

CHAPTER 12-7

TERRESTRIAL INSECTS:

HEMIMETABOLA – HEMIPTERA (NON-HETEROPTERA) AND THYSANOPTERA

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Figure 1. *Brachythecium buchananii* with capsules, overwintering home of *Schlechtendalia chinensis*, a gall aphid. Photo by Ivanov, with permission.

SUBORDER AUCHENORRHYNCHA

(Cicadas, Leafhoppers, Treehoppers, Planthoppers, and Spittlebugs)

Holzinger and Schlosser (2013) identified 93 species of **Auchenorrhyncha** fauna in Austrian peat bogs in the Bohemian Forest, indicating how common this group of **Hemiptera** is in bogs. Disturbance increases the number of species and densities in this group, but the number of species and densities of peatland specialists (**tyrphobionts**) decreases with disturbance.

CICADOMORPHA

Cicadellidae – Leaf Hoppers

Megophthalmus scanicus (3-4 mm; Figure 2) is among the few European **Cicadellidae** with a bryophyte association (Edwards 1874). This species overwinters among mosses. *Sorhoanus xanthoneurus* (3.1-3.4 mm; Figure 3), *Sorhoanus assimilis* (often the most frequent hemipteran; 2-2.9 mm; Figure 4), and *Stroggylocephalus livens* (5-6.5 mm; Figure 5) associate with *Sphagnum* (Figure 6) in bogs in Austria and seem to be true **tyrphobionts** (Holzinger & Schlosser 2013). Another

moderately common member of the family associated with *Sphagnum* is *Macustus grisescens* (5-6 mm; Figure 7).



Figure 2. *Megophthalmus scanicus*, a leaf hopper that overwinters among mosses in Europe. Photo by Tristan Bantock, with permission.



Figure 3. *Sorhoanus xanthoneurus*, a tyrphobiont associated with *Sphagnum* in Austria. Photo by Joe Botting, with permission.



Figure 4. *Sorhoanus assimilis* adult, a species commonly associated with *Sphagnum* in Austria. Photo by Gernot Kunz, with permission.



Figure 5. *Stroggylocephalus livens*, a tyrphobiont associated with *Sphagnum* in Austria. Photo by Gernot Kunz in Gallery, with permission.



Figure 6. *Sphagnum* blanket bog where several tyrphobionts in the *Cicadellidae* live. Photo through Creative Commons.



Figure 7. *Macustus grisescens*, a *Sphagnum* associate. Photo by Joe Botting, with permission.

Jassargus dentatus (Figure 8) occurs in association with *Sphagnum* in Slovenia and the Piedmont of Italy (Trivellone 2010). *Jassargus pseudocellaris* (Figure 9) is among the abundant hemipterans in Austrian bogs (Holzinger & Schlosser 2013).



Figure 8. *Jassargus dentatus*, a *Sphagnum* associate in parts of Europe. Photo by Gernot Kunz, with permission.



Figure 9. *Jassargus pseudocellaris*, a bog inhabitant in Austria. Photo by Tristan Bantock, with permission.

Paracephaleus curtus (Figure 10) lives on grass tufts of *Chionochloa rubra* (Figure 11) and mats of short plants, including mosses (Larivière *et al.* 2010).



Figure 10. *Paracephaleus curtus*, a species that sometimes lives among mosses. Photo by Marie-Claude Larivière, with permission.



Figure 11. *Chionochloa rubra* in New Zealand, home for *Paracephaleus curtus*. Photo by Ulrich Lange, through Creative Commons.

Spittlebugs are so-named for their production of a frothy medium that resembles human spit. This "spittle" provides them a place to hide from would-be predators, but it not only hides them, it has an acrid taste that deters the predators (Wikipedia 2015). It is good insulation against heat and cold, much like hiding in water, but with air spaces that make it an even better insulator. And it provides moisture, protecting the soft-bodied nymphs from dehydration. The nymphs are plant suckers, and it appears that bryophytes, at least *Polytrichum juniperinum*, are on the menu (Figure 12-Figure 13), as well as many tracheophyte species.



Figure 12. Spittlebug on *Polytrichum juniperinum*. Photo courtesy of Timea Deakova, with permission.



Figure 13. Spittlebug nymph. Photo by Diliff, through Creative Commons.

FULGOROMORPHA - PLANTHOPPERS

Delphacidae – Delphacid Planthoppers

The **Delphacidae** is a family of herbivores with a worldwide distribution. A sweep net revealed *Euconomelus lepidus* (1.8-3 mm; Figure 14) from mosses beside a lake in Scotland (Bratton 2012). This is one of the few species that seems to be associated with bryophytes.



Figure 14. *Euconomelus lepidus* lives in association with mosses near a lake in Scotland. Photo by Tristan Bantock, with permission.

