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 39.   **Galumnidae**, a mite group that is able to subsist in mosses. Photo by Scott Justis, with permission.

Figure 40.   *Galumna* sp. (shield-sided fungus mite) that can subsist on mosses. Photo from Flickr through Creative Commons.

The genus *Eustigmaeus* (Figure 33) is one of the common moss mites to feed on the bryophytes, and evidence suggests that the moss is indeed the intended food item.   Gerson (1972) reported, based on laboratory

experiments, that *Eustigmaeus frigida* mites (Figure 42) pierce stem and leaf tissues of mosses with their needlelike chelicerae, enabling them to suck the contents from the cells (David Walter, pers. comm. 6 June 2011), leaving behind skeletons of cell walls (Gerson 1972). Such feeding can cause the young moss shoots to discolor to a silvery grey and shrivel (Gerson (1972). David E. Walter (pers. comm. 15 September 2011) describe this as using "spike-like movable digits to puncture the leaves of the mosses on which they feed." Experiments by Gerson (1972) indicate that they will eat many moss species and survive on the diet. However, they only reproduced following a diet of a restricted few species. In addition to *Eustigmaeus frigida*, *E. rhodomela*, *E. clavata*, and *E. schusteri* also feed on various mosses and have similar life cycles to those of *E. frigida*.

Figure 41. *Galumna* representatives, members of a genus where some species are known to be able to subsist on mosses as food. Photo by Walter Pfliegler, with permission.
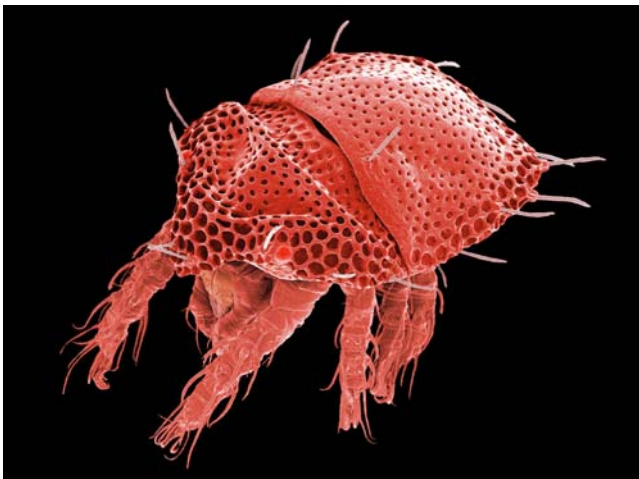

Figure 42. *Eustigmaeus frigida*, a common moss inhabitant that has specialized mouth parts for piercing mosses, but not those with thick leaves. Photo by David E. Walter, with permission.

Length of stylet plays a role in species of mosses that can be eaten by mites. Of five species Gerson observed on *Polytrichum* clumps (Figure 43), *E. frigida* has the shortest (23 μm) and narrowest (1 μm) stylet, compared to 32-58 μm long and 2-4 μm wide stylets among other residents (Gerson 1972). There was no survival of *E. frigida* on relatively large mosses: *Pogonatum urnigerum* (Figure 44),

Polytrichum commune (Figure 43), *Polytrichum piliferum* (Figure 45), *Leucobryum glaucum* (Figure 46), or *Atrichum altecristatum* (Figure 47-Figure 49).

Eustigmaeus (Figure 33) species, in particular, have special stylets that pierce stems and leaves and suck out cell contents (Gerson 1969). Like that of *E. frigida*, part of the specialization to feeding on certain mosses seems to be related to length of stylet (Gerson 1969). *Eustigmaeus clavata* and *E. microsegnis* have long (40 & 32 μm respectively), thick (3-4 μm) stylets and can survive on *Polytrichum* mats. *Eustigmaeus frigida* in Gerson's experiments has short (23 μm), thin (1 μm) stylets and are unable to survive on *Polytrichum* species with their thick dorsal cell walls and covering ventral lamellae.

Figure 43. *Polytrichum commune* in a peatland, a moss that is home for some mites but unsuitable for others. Photo by Michael Lüth, with permission.

Figure 44. *Pogonatum urnigerum*, a mite habitat. Photo by Michael Lüth, with permission.

Figure 45. *Polytrichum piliferum*, a mite habitat. Photo from bryology website at University of British Columbia, with permission.

Figure 46. *Leucobryum glaucum* cushion on forest floor, a habitat that is not suitable food for some mites. Photo by Janice Glime.

Figure 47. *Atrichum altecristatum*. Hydrated mosses showing lamellae in middle of leaf along costa. This large moss is inedible for many species of *Eustigmaeus.* Photo by Eric Schneider, with permission.

Figure 48. *Atrichum altecristatum* leaf cross section showing lamellae along the costa. Photo by John Hribljan, with permission.

Gerson (1987) reported mites from 38 species of bryophytes. Among these, all the active stages of **Eustigmaeus** fed on both leaves and stems of mosses, showing no preference for acrocarpous vs pleurocarpous taxa. However, as in earlier experiments, mites with short mouth parts were unable to feed on mosses with thick cell walls.

Woodring (1963) reared four species of mites through their 50- to 70-day life cycle on a diet exclusively of mosses. Josephine Milne (Bryonet 18 March 1996) found ca 18 species of mites, among other invertebrates, to be abundant on her cultures of the moss *Dicranoloma* (Figure 50) from a cool temperate rainforest in Australia. The mites fed especially on new leaves at the tips of the plants, frequently chewing out the young buds.
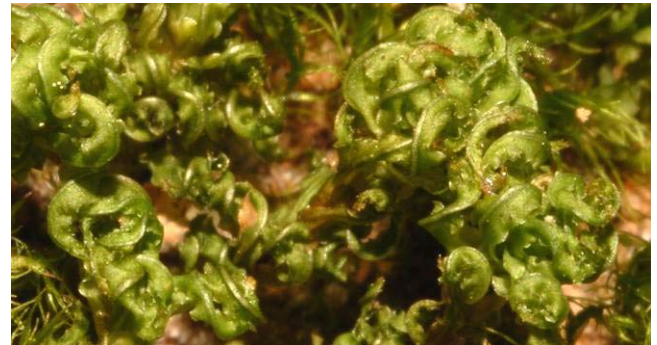

Figure 49. *Atrichum altecristatum*. Dehydrated mosses showing the contortion of the leaves. Photo by Eric Schneider, with permission.

Figure 50. *Dicranoloma billardierei*, potential home for many mite species. Photo by Michael Lüth, with permission.

Penthaleus species (Figure 51) are large, brightly colored mites that feed on plants and are frequent plant pests (Umina 2004). Russell (1979) discovered that at least some of them also eat bryophytes. By keeping one species in the lab, he was able to observe both adults and juveniles feeding on the moss *Orthotrichum* (Figure 91)from Oregon, USA. They subsisted on this food source for up to two weeks.

The Penthaleidae (Earth Mites; Figure 51) have needle-like mouthparts that permit them to puncture leaf cells or fungal hyphae and suck out the contents. These mites spend their early stages in the soil where they feed on fungi, algae, and bryophytes. In contrast, the older stages clamber onto the low-growing vascular plants where they feed on the leaves. The red-legged earth mites look black because of dense concentrations of chlorophyll from their food.   The red legs gain their color from carotenoids deposited in the cuticle – a possible adaptation to protect them from UV-light.

Early stages of the Earth mites, Penthaleidae (Figure 51-Figure 52), feed in the soil on fungi, algae, and bryophytes, whereas the older stages move to low-growing tracheophytes where they feed on the leaves (David Walter, pers. comm.).   They use their needle-like mouthparts to puncture leaf cells (or hyphae of fungi when they are in the

soil) and drain the cell contents. The red-legged earth mite is a well-known pest that looks nearly black due to dense accumulations of chlorophyll. Their legs are red, presumably protecting them from UV radiation.

(Figure 54-Figure 55), but the researchers were not so fortunate as to watch any banquet on these. Too bad for the springtails – they also form part of the diet of the mites! (Figure 56).

