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.
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.

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.

**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 & Collof 1991; Smith & Cook 1991; Hoffmann & Riveron 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 cardinals* 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 *Biscirius lapidarius* (only a single specimen) and *Bdella oblonga* from mosses at Deseirto de los Leones. The type specimen of *Bdella rio-termensia* 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 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).

**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 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 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 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).

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.

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

Figure 28. *Metabelba* sp., a moss-dwelling fungal eater. Photo by Walter Pfiegler, 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 Pfiegler, 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 Erythraeoida (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 (as Ledermuelleria). 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’Ttoole, 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 35-36), 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.

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.

Figure 35. Scutovertex sculptus, in a genus where some members live among mosses. Photo by S. E. Thorpe 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.

**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 37), *Galumna nervosa* (see Figure 38-Figure 40), *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 37. SEM of *Euphthiracaroid* mite from peatlands. Photo by Valerie Behan-Pelletier and Barb Eamer, with permission.

Figure 38. *Galumnidae*, a mite group that is able to subsist on mosses. Photo by Scott Justis, with permission.

Figure 39. *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 41) 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 40. *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 41. *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 42), *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 43), *Polytrichum commune* (Figure 42), *Polytrichum piliferum* (Figure 44), *Leucobryum glaucum* (Figure 45), or *Atrichum altecristatum* (Figure 46-Figure 48).

*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.
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 49) 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.

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**Pentaleus** species (Figure 50) 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* from Oregon, USA. They subsisted on this food source for up to two weeks.

The Pentaleidae (Earth Mites) 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, Pentaleidae (Figure 50-Figure 51), 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.

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. 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 52-Figure 53), 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 54).

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 55) 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.

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 55. *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 55) ate fungi and other food types within the moss mats on soil and on trees, as did *Hermannia gibba* (Figure 56). Other mites likewise used the moss habitat on tree trunks as a food source, with *Oribatula tibialis* (Figure 14) feeding on fungi, *Pthiracarus* sp. (Figure 57-Figure 58) feeding on litter, and others [*Achipteria coleoptrata*, *Chamobates cuspidatus* (see Figure 59-Figure 60), *Chamobates subglobus*, *Liacarus coracinus* (Figure 61), *Tectocepheus velatus* (Figure 103) 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, *Pthiracarus* 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 56), *Hermanniaella granulata*, *Hafenrefferia gilvipes* (see Figure 62), *Hypochthonius rufalus* (Figure 64-Figure 67), *Tectocepheus velatus* (Figure 103)].

Figure 56. *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.

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

<table>
<thead>
<tr>
<th>Family</th>
<th>Habitat</th>
<th>Food</th>
<th>Family</th>
<th>Habitat</th>
<th>Food</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cosmochthoniidae</td>
<td>moss, lichen, litter</td>
<td>algivorous</td>
<td>Lienodamaeida</td>
<td>moss, litter</td>
<td>unknown</td>
</tr>
<tr>
<td>Arborichthoniidae</td>
<td>moss, litter</td>
<td>unknown</td>
<td>Damaeidae</td>
<td>moss, litter</td>
<td>fungivorous</td>
</tr>
<tr>
<td>Brachychthoniidae</td>
<td>moss, soil, litter,</td>
<td>fungivorous, algivorous</td>
<td>Cepheididae</td>
<td>moss, litter</td>
<td>fungivorous</td>
</tr>
<tr>
<td>Epilohmanniidae</td>
<td>lichen</td>
<td>fungivorous</td>
<td>Erremaeidae</td>
<td>litter, moss, lichen</td>
<td>fungivorous</td>
</tr>
<tr>
<td>Nothridae</td>
<td>moss, litter</td>
<td>saprophagous</td>
<td>Megeremaecidae</td>
<td>litter, moss</td>
<td>fungivorous</td>
</tr>
<tr>
<td>Camisiidae</td>
<td>semi-aquatic, moss,</td>
<td>saprophagous</td>
<td>Zetorchestidae</td>
<td>moss</td>
<td>unknown</td>
</tr>
<tr>
<td>Trihypochthoniidae</td>
<td>litter, canopy</td>
<td>saprophagous</td>
<td>Tenialidae</td>
<td>moss, litter</td>
<td>fungivorous</td>
</tr>
<tr>
<td>Malacnothridae</td>
<td>semi-aquatic, moss,</td>
<td>fungivorous, algivorous</td>
<td>Liacaridae</td>
<td>moss, litter</td>
<td>fungivorous</td>
</tr>
<tr>
<td>Plasmobatidae</td>
<td>litter</td>
<td>fungivorous, saprophagous</td>
<td>Astegistidae</td>
<td>moss, litter</td>
<td>unknown</td>
</tr>
<tr>
<td>Liodidae</td>
<td>moss, canopy</td>
<td>saprophagous</td>
<td>Pelppidae</td>
<td>moss, litter</td>
<td>fungivorous</td>
</tr>
<tr>
<td>Plateremaeida</td>
<td>moss, dry litter</td>
<td>unknown</td>
<td>Gustavioidae</td>
<td>moss, litter</td>
<td>unknown</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Kodiakellidae</td>
<td>moss, litter</td>
<td>fungivorous</td>
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<td>Thyrisomidae</td>
<td>soil, litter, moss</td>
<td>fungivorous</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>Chamobatidae</td>
<td>semi-aquatic, moss</td>
<td>fungivorous, saprophagous</td>
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<td>Mycobatidae</td>
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<td>Oribatellidae</td>
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<td></td>
<td></td>
<td></td>
<td>Achipertiidae</td>
<td>litter, moss</td>
<td>saprophagous</td>
</tr>
<tr>
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<td></td>
<td></td>
<td>Tegoribatidae</td>
<td>litter, moss</td>
<td>saprophagous</td>
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<td></td>
<td></td>
<td>Galumnatidae</td>
<td>litter, moss</td>
<td>saprophagous, predaceous</td>
</tr>
</tbody>
</table>
Figure 57. *Phthiracarus* sp.; members of this genus live among mosses on tree trunks and eat litter. Photo by Walter Pfliegler, with permission.