Javesella opaca (see Figure 15, Figure 16) is a planthopper that feeds on mosses in the eastern United States (Wheeler 2003). Nymphs live on the upright leafy gametophytes of *Polytrichum commune* (Figure 17) and *Polytrichastrum alpinum* (Figure 18) where these mosses grow over flatrock areas. In South Carolina, USA, the late instars overwinter among *Polytrichum commune*, with adults developing by mid- to late March. Most of the adults are **brachypterous** (having short wings). It is interesting that these insects feed on the thick stems of the mosses, whereas in our experiments with pillbugs the stems were avoided in *Polytrichum* and only leaves were eaten. In Russia, *Javesella discolor* (Figure 19) lives in moss bogs, moist forests, and swamp meadows (Emeljanov 1988), where mosses play an important role in creating a suitable microclimate.



Figure 15. *Javesella pellucida*; *J. opaca* feeds on mosses in the eastern US. Photo by Tom Murray, through Creative Commons.



Figure 16. *Javesella opaca*, a moss feeder. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 17. *Polytrichum commune*, home for *Javesella opaca* in the eastern United States. Photo by Christopher Tracey, through Creative Commons.



Figure 18. *Polytrichastrum alpinum*, home and food for *Javesella opaca* in Europe. This species also overwinters here. Photo by Michael Lüth, with permission.



Figure 19. *Javesella discolor*, a species that lives in mossy bogs and other mossy habitats. Photo by Joe Botting, with permission.

Muellerianella extrusa (2.1-3.1 mm; Figure 20) occurs in association with *Sphagnum* in Austria (Holzinger & Schlosser 2013).



Figure 20. *Muellerianella extrusa*, a *Sphagnum* associate in Austria. Photo by Gernot Kunz, with permission.

Richardson *et al.* (2002) found that changes in subordinate plant species had a greater impact on the herbivorous insect community than on those living on the dominant dwarf shrubs. Moss-feeding bugs were reduced to as little as 65% of the controls when their plots were fertilized, whereas grass-feeding insect species showed a 400% increase. This benefitted the **Delphacidae**, a **graminivorous** (grass-eating) family, suggesting that for most of the species the mosses were not important.

Derbidae – Planthoppers

Wilson and Wheeler (2015) attempted to learn more about the life history of this little known family. They were able to rear *Cedusa hedusa* (Figure 21) successfully from fifth instars to adults. These were collected from populations of the moss *Polytrichum commune* (Figure 17) in Alabama, USA. Nevertheless, food of the nymphs remains unknown, as well as oviposition sites and food preferences of the adults.

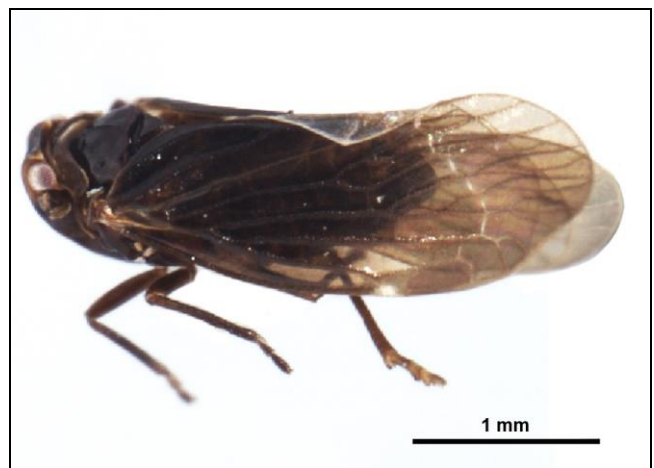


Figure 21. *Cedusa hedusa*, a species that lives on the moss *Polytrichum commune* in Alabama, USA. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Issidae – Planthoppers

Issus coleoptratus (3-4 mm; Figure 22-Figure 23) seems to spend most of its nymphal time among mosses (undocumented comment from Flickr). *Issus muscaeformis* (1.9-3.6 mm; Figure 24) has a name that suggests it has some relationship with mosses, but I can find no reference that places it in such a habitat. Consulted references include those that describe mosses as habitats for other insects.



Figure 22. *Issus coleoptratus* nymphal instar, a stage that lives among mosses. Photo through Creative Commons.



Figure 23. *Issus coleoptratus* adult, a moss-dwelling species. Photo by Sarefo, through Creative Commons.



Figure 24. *Issus muscaeformis* adult, a likely moss dweller. Photo by Roger S. Key, with permission.

The genus *Issus* (Figure 22-Figure 25) has an unusual means of locomotion (Burrows & Sutton 2013). It uses gears that intermesh, rotating like mechanical gears (Figure 25). These are located on the hind legs at the trochanter and rub together to propel the insect when it jumps. They insure that both legs have the same velocities and are synchronized. But as strange and unique as these are, they exist only in the nymphs, disappearing at the last molt. The adults must move like other insects.