Figure 51. **Penthaleus major**. Note the drop of liquid where the anus is. This anal position adapts the mite to its upside-down feeding position. Photo by Scott Justis, with permission.

Figure 53. **Bryum argenteum** protonemata with **Scutovertex** sp. feeding on it. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

Figure 52. This mite from an epiphytic leafy liverwort is most likely a member of the **Penthaleidae**. Its green color reveals a recent diet of chlorophyll, possibly the liverwort, or algae/Cyanobacteria growing on it. The brown mite just above it is a nymphal oribatid mite (**Achipteridae**?). Photo by Jessica Nelson and Duncan Hauser, permission status unknown.

When we know so little about organisms that eat bryophytes, it is a rare treat to find a report where the observers were able to watch the bryophyte herbivore closely. But Cronberg and coworkers (2008) did just that – they observed mites feeding on the protonemata of mosses (Figure 53). Whereas it appeared that the springtails lacked the apparatus necessary for protonemal dinners, the mites used their jaws to cut the protonemata into two pieces. They then consistently fed on only the distal (tip) piece. These mites also carried gemmae of **Bryum argenteum**

Figure 54. **Bryum argenteum**, showing the compact nature of this bryophyte. Mites can carry gemmae of this species. Photo by George Shepherd, through Creative Commons.

Figure 55. **Bryum argenteum** with gemmae; these gemmae can be dispersed by mites. Photo by Rui-Liang Zhu, with permission.

Most of the experiments and observations on mites that feed on bryophytes involve mosses, not liverworts. It would be an interesting experiment to give them choices of a range of mosses **and** liverworts to see if both are eaten. Liverworts are known to house a number of secondary compounds that serve as antiherbivore compounds, but then, many (perhaps most) mosses contain phenolic compounds that discourage herbivory as well (Mues 2000).

Other reports of bryophyte-feeding mites include those in laboratory enclosures where mosses were provided for cover and sources of moisture. Wallwork (1958) reported that adult *Achipteria coleoptrata* (Figure 57) ate living young stem tissue of mosses and survived on that diet for more than a month. It appears that bacteria in the gut are necessary to digest at least some cell types in tracheophytes, particularly those with lots of lignin (Haq & Konikkara 1989). It would be interesting to see if a gut flora is equally important in digesting non-lignified bryophytes.

Figure 56. Mite eating a springtail in the mountains of West Virginia, USA. Both can be found among mosses. Photo by Roy A. Norton, permission unknown.

The oribatid mites, known as moss mites, live among bryophytes, but rarely eat them (David walter, pers. comm.). Rather, the bryophytes provide a habitat where the mites can feed on fungi that live among the bryophytes, and at the same time they enjoy the protection of the bryophytes against large predators, UV light, and desiccation.
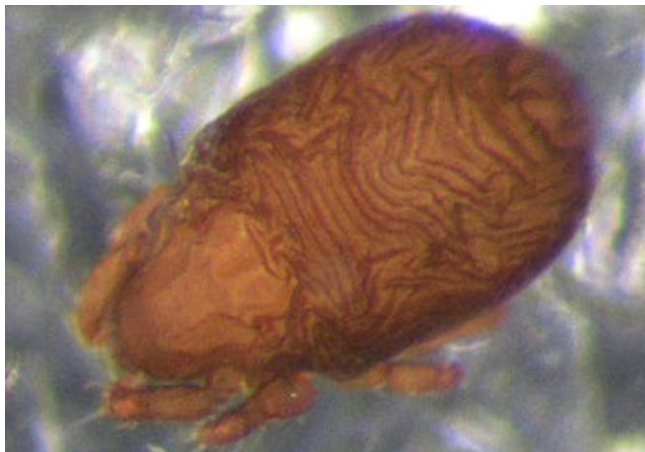

Figure 57. *Achipteria coleoptrata*, a mite that eats young moss stem tissue. Photo by the CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Community Food Sources

Bryophytes seem more likely to provide food for the mites indirectly by housing suitable food organisms, as can be seen for a number of moss-dwellers listed in Table 1. Smrž (2010) reported that *Achipteria coleoptrata* (Figure 57) ate fungi and other food types within the moss mats on soil and on trees, as did *Hermannia gibba* (Figure 58). Other mites likewise used the moss habitat on tree trunks as a food source, with *Oribatula tibialis* (Figure 14) feeding on fungi, *Phthiracarus* sp. (Figure 60-Figure 61) feeding on litter, and others [*Achipteria coleoptrata*, *Chamobates cuspidatus* (see Figure 62-Figure 63), *Chamobates subglobus*, *Liacarus coracinus* (Figure 64), *Tectocepheus velatus* (Figure 105) finding a variety of suitable foods there. *Melanozetes mollicomus* fed on the epiphytic mosses themselves. Among mosses on tree roots, *Melanozetes mollicomus* again fed on mosses, *Phthiracarus* on plant litter, *Achipteria coleoptrata* and *Damaeus auritus* (Figure 25) on fungi, and the remaining species used a variety of foods [*Hermannia gibba* (see Figure 58), *Hermanniella granulata*, *Hafenrefferia gilvipes* (see Figure 65), *Hypochthonius rufulus* (Figure 66-Figure 69), *Tectocepheus velatus* (Figure 105)].
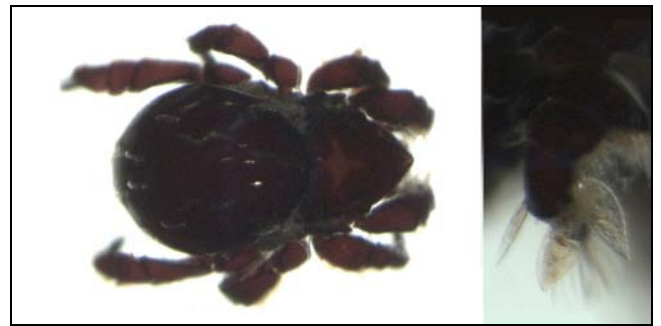

Figure 58. *Hermannia phyllophora*, a fungal mite that finds its fungal food within moss mats. Image on right shows leg scales. Photo by S. E. Thorpe, through Creative Commons.

Figure 59. *Hermanniella* sp., a mite that lives among mosses on tree roots. Photos by Walter Pfliegler, with permission.

Table 1. Oribatid mites found on mosses of mixed wood plains in Canada and their food habits. From Smith *et al*. 2011.

Family	Habitat	Food	Family	Habitat	Food
Cosmochthoniidae	moss, lichen, litter	algivorous	Licnodamaeidae	moss, litter	unknown
Arborichthoniidae	moss, litter	unknown	Damaeidae	moss, litter	fungivorous
Brachychthoniidae	moss, soil, litter, lichens	fungivorous, algivorous	Cepheidae	moss, litter	saprophagous
			Eremaeidae	litter, moss, lichen	fungivorous
Epilohmanniidae	litter, moss	unknown	Megeremaeidae	litter, moss	fungivorous
Nothridae	moss, litter	saprophagous	Zetorchestidae	moss	fungivorous
Camisiidae	semiaquatic, moss, litter, canopy,	saprophagous	Tenuialidae	moss	unknown
Trhypochthoniidae	semiaquatic, moss, litter, aquatic	fungivorous, algivorous	Liacaridae	moss, litter	saprophagous
			Astegistidae	moss, litter	fungivorous
Malaconothridae	semiaquatic, moss, litter	fungivorous, algivorous	Pelppiidae	moss, litter	fungivorous
			Gustavioidea	moss, litter	unknown
Nanhermanniidae	moss	fungivorous	Kodiakellidae	moss, litter	unknown
Hermanniidae	moss	fungivorous	Thyrisomidae	soil, litter, moss	fungivorous
Hermanniellidae	moss, litter	fungivorous, saprophagous	Chamobatidae	semiaquatic, moss	saprophagous
			Mycobatidae	moss, litter	fungivorous, saprophagous
			Oribatellidae	litter, moss	saprophagous
Plasmobatidae	moss, litter	unknown	Achipteriidae	litter, moss	saprophagous
Liodidae	moss, canopy	saprophagous	Tegoribatidae	litter, moss	saprophagous
Plateremaeidae	moss, dry litter	unknown	Galumnatidae	litter, moss	saprophagous, predaceous

Figure 60. *Phthiracarus* sp.; members of this genus live among mosses on tree trunks and eat litter. Photo by Walter Pfliegler, with permission.