Figure 58. *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 59. *Chamobates* sp., a mite that feeds on fungi among mosses on tree trunks. Photo by Walter Pfliegler, with permission.

Figure 60. Ventral surface of *Chamobates* sp., a fungal mite from mosses. Photo by Walter Pfliegler, with permission.

Figure 61. *Liacaridae* on moss, a family that can be found among mosses on tree trunks. Photos by Walter Pfliegler, with permission.

Figure 62. *Hafenrefferia* sp., mite that lives among mosses on tree roots and eats a variety of foods. Photo by Walter Pfliegler, with permission.
Some bryophytes may even provide a food source underground. The primitive leafy liverwort *Haplomitrium* (Figure 68) 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 63. *Hermanniella* sp., a moss that lives among mosses on tree roots. Photos by Walter Pfliegler, with permission.

Figure 64. *Hypochthonius rufulus* from Virginia Beach, USA, a mite that lives among mosses on tree roots. Photo by Scott Justis, with permission.

Figure 65. *Hypochthonius rufulus*, a mite that lives among mosses on tree roots. Photo by Walter Pfliegler, with permission.

Figure 66. SEM of *Hypochthonius rufulus* from a lateral view. Photo by David E. Walter, with permission.

Figure 67. 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.

Figure 68. *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 69). 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.

Determining the diet of such small animal by gut analysis has long been a challenge. However, modern techniques 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.

**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 71-Figure 72, Figure 74, Figure 79), *Penthaleus* (Figure 50)] 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.
Chapter 9-1: Arthropods: Mites (Acari)

Figure 73. 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 74) 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.

Figure 74. Halotydeus destructor, a mite that eats a diversified diet that includes mosses. Photo © Victorian Government of Australia, permission for educational use only.

Bryophytes may serve indirectly in providing food in at least some cases. For the mite Ameronothrus sp. (Figure 75), algae growing in association with the moss Schistidium maritimum (Figure 76) 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 75. Ameronothrus lineatus. Some members of this genus eat algae associated with the moss Schistidium maritimum. Photo by Steve J. Coulson, with permission.

Figure 76. 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 110), 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 77), 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.

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.

<table>
<thead>
<tr>
<th></th>
<th>Leaves</th>
<th>Leaves</th>
<th>Leafy Plant</th>
<th>Thalli</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinus resinosa</td>
<td>35.41</td>
<td>13.44</td>
<td>19.37</td>
<td>23.56</td>
</tr>
<tr>
<td>Angiosperm tree</td>
<td>43.89</td>
<td>11.59</td>
<td>20.43</td>
<td>11.04</td>
</tr>
<tr>
<td>Polytrichastrum</td>
<td>16.51</td>
<td>14.07</td>
<td>24.37*</td>
<td>12.90</td>
</tr>
<tr>
<td>Cladonia cristatella</td>
<td>19.93</td>
<td>66.54*</td>
<td>2.98*</td>
<td>0.78*</td>
</tr>
</tbody>
</table>

*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.

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 50) 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 79) 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 78). 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 74) 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 78).

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 80) and liverwort *Riccia crystallina* (Figure 81) were also present. At Bundoora, *Tortula truncata* (Figure 82; formerly *Pottia truncata*), *Fissidens littatus*, *Ceratodon purpureus* (Figure 83-Figure 84), *Barbula unguiculata* (Figure 85), *Zygodon hookeri*, and *Bryum* sp. (see Figure 80) were present, as well as Cyanobacteria.

It appears that the microflora, including mosses, is important for the early life stages. Macleman *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 78). Even adults would retreat there under unfavorable microclimate conditions on their tracheophyte food plants.
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 86), *Hypnum* (Figure 87), *Didymodon* (Figure 88), and *Ceratodon purpureus* (Figure 83-Figure 84). One tiny mite even lays its eggs in the tiny capsules of *Orthotrichum pusillum* (Keeley 1913; Figure 89). 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?
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 91). 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.

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.