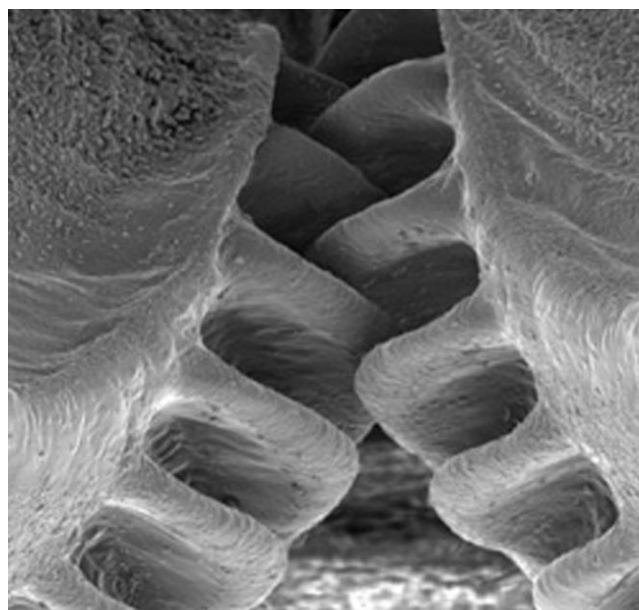


Figure 25. *Issus coleoptratus* interactive gears in the hind legs. Photo by Malcolm Burrows & Gregory Sutton, through Creative Commons.

SUBORDER STERNORRHYNCHA

(aphids, whiteflies, and scale insects)

Anyone who has kept a greenhouse will probably cringe at the mention of these insects. All are pests in that environment. And you might just introduce some of them with mosses you bring in.

Eriococcidae – Scale Insects

One of these greenhouse horrors is the scale insect (Figure 26). These seem like unlikely moss inhabitants, but Henderson (2007) considered mosses and ferns to be the most likely candidates as host plants for *Affeldococcus kathrinae* (0.4-0.65 mm). This very tiny species lacks a specific host tree, but lives in the high canopy epiphyte mat of the rata (*Metrosideros* spp.; Figure 27) in New Zealand. This led Henderson to conclude the epiphytic bryophytes and/or ferns might be the hosts.



Figure 26. *Eriococcus coriaceus* on *Eucalyptus* in Australia, representing a family with one known species of moss dwellers (*Affeldococcus kathrinae*). Photo by Arthur Chapman, through Creative Commons.



Figure 27. Rata forest (*Metrosideros umbellata*), Enderby Island, New Zealand. These forests have mostly mosses and ferns as ground cover and provide a suitable home for *Affeldococcus kathrinae*. Photo by John Barkla, with permission.

Aphididae (including Pemphigidae) - Aphids

Although incidences of **bryophagy** (eating bryophytes) are not well known among aphids, there are actually species that specialize on bryophytes, and others that eat them for special purposes (Hille Ris Lambers 1954; Müller 1973; Smith & Knowlton 1975; Stekol'Shchikov & Shaposhnikov 1994). Moss aphids pierce the cells, then

suck the contents from the cells (Thomas & Lombard 1991; Longton 1992). Aphids are common enough among mosses that there is a whole group known as the moss aphids (Müller 1973; Smith & Knowlton 1975).

Aphids are not common moss inhabitants, with the exception of the gall aphids, but perhaps we aren't looking in the right places. Recently Robin Stevenson found *Sphagnum* forming sleeves around young saplings of *Pinus sylvestris* and *Betula* spp. (Stevenson & Masson 2015). He pursued these strange sleeves, determining that they were formed by ants (*Lasius platythorax*). But why? Upon tearing them apart, he found lots of aphids (*Symydobius oblongus*; Figure 28-Figure 29) were running about. Ants are well known for tending aphids, using the "honey dew" excreted from two tubercles at the ends of the alimentary (digestive) canals (Figure 28). See Chapter 12-10 on Hymenoptera for more details on this relationship.



Figure 28. *Symydobius oblongus* nymph, a species that lives in *Sphagnum* sleeves created by ants on young birch and pine saplings in bogs. Note the two tiny white tubercles near the end of the abdomen where ants are able to harvest honey dew. Photo from <www.influentialpoints.com>, through Creative Commons.



Figure 29. *Symydobius oblongus* adult, a species that lives in *Sphagnum* sleeves created by ants on young birch and pine saplings in bogs. Photo from <www.aphotofauna.com>, with permission.

Gall Aphids

Some moss aphids form galls (Figure 85-Figure 86), but not on the mosses. Instead, the mosses act as alternate hosts (Chiuh 1976). One of the few remaining agricultural uses of mosses is the culturing of mosses as the winter host for Chinese gall aphids (Li *et al.* 1988, 1999; Liu & Li 1992, 1993; Liu *et al.* 1994). This has led to studies on the effects of temperature and water content on the vitality of these host mosses in winter (Liu *et al.* 1994) and on the physioecology of these mosses (Liu 2000).

Liu and coworkers (Liu 2000; Liu *et al.* 2000) studied the hosts *Plagiomnium acutum* (Figure 30), *P. maximoviczii* (Figure 41), *Thuidium cymbifolium* (Figure 31), and *Chrysocladium retrorsum* (Figure 32), hoping to cultivate them at optimal conditions. These mosses are able to maintain a net photosynthetic gain at temperatures as low as -15 to -10°C. The optimum temperatures for *T. cymbifolium* and *C. retrorsum* were in the range of 25-36°C in spring, dropping to 20-30°C in winter.



Figure 30. *Plagiomnium acutum*, overwintering host for gall aphids in China. Photo through Creative Commons.