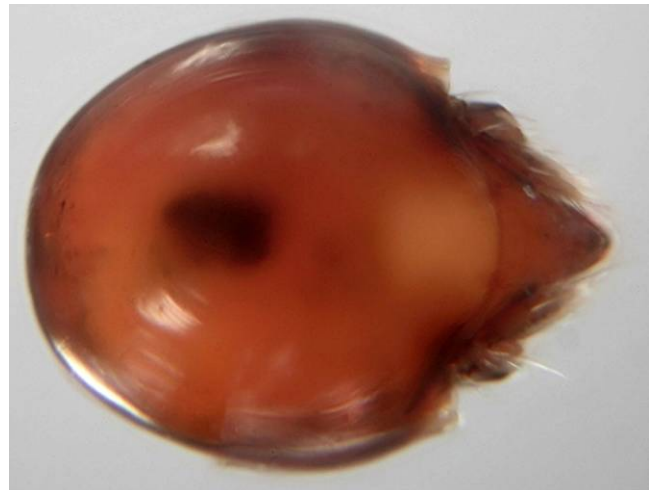Figure 62. *Chamobates* sp., a mite that feeds on fungi among mosses on tree trunks. Photo by Walter Pfliegler, with permission.

Figure 61. *Phthiracarus* sp. This mite looks like a tiny seed and members of the genus live among mosses on tree trunks. Photo by Walter Pfliegler, with permission.
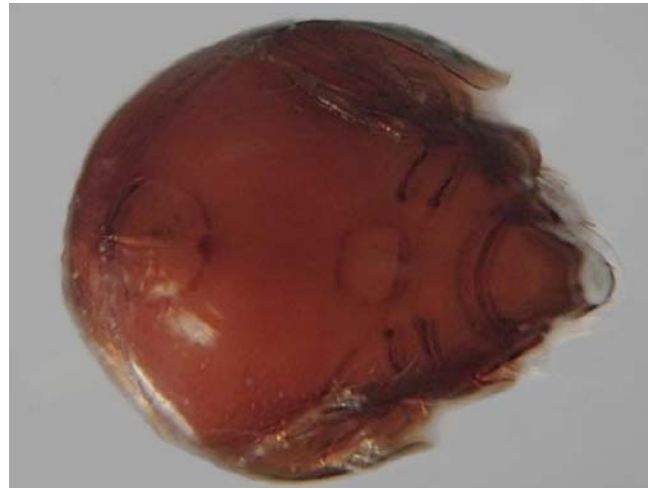

Figure 63. Ventral surface of *Chamobates* sp., a fungal mite from mosses. Photo by Walter Pfliegler, with permission.

Figure 64. **Liacaridae** on moss, a family that can be found among mosses on tree trunks. Photos by Walter Pfliegler, with permission.

Figure 65. *Hafenrefferia* sp., mite that lives among mosses on tree roots and eats a variety of foods. Photo by Walter Pfliegler, with permission.

Figure 66. *Hypochthonius rufulus* from Virginia Beach, USA, a mite that lives among mosses on tree roots. Photo by Scott Justis, with permission.

Figure 67. *Hypochthonius rufulus*, a mite that lives among mosses on tree roots. Photo by Walter Pfliegler, with permission.

Figure 68. SEM of *Hypochthonoius rufulus* from a lateral view. Photo by David E. Walter, with permission.
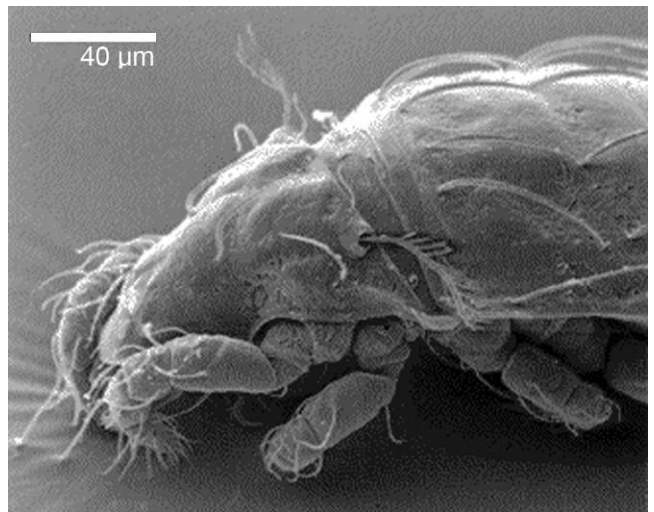
Figure 69. SEM image showing details of head region of *Hypochthonius* sp., a moss-dweller on tree roots   Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Some bryophytes may even provide a food source underground. The primitive leafy liverwort *Haplomitrium* (Figure 70) extends its stem below ground, where it is inhabited by endophytic fungi (Carafa *et al.* 2003). Whether these are available as food for mites remains a question, but many bryophytes have fungal associates that could provide food sources.

Figure 70. *Haplomitrium gibbsiae*, a leafy liverwort that has underground endophytic fungi – an unevaluated potential food source for mites. Photo by Jan-Peter Frahm, with permission.

Wolf and Rockett (1984) experimented with the diet of *Rhysotritia* (Figure 71). They found that those mites taken from their natural habitat contained significantly fewer bacteria in their guts than those maintained in the lab in a soil-moss habitat. This suggests that bryophytes can provide significant bacterial food sources to the mite inhabitants.

Figure 71. *Rhysotritia* sp. from Norfolk, VA, USA; this mite can subsist on bacteria among mosses. Photo by Scott Justis, with permission.

At least some aquatic mites use mosses for food. Gerson (1982) reported that some use the moss *Cratoneuron filicinum* (Figure 72) for food.

Spider mites at Kadoorie Farm & Botanic Garden in Hong Kong also use bryophytes as food. The mites, reported as *Tetranychus* sp. (Figure 74) [but not spider mites, and probably *Halotydeus* (Figure 73-Figure 74) according to David Walter, pers. comm. 6 June 2011], actually eat the gemmae of the epiphytic moss *Octoblepharum albidum* (Figure 75), leaving only the basal cells where the gemmae attach to the leaf margins (Zhang *et al.* 2002, 2003). *Halotydeus signiensis* in the South Orkney Islands and *H. bakerae* in Australia are described from mosses (Walter 2006; David Walter, pers. comm. 7 June 2011). Their food relationships are not described.

Figure 72. *Cratoneuron filicinum*, a moss that serves as food for some mites. Photo by Michael Lüth, with permission.

Determining the diet of such small animal by gut analysis has long been a challenge. However, modern technieques using DNA matching may permit the identification of food eaten by mites collected from the field (see Remén *et al.* 2010), at least to the phylum level, and eventually to much lower levels as our bank of DNA fingerprints increases.

Figure 73. *Halotydeus* sp., member of a genus with moss-dwelling members. Photo by Walter Pfliegler, with permission.

Importance of Bryophytes for Food

David Walter (pers. comm. 6 June 2011) suggests that mosses may be most important as food for earth mites [species of *Halotydeus* (Figure 73-Figure 74, Figure 76, Figure 81), *Penthaleus* (Figure 51)] in early spring before tracheophytes emerge from the ground or produce their leaves. Bryophytes are often the only green plants around, aside from tough conifers, when the snow melts and mites become active. He suggests that bryophytes might also be more important for the early instars – those 6-legged ones like I saw late at night when I was trying to identify the moss. This seems like a fertile topic for experimentation, looking for changes in diet between early and late life cycle stages. It would be interesting to see if older instars or adults might have a wider array of mosses in their diets, or abandon them altogether for tracheophytes.