<table>
<thead>
<tr>
<th>Survival and Oviposition</th>
<th>Survival but no Oviposition</th>
<th>No Survival</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amblystegium serpens</td>
<td>Bryum argenteum</td>
<td>Atrichum altecristatum</td>
</tr>
<tr>
<td>Barbula unguiculata</td>
<td>Bryum pseudotriquetrum</td>
<td>Leucobryum glaucum</td>
</tr>
<tr>
<td>Brachythecium salebrosum (+)</td>
<td>Dicranum scoparium</td>
<td>Pogonatum urnigerum</td>
</tr>
<tr>
<td>Brachythecium sp.</td>
<td>Dirichium pusillum</td>
<td>Polytrichum commune</td>
</tr>
<tr>
<td>Ceratodon purpureus</td>
<td>Fissidens taxifolius</td>
<td>Polytrichum piliferum</td>
</tr>
<tr>
<td>Didymodon tophaceus</td>
<td>Funaria hygrometrica</td>
<td></td>
</tr>
<tr>
<td>Drepanoclados aduncus</td>
<td>Hedwigia ciliata</td>
<td></td>
</tr>
<tr>
<td>Callicladium haldanianum (+)</td>
<td>Plagiomnium cuspidatum</td>
<td></td>
</tr>
<tr>
<td>Calliergonella lindbergii (+)</td>
<td>Plagiionmnium ellipticum</td>
<td></td>
</tr>
<tr>
<td>Hypnum reptile (+)</td>
<td>Pleurozium schreberi</td>
<td></td>
</tr>
<tr>
<td>Leptodictyum riparium (+)</td>
<td>Pohlia wahlenbergii</td>
<td></td>
</tr>
<tr>
<td>Thuidium delicatulum (+)</td>
<td>Racomitrium heterostichum</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rhodobryum roseum</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sphagnum magellanicum</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sphagnum recurvum</td>
<td></td>
</tr>
</tbody>
</table>
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 92) or Collembola (*Isotoma caerulea*) can be even more intimate. In their experiments, these arthropods served as sperm vectors for the moss (Figure 93). 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 94). The springtails seem to be more effective than the mites.

![Figure 92. *Scutovertex sculptus*, member of a genus known to disperse the sperm of the moss *Polytrichum*. Photo by S. E. Thorpe, through Creative Commons](image)

Figure 92. *Scutovertex sculptus*, member of a genus known to disperse the sperm of the moss *Polytrichum*. Photo by S. E. Thorpe, through Creative Commons

![Figure 93. 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.](image)

Figure 93. 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.

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 94. 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 95) and *Rhombognathus gressitti* (an intertidal species) likewise use mosses for egg-laying sites in the Antarctic, as do *Stereotydeus, Protereunetes, Oppia* (Figure 96), and *Halozetes*.

![Figure 95. *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.](image)

Figure 95. *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 96. *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.](image)

Figure 96. *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 97), 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).

Adaptations of Parasitengonina

One of the major subgroups of Parasitengonina is the Hydrachnidae (formerly Hydracarina; Figure 98). 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).

The terrestrial subgroups include the Erythraeoidea and the Trombidiidae, both of which include a few terrestrial species. Among the Trombidiidae, 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 thalloid 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 99) 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).

**General**

**Carabodes labyrinthicus** (Figure 100) 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 75) occurs in both, although it seems to be more common among lichens. **Centroribapes uropygiun** occurs in both. **Chamobates cuspidatus** (see Figure 59-Figure 60) 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 101) and **Tectocepheus sarekensis** (see Figure 103) 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 102) 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.
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.

The Arctic *Diapterobates notatus* (Figure 105-Figure 107) can occur in large numbers in moss and lichen litter. *Halozetes belgicae*, an Antarctic species, lives among both lichens and mosses. *Lamellovertex caelatus* occurs on both in areas with cool climates. *Sphaerozetes arcticus* dwells among mosses and lichens in northern Canada and Alaska.

**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 100), on the other hand, prefers mosses. *Hydrozetes capensis* (see Figure 104) was found in dripping mosses and lichens in a canal.

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**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 102), 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 cladonica, named for the lichen genus Cladonia, also occurs among mosses, including Sphagnum.

**Coastal**

Hermannia scabra (see Figure 56) lives among mosses and lichens in coastal as well as inland sites (Seyd & Seaward 1984). Oribatella calcarea is common among lichens in the intertidal zone, but are also known from mosses, including Sphagnum, in coastal areas. Oribatula venusta (see Figure 109) 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 109) 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).

**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. Pherelioodes wohnkei occurs among arboreal mosses and lichens in Guatemala. Poroliodes farinosus occurs among lichens, especially Parmelia (Figure 102), but also among arboreal mosses and liverworts.

**Coastal**

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

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Camouflage does not seem to be highly selected. For example, larvae of *Mycobates parmeliae* (see Figure 111) are bright orange and blend with their lichen habitat of *Xanthoria parietina* (Figure 112), 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.

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.

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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**Summary**

Mites (*Acari = Aracina*) 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.

**Literature Cited**