Figure 31. *Thuidium cymbifolium* with capsules, a host plant for gall aphids, including *Schlechtendalia elongallis*. Photo by Li Zhang, with permission.



Figure 32. *Chrysocladium retrorsum*, a host plant for gall aphids. Photo by Yao Kuiyu, through Creative Commons.

Li *et al.* (1999) compared photosynthetic capacity in the two gall aphid hosts *Plagiomnium acutum* and *Herpetineuron toccoeae*. *Plagiomnium acutum* had lower photosynthesis on sunny days and higher on cloudy and rainy days compared to that of *H. toccoeae*. Consistent with its preferred bright days, *H. toccoeae* also had lower transpiration rates than did *P. acutum*, permitting the former to tolerate high temperatures and dry environments.

There are at least 24 known species of moss hosts in China, and their cultivation is critical to the production of the gall nuts (Li 1990). In China, the gall aphid species are generally highly specialized on only a few winter moss hosts (Chiuh 1976; Li *et al.* 1988). Among those used are *Mnium lycopodioides* (Figure 33), *M. thomsonii* (Figure 34), *Orthomnion dilatatum*, *Plagiomnium rhynchophorum*, *Brachythecium albicans* (Figure 35), *B. buchananii* (Figure 1), *B. velutinum* (Figure 36), *B. rutabulum* (Figure 37), *Homalothecium leucodonticaule* (Figure 38), *Hypnum callichroum* (Figure 39), and *Erythrodontium julaceum* (Figure 40). The first four of these are winter hosts of the Chinese gall aphid *Schlechtendalia chinensis* (Aphididae; Figure 42). The virus-carrying *Melaphidini* (Pemphigidae, a segregate from Aphididae) species shift their habitat between *Rhus* (sumac; Figure 85) and bryophytes (Eastop 1977).



Figure 33. *Mnium lycopodioides*, a winter host of the Chinese gall aphid *Schlechtendalia chinensis*. Photo by Michael Lüth, with permission.



Figure 34. *Mnium thomsonii*, a winter host of the Chinese gall aphid *Schlechtendalia chinensis* (Figure 42). Photo by Hermann Schachner, through Creative Commons.



Figure 37. *Brachythecium rutabulum* with capsules, an alternate host for gall aphids in China. Photo by Malcolm Storey from DiscoverLife, through Creative Commons.



Figure 35. *Brachythecium albicans*, an alternate host for gall aphids in China. Photo by Janice Glime.



Figure 38. *Homalothecium leucodonticaule* (= *Homalothecium laevisetum*), a species used by Chinese gall aphids. Photo through Creative Commons.



Figure 36. *Brachythecium velutinum* with capsules, an alternate host for gall aphids in China. Photo by Michael Lüth, with permission.



Figure 39. *Hypnum callichroum*, an alternate host for gall aphids in China. Photo by Michael Lüth, with permission.



Figure 40. *Erythrodontium julaceum*, an alternate host for gall aphids in China. Photo by Michael Lüth, with permission.

Plagiomnium maximoviczii (Figure 41) is also a common species that serves as the winter host for the Chinese gall aphids (Horikawa 1947; Tang 1976; Lao *et al.* 1984; Li *et al.* 1988). The aphids *Schlechtendalia chinensis* (Pemphigidae; Figure 42), *Nurudea shiraii*, and *Nurudea yanoniella* (Pemphigidae) are important commercially in China because of the galls they make on the sumac (*Rhus*) tree (Tang 1976; Min & Longton 1993). These galls are highly prized for medicines (expectorant; treatment of cankers and wounds) and the chemical industry (black dyes for dyers and tanners; ink) (Fagan 1918). The aphids migrate to the mosses for the winter, using them for both shelter and food (Chiu 1976; Tang 1976; Lai *et al.* 1990).

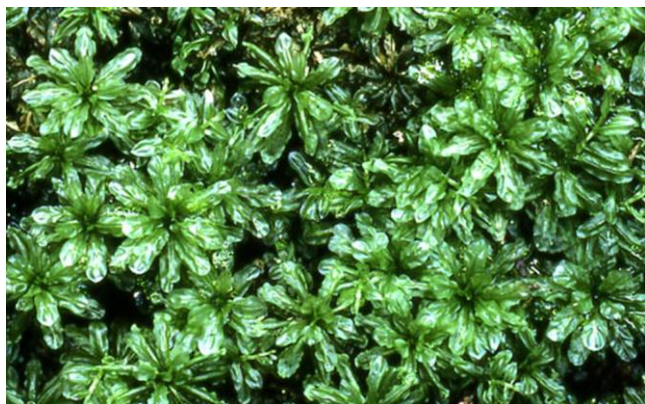


Figure 41. *Plagiomnium maximoviczii*, a winter host for Chinese gall aphids. Photo from Hiroshima University Digital Museum of Natural History, with permission.