Figure 74. **Halotydeus** sp. on leaves of the moss **Octoblepharum albidum**. Note its resemblance to **Penthaleus** (Figure 51), but its absence of a dorsal anus. The arrow indicates the location of gemmae. Photo by Li Zhang from Zhang *et al.* 2002, with permission.

Figure 75. Gemmae of **Octoblepharum albidum**. These can be dispersed by bryophytes. Photo by Li Zhang from Zhang *et al.* 2002, with permission.

Ridsdill-Smith and Pavri (2000) demonstrated that the diet of the mite **Halotydeus destructor** (known to feed on mosses; Figure 76) does not depend on a specific plant species. Rather, a diversified diet can provide nutrients for these mites as the seasons and weather change. Its ability to use plants with different nutrient suitability not only permits it to live through the changing seasons, but permits it to take advantage of the differing microclimates from soil to plant leaves. This feeding strategy contributes to its being very abundant, and unfortunately, enables it to be an agricultural pest.

Bryophytes may serve indirectly in providing food in at least some cases. For the mite **Ameronothrus** sp. (Figure 77), algae growing in association with the moss **Schistidium maritimum** (Figure 78) in a coastal splash zone at Yachats, Oregon, USA, provided a food source (Merrifield 1994). These mites emerged from perichaetia, mature capsules, and spent capsules, as well as from samples extracted with a Baermann funnel. A student of Stefan Schneckenburger (Bryonet 7 July 2015) likewise found eggs and adults of small mites in the capsules of **Schistidium** and other **lithophytic** (rock-dwelling) mosses. These capsules had no spores and the opercula were secured.

Figure 76. **Halotydeus destructor**, a mite that eats a diversified diet that includes mosses. Photo © Victorian Government of Australia, permission for educational use only.

Figure 77. **Ameronothrus lineatus**. Some members of this genus eat algae associated with the moss **Schistidium maritimum**. Photo by Steve J. Coulson, with permission.

Figure 78. **Schistidium maritimum** with sporophyte. Algae on this moss provide food for some species of mites. Photo by Des Callaghan, with permission.

Lawrey (1987) suggests that mosses are not that different from tracheophytes in their nutritional value. The sugars seem to be the same, although *Sphagnum* has some that are different (Maass & Craigie 1964), and there are lots of mosses that have not been analyzed. Caloric content likewise is similar to that of tracheophytes. Lipids seem to be highest in the spores (Lawrey 1987), perhaps accounting for reports of mites in capsules (Merrifield 1994). The essential elements may be lower in bryophytes – not surprising because of the low nutrient conditions in which many mosses live, with N being quite variable and K and Mg somewhat lower than in tracheophytes (Prins 1981). But mosses seem to have lower concentrations of those soluble carbohydrates and hemicelluloses that are easily digested, exhibiting instead higher concentrations of structural components such as cellulose and polyphenolic lignin-like compounds – compounds that are harder to digest. Tracheophytes, by contrast, have lots of leaf parenchyma cells that lack lignin. While bryophytes all lack lignin, their polyphenolic compounds with lignin-like structure and properties, often serve as chemical deterrents to herbivory. The highly structured *Polytrichastrum* (=*Polytrichum*) *ohioense* has less "desirable" structural compounds than those found in the lichen *Cladonia cristatella* (Figure 112), *Pinus resinosa* (red pine), or angiosperm tree leaves (Table 2), but I must question if the highly evolved structure of this moss with known cuticle and conducting cells is really a reliable representative of the mosses. This chemical structure could explain why mites in the study by Gerson (1972, 1987) did not survive when provided with only *Polytrichum* as food.

Presence of mites among bryophytes may be more a function of the substrate than of the food source. As Lawrey (1987) concluded, the habitat may be more important than the nutrition. But given a choice among otherwise suitable habitats, it appears that nutrition does play a role (Young & Block (1980). In an experimental study on the Antarctic mite *Alaskozetes antarcticus* (Figure 79), the mites maintained on lichens had the highest respiration rate and metabolism compared to those on the green alga *Prasiola crispa* or on **guano** (bird droppings). The mites also selected the lichens as food among these three choices.

Figure 79. *Alaskozetes antarcticus*, a common Antarctic moss-dweller. Photo by Richard E. Lee, Jr., permission pending.

Krantz and Lindquist (1979) consider the **Penthalodidae** and **Eupodidae** to survive in moss substrates, whereas other species are fungivores. Later, McDonald *et al*. (1995) stated that the early life stages of *Penthaleus* (Figure 51) species were "likely to feed on lower plants and microflora found on the soil surface."

The observations of mites feeding on associated algae and fungi were followed by studies on the suitability and use of microflora as food for moss-feeding mites. Maclennan *et al*. (1998) compared the success of development for the plant pest *Halotydeus destructor* (**red-legged earth mite**; Figure 81) when reared on sand, bare soil, microflora from two locations, wheat, vetch, and combinations of microflora with wheat or vetch. This species is a pest in Australia, New Zealand, and southern Africa (Ridsdill-Smith 1997; Umina 2004). Maclennan *et al*. (1998) found that the microflora (including mosses, algae, and detrital matter) was an important supplement to the plant diet (Figure 80). When overgrazing caused the tracheophyte canopy to decline (Grimm *et al*. 1995), the loss of cover caused the microflora to decline. Maclennan *et al*. suggest that the mite densities dropped in response to the declining microflora.

As mentioned by David E. Walter (pers. comm. 6 June 2011), feeding by the immature stages on the microflora avoided competition with the adults. But when tracheophyte food is unavailable, *Halotydeus destructor* (Figure 76) is able to feed for 26 days (duration of the experiment and well into adulthood) on microflora alone in some sites (Bundoora) (Maclennan *et al*. 1998). And even the tracheophyte wheat was not sufficient to sustain them when eaten without microflora as a supplement (Figure 80).

The additional advantage of the mosses and microflora is their ability to provide a suitable microhabitat at times when the tracheophytes are inhospitable. In this study, the microflora crust at Dookie was dominated by the alga *Vaucheria*, but the moss *Bryum dichotomum* (Figure 82) and liverwort *Riccia crystallina* (Figure 83) were also present. At Bundoora, *Tortula truncata* (Figure 84; formerly *Pottia truncata*), *Fissidens vittatus*, *Ceratodon purpureus* (Figure 85-Figure 86), *Barbula unguiculata* (Figure 87), *Zygodon hookeri*, and *Bryum* sp. (see Figure 82) were present, as well as Cyanobacteria.

Table 2. Comparison of structural components of a bryophyte (*Polytrichum ohioense*) with two trees and a lichen (*Cladonia cristatella*). Values represent percent of oven-dry weight; n=5. From Lawrey 1977.

Pinus resinosa leaves	35.41	13.44	19.37	23.56
Angiosperm tree leaves	43.89	11.59	20.43	11.04
Polytrichastrum ohioense leafy plant	16.51	14.07	24.37*	12.90
Cladonia cristatella thalli	19.93	66.54[+]	2.98[+]	0.78[+]

*Mosses don't have a true lignin.
[+]Lichens have chitin and lichenin as cell wall components and do not have true hemicellulose, cellulose, or lignin.
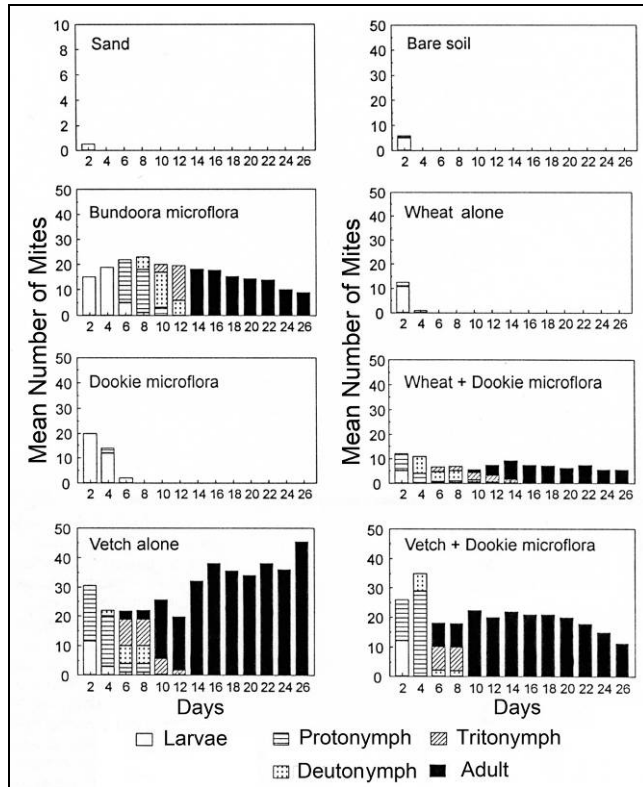
Figure 80. Mean density estimates and development of the red-legged mite *Halotydeus destructor* on sand and soil substrates compared to plants along and with microflora at two sites. Redrawn from Maclennan *et al.* 1998.

Figure 81. *Halotydeus destructor*, the tiny black mite with red legs, includes mosses in its diet. The larger, red mite is *Anystis* (Prostigmata), a predator of *Halotydeus* species! Photo from <agspsrv34.agric.wa.gov.au>, for educational use only.

Figure 82. *Bryum dichotomum*, a moss that is a likely mite habitat. Photo by Barry Stewart, with permission.

Figure 83. *Riccia crystallina*, a thallose liverwort that provides cover for mites. Photo by Des Callaghan, with permission.

It appears that the microflora, including mosses, is important for the early life stages. Maclennan *et al.* (1998) found that the larvae and protonymphs spent almost no time on the wheat or vetch, but rather developed in the moss layer (Figure 80). Even adults would retreat there under unfavorable microclimate conditions on their tracheophyte food plants.

Figure 84. *Tortula truncata* (formerly *Pottia truncata*), a tiny moss that houses mites. Photo by Michael Lüth, with permission.

Figure 85. *Ceratodon purpureus* in its hydrated condition, making it desirable to keep mites hydrated. Photo by Andrew Spink <http://www.andrewspink.nl/mosses/>, with permission.

Figure 86. *Ceratodon purpureus*, a widespread species that hosts mites. Photo by Christian Hummert, through Creative Commons.

Figure 87. *Barbula unguiculata*, a common open habitat species that provides moist cover for mites. Photo by Michael Lüth, with permission.

In prairie, desert, and other dry habitats where cryptogamic crusts develop, the bryophytes may be particularly important to serve as sources of food for the mites. They are almost a necessity because the bryophytes provide the only locations with sufficient moisture for most species. The co-habitants of fungi, algae, and some Cyanobacteria provide potential food for some mite inhabitants (Lukešová & Frouz 2007). On the other hand, all oribatid mites tested rejected the Cyanobacterium *Nostoc*.

Reproductive Site

Gerson (1969) brought mites, collected from mosses in Quebec, Canada, into the laboratory and allowed them to breed and lay eggs. Among the available mosses, they laid eggs on *Brachythecium* (Figure 88), *Hypnum* (Figure 89), *Didymodon* (Figure 90), and *Ceratodon purpureus* (Figure 85-Figure 86).

One tiny mite even lays its eggs in the tiny capsules of *Orthotrichum pusillum* (Keeley 1913; Figure 91). The eggs are sticky, so the spores adhere, giving the appearance of an oval mass of tiny beads of spores. The eggs are so glutinous that even boiling fails to dislodge the adhering spores. But is this a common occurrence, or just a lucky

one-time find? And what is the fate of the spores when the young mites hatch? Do the mite children eat the spores, or do the mites become unwitting dispersal agents?

Figure 88. *Brachythecium rutabulum*, a substrate that has been used by mites in the laboratory as an egg-laying site. Photo by Janice Glime.

Figure 89. *Hypnum pratense*, a potential egg-laying site for mites. Photo by Michael Lüth, with permission.

Figure 90. *Didymodon fallax* (formerly in *Barbula*), a moss where mites are known to lay eggs. Photo by Michael Lüth, with permission.
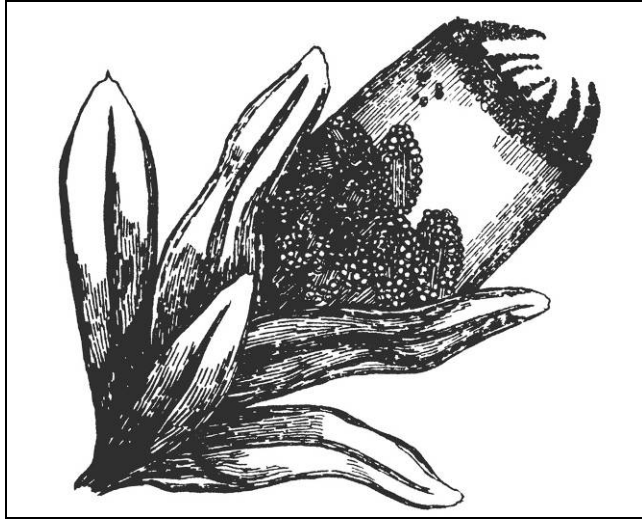
Figure 91. This capsule of **Orthotrichum pusillum** houses the eggs of a tiny mite. Spores of the moss adhere to the eggs, forming clusters. Drawing modified from Keeley 1913.

Figure 92. **Orthotrichum pusillum**, a moss known to house mite eggs in its capsules. Photo by Robert Klips, with permission.

Eustigmaeus (formerly **Ledermuelleria**; Figure 33) lays eggs on a variety of mosses, but it also seems to avoid some, and there is evidence that eggs or young will not survive on some species (Table 3; Gerson 1987). These mites have a life cycle of 30 days with isolated females producing only male offspring (Gerson 1972). The female lays about 21 eggs, and reproduction seems unrelated to day length.

Johnstoniana exima (formerly *J. tuberculata*) is one of the mites with a parasitic larval stage. This small species lives in moist areas near lakes, where it is completely hidden just below the litter surface (Wohltmann *et al*. 1994). This litter could include mosses, but specific documentation seems to be lacking. The female lays her eggs in autumn and both sexes die shortly afterwards. The eggs overwinter, with larvae emerging in May and June. This emergence synchronizes perfectly with that of the host for the larvae, the cranefly **Limonia** sp. (see Figure 93). This synchronization suggests that the same factors control the development and hatching in both the mite and the adult cranefly. Since **Limonia** often lives among bryophytes [*e.g.* **L. sexocellata**, **L. capicola** in South Africa (Harrison & Barnard 1972); species in Colorado (Ward & Dufford 1979)], it is likely that the bryophyte habitat may play an important role when the mite attempts to locate a host.

But this overwintering pattern is not true for all **Johnstoniana** species. **Johnstoniana parva** requires a humid habitat, which they are able to find in the litter, and presumably mosses (Wendt *et al*. 1994). It has two egg-laying periods. After insemination in the autumn, overwintering eggs enter diapause in the bedrock. Other females are inseminated in the fall, then these adults hibernate for the winter and lay their eggs in late spring.

At least some of the aquatic mites use pheromones to find their mates (Smith & Hagman 2002). **Arrenurus manubriator** males respond to water in which females of the species have been kept previously. When put into water with these pheromones, the male assumes a readiness posture in readiness for coupling.

Figure 93. **Limonia nubeculosa**, member of a genus of common moss-dwelling craneflies (Diptera) and hosts to mite larvae. Photo by James K. Lindsey, with permission.

Table 3. Survival and oviposition of *Eustigmaeus frigida* on various moss species. + = presence of *E. frigida* on that species in the field. From Gerson 1987.