Schlechtendalia

Schlechtendalia chinensis (Figure 42) makes its galls on *Rhus chinensis*. It uses *Plagiomnium maximoviczii* (Figure 41), *P. cuspidatum* (Figure 43), and *P. vesicatum* (Figure 44) for its winter shelter (Chiu 1976). When the galls burst open at maturity, the aphids emerge and migrate to their moss hosts. There they produce 20-30 nymphs that will develop into spring migrants. The newly emerged nymphs move to the moss stalks near the ground and cover their bodies with a waxy secretion in preparation for winter. In early spring they develop into the winged females that give live birth. These females are spring

migrants that move to the *Rhus chinensis* (sumac; Figure 45) where they will feed. Their offspring will be wingless. These become wingless adults and will be ready to mate in 4-8 days.



Figure 42. *Schlechtendalia chinensis* gall, a species that uses mosses as overwintering hosts. Photo from SanHerb, with permission.



Figure 43. *Plagiomnium cuspidatum*, one of the winter hosts of the Chinese gall aphid *Schlechtendalia chinensis* (Figure 42). Photo by Michael Lüth, with permission.



Figure 44. *Plagiomnium vesicatum* (formerly included in *Mnium*), a winter host for the Chinese gallnut *Schlechtendalia chinensis* (Figure 42). Photo from the Digital Museum, University of Hiroshima, with permission.



Figure 45. *Rhus chinensis*, host of the Chinese gall aphid *Schlechtendalia chinensis* (Figure 42). Photo from Kinmen National Park Digital Archives, through Creative Commons.

The females lay their eggs on the mosses (Lai *et al.* 1990). Because the host tree, the sumac, grows on dry slopes and the mosses tend to grow on more humid stream banks, there are few places where the mosses are sufficiently close to the trees for the relationship to work for the aphids (Zhang, pers. comm.). Hence, it is desirable to create more suitable habitats, possibly by cultivating mosses, placing them near the sumac at the appropriate season, then culturing the mosses through the winter in a favorable environment.

In addition to the *Plagiomnium* species, *Schlechtendalia* (Figure 42) also uses *Homomallium* (Figure 46), *Palamocladium* (Figure 47) (Liu & Li 1994), and *Herpetineuron toccoe* (Figure 48) (Li *et al.* 1999).



Figure 46. *Homomallium incurvatum*, member of a genus that provides a winter host for *Schlechtendalia chinensis* (Figure 42) in China. Photo by Hermann Schachner, through Creative Commons.

Kaburagia

Another gall-making aphid, *Kaburagia rhusicola* (1.3–1.5 mm), likewise uses mosses for winter hosts in China (Lai & Zhang 1994). These mosses include *Brachythecium* spp. (Figure 35–Figure 37), *Entodon* (Figure 49), and *Oxyrrhynchus* (= *Eurhynchium*?; Figure 94). In northern China, this aphid species moves from galls in late summer, and hibernates in an immature stage on the secondary host, the moss *Eurohypnum leptothallum* (Figure 50) (Chinese Academy of Forestry Science Institute

of Resource Insects 2014; The Aphids 2015). This institution has patented the procedure for growing the aphids on *E. leptothallum*. *Kaburagia ensigallis* (perhaps the same species as *K. rhusicola*) uses *Brachythecium buchananii* (Figure 1) as a host plant (Lou & Chen 2000).



Figure 47. *Palamocladium leskeoides*, member of a genus that provides a winter host for *Schlechtendalia chinensis* (Figure 42) in China. Photo courtesy of Claudio Delgadillo Moya.



Figure 48. *Herpetineuron toccoe*, a species that provides a winter host for *Schlechtendalia chinensis* (Figure 42) in China. Photo by Michael Lüth, with permission.



Figure 49. *Entodon* cf. *myurus* with capsules, member of a genus that provides a winter host for *Kaburagia rhusicola* in China. Photo by Michael Lüth, with permission.



Figure 50. *Eurohypnum leptothallum*, where *Kaburagia rhusicola* migrates in late summer in China and hibernates for the winter. Photo from <prologue.blog.naver.com>, through Creative Commons.

Muscaphis

But China does not have a corner on the gall aphid/moss association. Among the moss inhabitants is *Muscaphis escherichi* (1.7-2.7 mm; Figure 51), a bryophagous species on *Sorbus*, but when it is seasonally unavailable as a suitable habitat, they live primarily on the moss *Rhytidiadelphus loreus* (Figure 52) in the state of Washington, USA (Russell 1979). In Europe *M. escherichi* is common on many species of mosses, but researchers have had poor success in rearing it on any species but *Plagiothecium laetum* (Figure 53) and males have never been found on mosses (Stekolshchikov & Shaposhnikov 1993). *Muscaphis cuspidata* (0.9-1.3 mm) lives on *Calliergonella cuspidata* (Figure 54) and *Drepanocladus aduncus* (Figure 55), either close to the water or just below the water level. *Muscaphis mexicana* (1.7-2.1 mm) migrates to unidentified mosses, where wingless yellow or yellowish green aphids (0.6-0.8 mm) are produced (The Aphids 2015). The species *Muscaphis musci* (1.1-1.5 mm; Figure 56) occurs on many species of mosses, including those in *Amblystegium* (Figure 57), *Atrichum* (Figure 58), *Barbula* (s.l.; Figure 59), *Brachythecium* (Figure 37), *Bryum* (Figure 60), *Calliergonella*, *Eurhynchium* (Figure 94), *Hylocomium* (Figure 61), *Mnium* (probably *Plagiomnium*) (Figure 33-Figure 44), *Polytrichum* (s.l.) (Figure 17), *Pseudoscleropodium* (Figure 62), and *Tortula* (s.l.; Figure 63). In Denmark, Wilkaniec & Borowiak-Sobkowiak (2009) report *Muscaphis musci* from *Calliergonella cuspidata*, *Brachythecium rutabulum* (Figure 37), *Atrichum undulatum* (Figure 58), and *Plagiomnium undulatum* (Figure 64). *Muscaphis utahensis* (0.7-1.1 mm; Figure 65) occurs on mosses in the western USA and is thus far known only from the moss *Cratoneuron filicinum* (Figure 66) (Stekolshchikov & Shaposhnikov 1993). In most of the *Muscaphis* species, the bryophytes serve as alternate hosts and oviposition sites.