Survival and Oviposition	Survival but no Oviposition	No Survival
Amblystegium serpens	*Bryum argenteum*	*Atrichum altecristatum*
Barbula unguiculata	*Bryum pseudotriquetrum*	*Leucobryum glaucum*
Brachythecium salebrosum (+)	*Dicranum scoparium*	*Pogonatum urnigerum*
Brachythecium sp.	*Ditrichum pusillum*	*Polytrichum commune*
Ceratodon purpureus	*Fissidens taxifolius*	*Polytrichum piliferum*
Didymodon tophaceus	*Funaria hygrometrica*	
Drepanocladus aduncus	*Hedwigia ciliata*	
Callicladium haldanianum (+)	*Plagiomnium cuspidatum*	
Calliergonella lindbergii (+)	*Plagiomnium ellipticum*	
Hypnum reptile (+)	*Pleurozium schreberi*	
Leptodictyum riparium (+)	*Pohlia wahlenbergii*	
Thuidium delicatulum (+)	*Racomitrium heterostichum*	
	Rhodobryum roseum	
	Sphagnum magellanicum	
	Sphagnum recurvum	

But mites are not the only things reproducing. West (1984) found mites and Collembola to be particularly important in *Polytrichum* clumps on South Georgia in the sub Antarctic. He found that different species of *Polytrichum* had different species of mites, using it as food, shelter, or both. Cronberg *et al*. (2006) found that the relationship between mosses and mites (*Scutovertex minutus*; Figure 94) or Collembola (*Isotoma caerulea*) can be even more intimate. In their experiments, these arthropods served as sperm vectors for the moss (Figure 95). This breakthrough discovery helps to explain how sperm may reach females 10 cm, even 1 m, away (Milius 2006). Mosses as close as 2-4 cm failed to reproduce unless cultures were in the company of these arthropods. In fact, it appears that the mites and springtails actually move to the fertile males and females more often than to "sterile" (non-fertile) shoots (Figure 96). The springtails seem to be more effective than the mites.

Figure 95. Comparison of sporophytes produced, indicating fertilizations, with male and female moss patches (*Bryum argenteum*) at 3 distances apart. Bars are mean number of sporophytes produced by 7 replicates. Vertical lines represent standard errors. Redrawn from Cronberg *et al*. 2006.
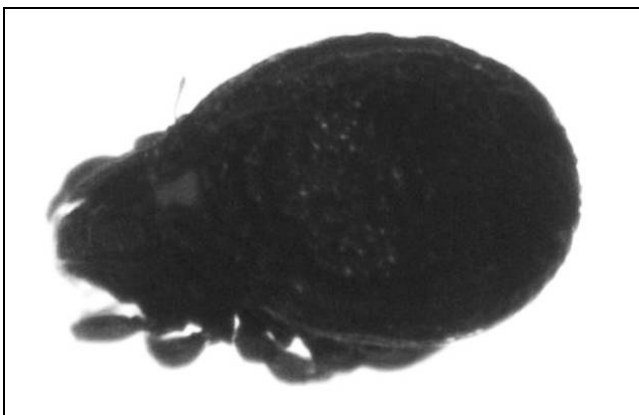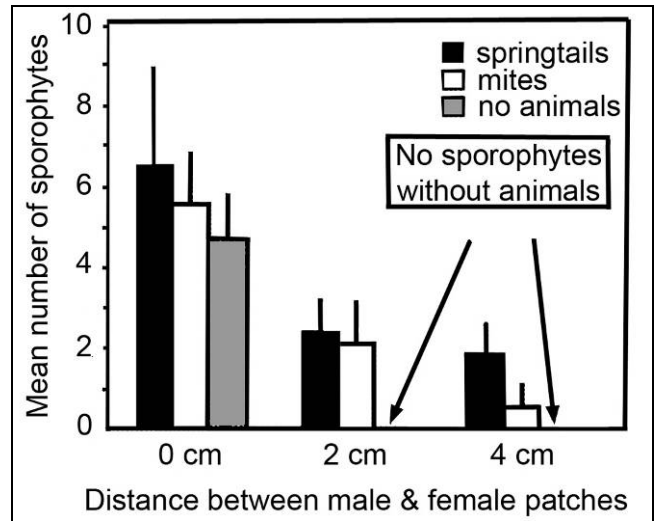

Figure 94. *Scutovertex sculptus*, member of a genus known to disperse the sperm of the moss *Polytrichum*. Photo by S. E. Thorpe, through Creative Commons.

The mite *Eustigmaeus bryonemus* (see Figure 33) in Brazil not only feeds on mosses, but it lays its eggs there as well (Flechtmann 1984). Its bright red eggs are laid mostly on the middle and lower leaves of fresh moss shoots. These are placed on the surface and not glued.

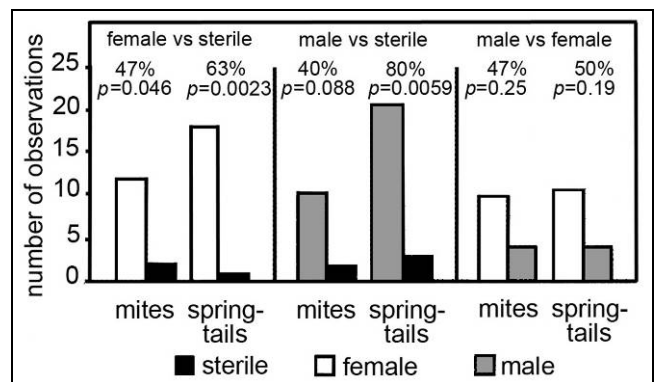Figure 96. Preferences of mites (*Scutovertex minutus* & *S. sculptus*) and springtails (*Isotoma caerulea*) for fertile male, fertile female, and sterile plants of *Bryum argenteum*. Percentages are proportion of 30 replicate moss shoots on which animals were present. Bars represent numbers of animals present on fertile or sterile shoots. Probability is based on G test. Redrawn from Cronberg *et al*. 2006

Tydeus tilbrooki, the smallest arthropod in the Antarctic, lays its eggs among mosses, especially *Polytrichum* species that are encrusted with lichens (Gressitt 1967). It eats fungal hyphae and lichens there. *Rhagidia gerlachei* (see Figure 97) and *Rhombognathus gressitti* (an intertidal species) likewise use mosses for egg-laying sites in the Antarctic, as do *Stereotydeus*, *Protereunetes*, *Oppia* (Figure 98), and *Halozetes*.

Figure 97. *Rhagidia* sp. The tiny mites are most likely larvae of the same species. In the Antarctic, members of this genus lay eggs among mosses. Photo by Andrew Lewington @ <http://www.cavelife.org.uk/>, with permission.
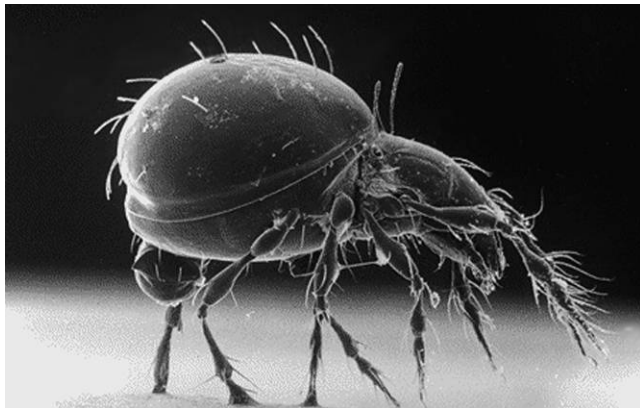

Figure 98. *Oppia* sp. is a member of a genus that lays its eggs in mosses in the Antarctic. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Parasitic Mites

Many of the mites have larval stages that are parasites on other organisms. This group, known as the **Parasitengonina**, belong to the **Prostigmata** (Krantz & Walter 2009). Compared to the oribatids (moss mites), they are large mites, often display a bright reddish coloration (Figure 99), and are characterized by their particular life cycle, beginning with a parasitic larva. Although most of these larvae parasitize other arthropods (primarily flying insects), humans are familiar with the chiggers that parasitize humans and other vertebrates. The life cycle of this mite group is in an interesting one that makes them both parasites and predators. The parasitic larva matures into a **protonymph**, an immobile stage within the larval skin. This is followed by a predatory stage, the **deutonymph**, that feeds on other arthropods. The third and final nymphal stage is the **tritonymph**, once

more an immobile stage within the deutonymphal skin. This emerges from its "skin" prison as an **adult** that once again preys on other arthropods). Only a few Parasitengonina have a life cycle that varies from this pattern by having free-living larvae or additional moults (Wohltmann 2000).