Figure 51. *Muscaphis escherichi*, a bryophagous species that lives on *Rhytidiadelphus loreus* in the western USA. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 52. *Rhytidiadelphus loreus*, the primary home for *Muscaphis escherichi* (Figure 51) in Washington, USA. Photo by Michael Lüth, with permission.



Figure 53. *Plagiothecium laetum*, the only species that seems to result in successful rearing of *Muscaphis escherichi*. Photo by Kristian Peters, with permission.



Figure 54. *Calliergonella cuspidata*, home to *Muscaphis cuspidata*. Photo by Michael Becker, through Creative Commons.



Figure 55. *Drepanocladus aduncus*, home to *Muscaphis cuspidata*. Photo by Michael Lüth, with permission.



Figure 56. *Muscaphis musci*, an aphid that occurs on many bryophyte species. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 57. *Amblystegium serpens*, a genus that is home for *Muscaphis musci* (Figure 56). Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.



Figure 58. *Atrichum undulatum*, home to *Muscaphis musci* (Figure 56). Photo by Janice Glime.

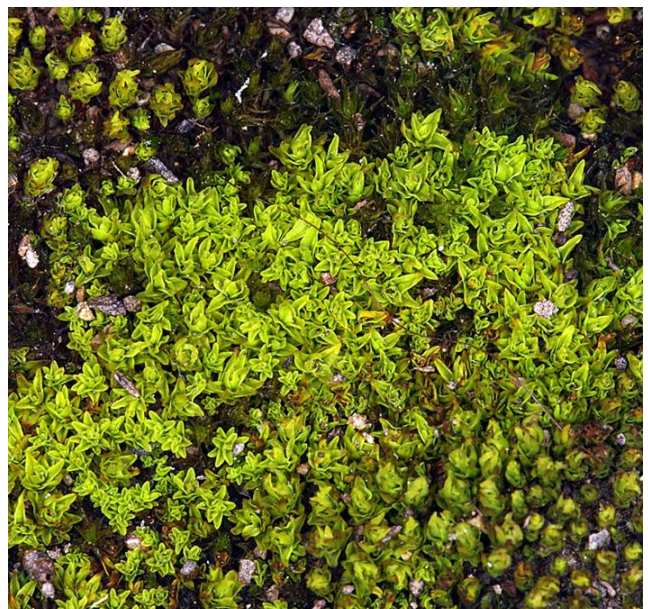


Figure 59. *Barbula convoluta*, home for *Muscaphis musci* (Figure 56). Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 60. *Bryum capillare*, home for *Muscaphis musci* (Figure 56). Photo by James K. Lindsey, with permission.

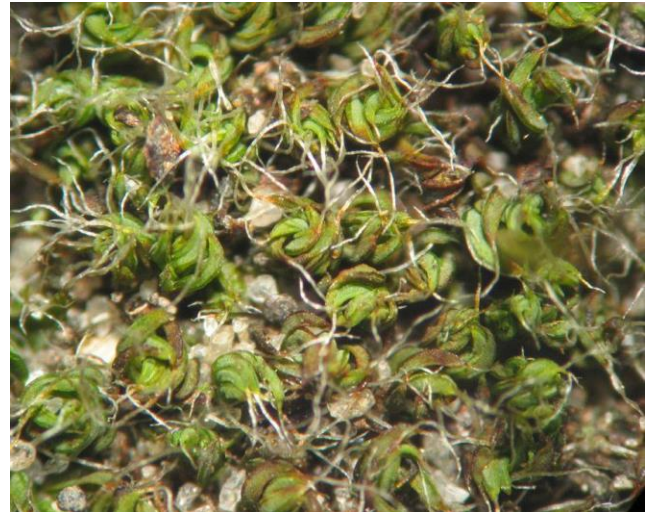


Figure 63. *Tortula muralis* dry. This species is in a genus that provides a home for *Muscaphis musci* (Figure 56). Photo by Kristian Peters, through Creative Commons.



Figure 61. *Hylocomium splendens* where you might find *Muscaphis musci* (Figure 56). Photo by Janice Glime.