Figure 99. A water scorpion (**Heteroptera: Nepidae**) infected by parasitic mites, larvae of a species of *Hydrachna*. Photo by Walter Pfliegler, with permission.

Andreas Wohltmann (pers. comm. 17 September 2011) considers that "mosses (and lichens) constitute part of the microhabitat of almost all Parasitengonina except a few species (e.g. desert-dwelling species such as *Dinothrombium* spp. and possibly some subterranean watermites) and thus Parasitengonina mites can be sampled in these substrates during mating, oviposition or searching for prey (or suitable hosts in the case of larvae)." Nevertheless, no evidence exists to suggest that any of the Parasitengonina feed on mosses or that any life cycle is dependent on them for mating or oviposition. Based on his field sampling, Wohltmann has concluded that there seems to be a greater correlation between bryophytes and Parasitengonina among the species in semiaquatic habitats than elsewhere.

Stur *et al*. (2005) examined non-biting midges (Chironomidae) in spring habitats in Luxembourg in search of parasitic water mite larvae. There were several species of midges what were not parasitized, and they suggested that general unavailability of the host or life cycle incompatibility could account for the abasnce of parasites. But they also suggested that two species of *Chaetocladius* among the mosses, along with their moss-dwelling life style, might also account for the lack of parasites on the sampled *Chaetocladius*. They suggested that the semiterrestrial moss-dwelling life style of these two *Chaetocladius* species made them less available to these aquatic parasitic mite larvae.

Adaptations of Parasitengonina

One of the major subgroups of **Parasitengonina** is the **Hydrachnidae** (formerly Hydracarina; Figure 100). As its

name suggests, this is a group that lives in a broad range of aquatic habitats, many of which have bryophytic substrates (Andreas Wohltmann, pers. comm. 17 September 2011).

Figure 100. *Hydrachna cruenta* amid *Elodea canadensis* leaves. This large mite is 3 mm in diameter. Photo by Andreas Wohltmann, with permission.

The terrestrial subgroups include the **Erythraiae** and the **Trombidiae**, both of which include a few terrestrial species. Among the **Trombidiae**, the members of the family **Johnstonianidae** are all amphibious. In contrast to the aquatic mites, terrestrial **Parasitengonina** have dense body hairs (**hypertrichy**) that prevent the cuticle from getting wet (Andreas Wohltmann, pers. comm. 17 September 2011). This causes an air bubble to form around the body when it gets wet. Water mites have few hairs and the body makes direct contact with the water. This lowers the **hemolymph osmolality** and reduces osmotic pressure, permitting them to live in fresh water without exploding.

The **Erythraeoidea** have a higher drought resistance than members of the **Trombidioidea** (Wohltmann 1998). This greater resistance results from differences in the body plan much like some of the characteristics that protect bryophytes. These include a reduction of body openings (bryophytes have none in their gametophytes, except in thallose liverworts) and lipids that help to seal others. This combination reduces water loss. But also like most bryophytes, the **Trombidioidea** are able to gain moisture from the atmosphere, although this has not been observed for erythraeoid eggs or protonymphs. In the **Trombidioidea**, this vapor uptake can increase fresh body mass by about 50% prior to the protonymph stage. Wohltmann suggests that this increase in body mass may serve to stretch the cuticle and provide more space for the next developing instar. Hence, it might not have any relationship to drought resistance. In fact, one might speculate that stretching the cuticle could even reduce its resistance to losing water.

Bryophytes or Lichens?

Both bryophytes and lichens are small turfs that provide spaces and protection. Hence we should expect many species to live among both. But it appears that we do not really know very much about why they choose one or the other, or both.

Some species occur predominantly on lichens, and others on bryophytes. *Halozetes crozetensis* is predominately among mosses, but occurs in lichens as well, with the choice apparently depending on the location and its climatic factors (Seyd & Seaward 1984). Some seem to be facultative moss dwellers, using them only when the lichens are unavailable. *Scutovertex minutus* (see Figure 35-Figure 36) and *Zygoribatula frisiae* (see Figure 101) live among mosses when lichens are absent, but are common lichen inhabitants. *Lepidozetes singularis* occurs among mosses in the Black Forest, but lives among lichens elsewhere (Seyd & Seaward 1984).

Figure 101. *Zygoribatula bulanovae*. Some members of this genus prefer lichens but use mosses when no lichens are available. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

General

Carabodes labyrinthicus (Figure 102) is widespread on mosses as well as lichens (Seyd & Seaward 1984). *Ommatocepheus ocellatus* likewise is known from mosses and liverworts as well as lichens, and is known to feed on saturated lichens. *Tricheremaeus serratus* occurs with both lichens and bryophytes. *Adoribatella punctata* occurs in both, as does *Alaskozetes antarcticus*, a detritivore. *Ameronothrus lineatus* (Figure 77) occurs in both, although it seems to be more common among lichens. *Centroribates uropygium* occurs in both. *Chamobates cuspidatus* (see Figure 62-Figure 63) is primarily a moss dweller, but occurs also on lichens. *Leiosoma palmicincta* occurs on both and survived from egg to adult on lichens alone. *Eremaeus oblongus* (see Figure 103) and *Tectocepheus sarekensis* (see Figure 105) occur in a wide range of habitats that include mosses and lichens. In Sierra de Cazorla, *Ghilarovus hispanicus* lives among mosses and lichens on rocks. *Tegoribates bryophilus* in Colorado, USA, and *Metrioppia helvetica* are known from mosses and lichens. *Parachipteria petiti* was taken from the lichen *Parmelia* (Figure 104) as well as from mosses and liverworts. *Micreremus brevipes* seems especially fond of pine forests, where it can be found among litter, but also among corticolous lichens, and mosses.

Figure 102. *Carabodes labyrinthicus*, a mite that lives on both mosses and lichens. Photo by Monica Young, through Creative Commons.

Figure 103. *Eremaeus* female, a genus that can be found on both lichens and mosses. Photo by Walter Pfliegler, with permission.

Figure 104. *Parmelia saxatilis* growing over a moss and often sharing mite fauna. Photo by Rick Demmer, USDA Forest Service, through public domain.

As food sources, it appears that there are at least preferences between bryophytes and lichens. That is not surprising because the lichen provides primarily fungal food that is relatively easy to eat once the outer covering of the lichen has been penetrated. But in bryophytes, the thick cellulose walls provide a somewhat different challenge for the tiny mites. Some overcome this with a stylet type of apparatus that is able to penetrate the bryophyte cells. Nevertheless, some mites are associated with both mosses and lichens (Travé 1963, 1969), but their food preferences

may still be similar, relying more on the associated organisms than on the bryophyte itself.

Figure 105. *Tectocepheus velatus*, a member of a genus that lives on both mosses and lichens. Photo by Monica Young, through Creative Commons.

Cool Sites

In the cold climate of Spitsbergen, numerous mites occupy lichens, but some at least are also found on mosses (Seyd & Seaward 1984). These include *Calyptozetes sarekensis*, but this species is more abundant among lichens. *Camisia invenusta*, a mite of mountain summits and other cool areas, inhabits both, but is more common among lichens and mosses on rocks than in the canopy. *Carabodes willmanni* (see Figure 102), on the other hand, prefers mosses. *Hydrozetes capensis* (see Figure 106) was found in dripping mosses and lichens in a canal.