Figure 64. *Plagiommium undulatum*, a home for *Muscaphis musci* (Figure 56). Photo by Michael Lüth, with permission.



Figure 62. *Pseudoscleropodium purum*, a species inhabited by *Muscaphis musci* (Figure 56). Photo by Michael Lüth, with permission.

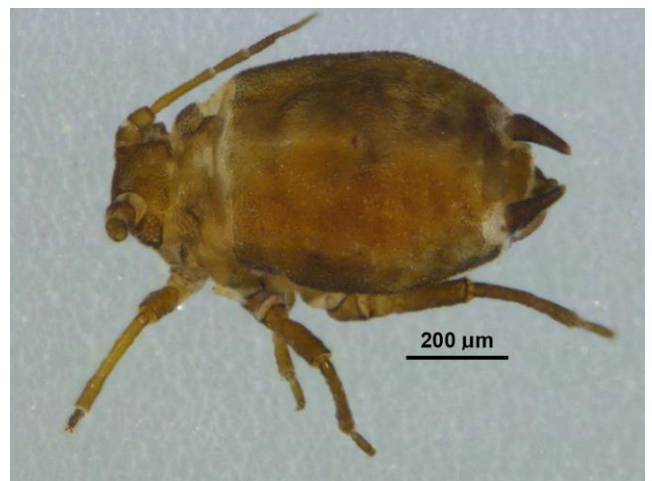


Figure 65. *Muscaphis utahensis*, a species lives on the moss *Cratoneuron filicinum*. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 66. *Cratoneuron filicinum*, home for *Muscaphis utahensis* (Figure 65). Photo by David Holyoak, with permission.

Myzodium

Another moss-dwelling aphid is the genus *Myzodium* (0.9-1.9 mm; Figure 67), one of the few genera of aphids that builds nests among *Sphagnum* (Figure 6) (Gerson 1969), and at least some of them eat mosses.

Aphids tap into the phloem of vascular plants to obtain nutrients. Clever researchers have used this behavior as a means to determine what substances are travelling in the phloem. Thomas and Lombard (1991; Thomas 1993) have used these tiny moss-dwelling aphids on *Polytrichum commune* (Figure 17) to obtain similar information on this moss. Their impact is sufficient to reduce the flow of labelled materials to other individuals that share rhizomes with the infested individuals. *Myzodium* sp. (~1.5-1.9 mm; Figure 67-Figure 68) not only diverts the nutrients from the **leptoids** (moss food-conducting cells) but also alters the normal source-to-sink flow within the moss turf.

Russell (pers. comm.) found many nymphs of *Myzodium modestum* (1.2-1.9 mm; Figure 67-Figure 68), a **bryophagous** species (eats bryophytes) (Müller 1973), overwintering on *Polytrichum* sp. (Figure 17) in early September at Waldo Lake, Oregon, USA. This species lives on other mosses as well, including *Dicranella crispa* (Figure 69), *Dicranum* sp. (Figure 113), *Oligotrichum aligerum* (Figure 70), *Pleurozium schreberi* (Figure 114), *Pogonatum dentatum* (Figure 71), *Polytrichastrum alpinum* (Figure 72), *Polytrichastrum formosum* (Figure 73), *Polytrichastrum longisetum* (Figure 74), *Polytrichum commune* (Figure 17), *Polytrichum juniperinum* (Figure 75), *Racomitrium* sp. (Figure 76), *Roellia roellii* (Figure 77), *Sanionia uncinata* (Figure 78), and *Sphagnum rubellum* (Figure 79) (Pike *et al.* 2010). This list attests to a wide variety of habitats including bogs, alpine, forest, boreal, and others as well as a wide range of bryophyte families from primitive to advanced, and it includes both acrocarpous and pleurocarpous mosses. *Polytrichum juniperinum* seems to have the most collection records. Unlike many species on tracheophytes, *Myzodium modestum* is not attended by ants.



Figure 67. *Myzodium* sp. nymphs, often born among *Sphagnum* (Figure 6). Photo by Andrew Jensen through Creative Commons.

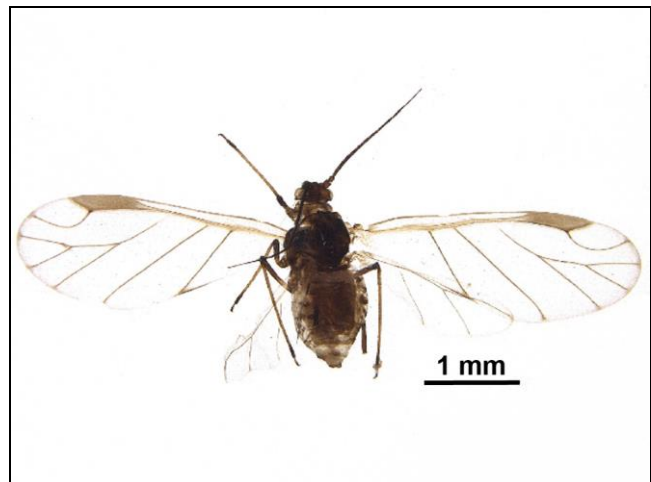


Figure 68. *Myzodium modestum* adult; nymphs spend the winter among mosses and feed on them by injecting a stylet into the leptoids. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 69. *Dicranella crispa*, home for *Myzodium modestum* (Figure 68). Photo by Ivanov, with permission.