Figure 106. SEM of *Hydrozetes*, a lichen and moss-dwelling genus common in peatlands. Photos by Valerie Behan-Pelletier and Barb Eamer, with permission.

The Arctic *Diapterobates notatus* (Figure 107-Figure 109) can occur in large numbers in moss and lichen litter. *Halozetes belgicae*, an Antarctic species, lives among both lichens and mosses. *Hermannia reticulata* (Figure 110) occurs on both in areas with cool climates. *Lamellovertex caelatus* occurs among mosses in the Swiss Alps. *Sphaerozetes arcticus* dwells among mosses and lichens in northern Canada and Alaska.

Figure 107. Dorsal view of **Diapterobates** sp., member of a genus that inhabits Arctic moss litter. Photo by Walter Pfliegler, with permission.

Figure 108. **Diapterobates** sp., ventral view. Photo by Walter Pfliegler, with permission.

Figure 109. **Diapterobates notatus**, inhabitant of Arctic moss litter. Photo by Steve Coulson using multifocus stacking, with permission.

Sphagnum

Camisia segnis likewise occurs in cooler areas and inhabits both lichens and mosses, including **Sphagnum** (Seyd & Seaward 1984). It is known to eat lichens, but I don't know if it eats mosses. **Carabodes areolatus** and **C. marginatus** live among both lichens and mosses, including **Sphagnum**. **Carabodes minusculus** seems to prefer

lichens, but nonetheless, it does occupy mosses, including **Sphagnum**. Immature **Mycobates parmeliae**, as its name implies, lives most commonly among lichens such as **Parmelia** (Figure 104), but as adults it is most frequently in mosses and liverworts (Travé 1963), including **Sphagnum**. This suggests a change in resource needs, but we don't know which one(s). **Trhypochthonius cladonicola**, named for the lichen genus **Cladonia**, also occurs among mosses, including **Sphagnum**.

Figure 110. **Hermannia reticulata**, a moss and lichen inhabitant in cool climates. Photo from Bold Systems, Biodiversity Institute of Ontario, through Creative Commons.

Arboreal

Many of the mites that occur in arboreal habitats also occur on rocks and some can be found in association with both bryophytes and lichens. **Phauloppia coineaui** occurs among both mosses and lichens on rocks and in trees, but they seem to prefer lichens (Seyd & Seaward 1984). **Pseudachipteria magnus** is predominately a moss dweller, but it also can occur in saxicolous and arboreal lichens. **Liodes theleproctus** lives among lichens, mosses, and liverworts on rocks and in trees in the Pyrénées. **Strenzkea depilata** occurs among lichens, mosses, and liverworts on rocks and trees. Others seem to be predominately arboreal. **Humerobates rostrolamellatus** is arboreal and feeds on fungi and lichens, but it also occurs among mosses. **Lucoppia nemoralis** prefers to live among mosses and lichens on trees, including the trunk. The arboreal **Phauloppia lucorum** can be extremely abundant in lichens, but is known from mosses; it feeds on lichens. **Cymbaeremaeus cymba** lives predominately among arboreal lichens and mosses. **Licneremaeus discoidalis** lives among arboricolous mosses and lichens in Guatemala. **Phereliodes wehnckei** occurs among arboreal mosses and lichens in Guatemala. **Poroliodes farinosus** occurs among lichens, especially **Parmelia** (Figure 104), but also among arboreal mosses and liverworts.

Coastal

Hermannia scabra (see Figure 58) lives among mosses and lichens in coastal as well as inland sites (Seyd & Seaward 1984). **Oribatella calcarata** is common among lichens in the intertidal zone, but are also known from mosses, including **Sphagnum**, in coastal areas. **Oribatula**

venusta (see Figure 111) has been taken from mosses as well as lichens on the sea shore as well as inland.

From this somewhat extensive list, it would appear that lichens and bryophytes may offer a number of common features suitable for mites. Lichens can offer cover, except for the crustose forms, and food, possibly from the fungal component (Seyd & Seaward 1984). The difference in food, with lichens providing fungi, may be a major factor dividing the species. For example, although *Oribatula exsudans* (see Figure 111) was collected from mosses, its fecal pellets contained no mosses – only pollen grains, fungal spores, fungal mycelia, and portions of lichen thallus (Seyd & Seaward 1984).

Figure 111. *Oribatula tibialis,* member of a genus that includes mites that live on both lichens and mosses. Photo by CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Interestingly, for oribatids that occupy both bryophytes and lichens, the lichen is primarily species of *Cladonia* (Figure 112; Seyd & Seaward 1984) and presumably also *Cladina*. This group of lichens has a 3-d structure somewhat like that of a moss, providing a labyrinth of internal spaces that serve as a refuge.

Figure 112. *Cladonia cristatella*, a fruticose lichen that often occurs with mosses and shares many species of mite fauna. Photo by Charles Peirce, USDA Forest Service, through public domain.

Camouflage does not seem to be highly selected. For example, larvae of *Mycobates parmeliae* (see Figure 113) are bright orange and blend with their lichen habitat of *Xanthoria parietina* (Figure 114), but the adults apparently move to bryophytes, where bright orange does not match

the color pattern (Seyd & Seaward 1984). This seeming contradiction may be explained, however, by the better covering ability of the bryophytes.

Figure 113. *Mycobates perates*, member of a genus containing bright orange lichen dwelling larvae (*M. parmeliae*), but that then switch to mosses as adults. Photo by Monica Young, through Creative Commons.

Figure 114. *Xanthoria parietina*, host of the larvae of *Mycobates parmeliae*, a mite that lives among bryophytes as adults. James K. Lindsey, with permission.

Gall Formers?

Galls are unknown on extant thalloid liverworts or hornworts (Aller Hernick *et al*. 2008). But researchers have also reported that some thallose liverworts (*Metzgeriothallus sharona*) from the Middle Devonian had minute galls that might have been created by mites (Aller Hernick *et al*. 2008; Labandeira 2014). These liverworts are only revealed by projecting polarized light on the shale and siltstone surfaces.

Summary

Mites (**Acari** = Acarina) are common bryophyte inhabitants, especially the oribatids, resembling tiny spiders (mostly less than 1 mm) with 8 legs but no separation between the thorax and abdomen. Bryophytes provide a moist environment where movement up and down permits the mites to find the microclimate that best fulfills their needs and avoids damaging UV-B radiation. The bryophytes provide protective conditions suitable for many species to use for egg-laying.

Some mites use sucking mouth parts to extract food from bryophyte cells. Stylet size in *Eustigmaeus*, a common genus among bryophytes, determines which bryophytes are edible. Some eat protonemata and others both eat and disperse gemmae. Some available bryophytes are avoided and on some, there is no survival for mites that do survive on other bryophyte taxa when the bryophytes are the sole source of food. Other mites are fungal eaters that take advantage of the soil-bryophyte interface where conditions are good for fungal growth, and others feed on organisms living among the bryophytes. On the other hand, the mites often serve as food for other inhabitants of the bryophytes. The bryophytes may be most important as a food source in early spring when herbaceous tracheophytes have not yet developed. Some mites live in liverwort lobules, taking advantage of the moisture, protection from predators, and liverwort food source.

During their travels among the bryophytes, mites can disperse sperm (and other propagules), and it seems that the reproductive structures of some bryophytes may actually attract them. Hairs protect the terrestrial members by providing trapped air spaces when they get wet. Aquatic members have few hairs.

Members of the Parasitengonina generally occur in habitats where mosses may provide substrate during their life cycle. These mites have a **parasitic larva**, an immobile **protonymph,** a free-living predatory **deutonymph**, another immobile stage – the **tritonymph**, and finally a free-living predatory **adult**.

Lichens provide some of the same advantages as bryophytes, offering small spaces where the mites can escape UV radiation, desiccation, and predation, but lichens offer different food choices, including the lichens themselves, contributing to a degree of specificity in the choice of bryophyte vs lichen.

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