Figure 70. *Oligotrichum aligerum*, a species inhabited by *Myzodium modestum* (Figure 68). Photo by Martin Hutten, with permission.



Figure 71. *Pogonatum dentatum*, a northern moss species that hosts *Myzodium modestum* (Figure 68). Photo by Michael Lüth, with permission.



Figure 72. *Polytrichastrum alpinum*, a species inhabited by *Myzodium modestum* (Figure 68). Photo by Andrew Hodgson, with permission.



Figure 73. *Polytrichastrum formosum*, a species inhabited by *Myzodium modestum* (Figure 68). Photo by David T. Holyoak, with permission.



Figure 74. *Polytrichastrum longisetum*, a species inhabited by *Myzodium modestum* (Figure 68). Photo by Hermann Schachner, through Creative Commons.



Figure 75. *Polytrichum juniperinum* male with new growth from antheridial splash cups. This species is home to *Myzodium modestum* (Figure 68). Photo by Janice Glime.

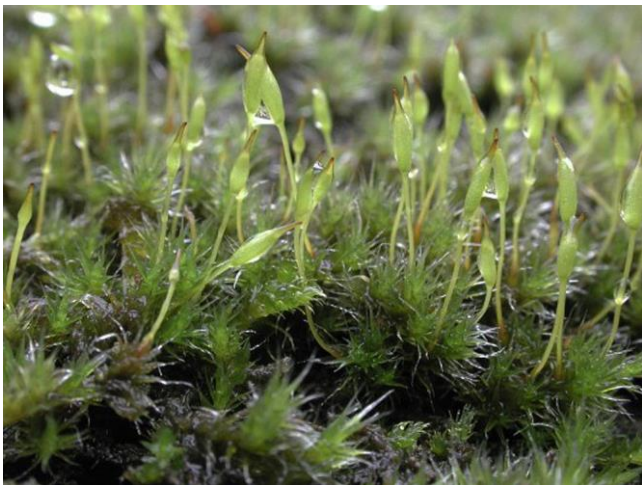


Figure 76. *Racomitrium heterostichum*, home to *Myzodium modestum* (Figure 68). Photo by Jan-Peter Frahm, with permission.



Figure 77. *Roellia roellii*, home to *Myzodium modestum* (Figure 68). Photo by Martin Hutten, with permission.



Figure 78. *Sanionia uncinata*, home to *Myzodium modestum* (Figure 68). Photo by Janice Glime.

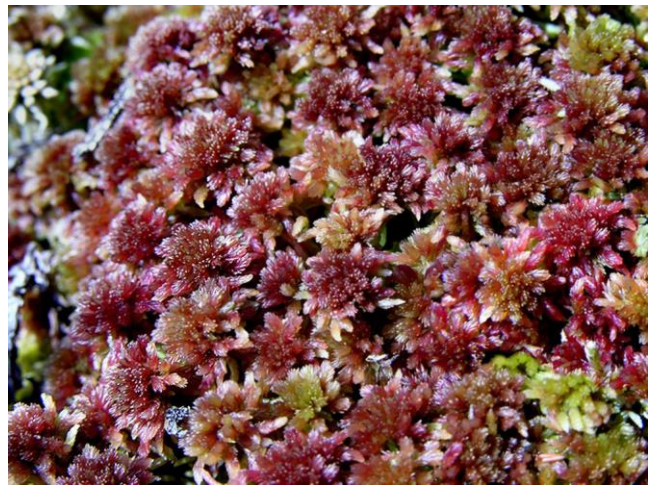


Figure 79. *Sphagnum rubellum*, home to *Myzodium modestum* (Figure 68). Photo by J. C. Schou <<http://www.biopix.com/>>, with permission.

Myzodium mimulicola (0.9-1.9 mm; Figure 80) occurs on *Aulacomnium palustre* (Figure 81), *Brachythecium frigidum* (Figure 82), *Straminergon stramineum* (Figure 83), *Philonotis fontana* (Figure 84), and *Sanionia uncinata* (Figure 78), another mixture of acrocarpous and pleurocarpous mosses, in western North America (Pike *et al.* 2010).



Figure 80. *Myzodium mimulicola* adult, a species that occurs on several moss species in western North America. Photo by Andrew Jensen, through Creative Commons.



Figure 81. *Aulacomnium palustre* with gemmae, a species that is home to *Myzodinium mimulicola* (Figure 80). Photo by Bob Klips, with permission.



Figure 82. *Brachythecium frigidum*, a species that is home to *Myzodinium mimulicola* (Figure 80). Photo by David Wagner, with permission.



Figure 83. *Straminergon stramineum*, a species that is home to *Myzodinium mimulicola* (Figure 80). Photo by David T. Holyoak, with permission.



Figure 84. *Philonotis fontana*, a species that is home to *Myzodinium mimulicola* (Figure 80). Photo by Michael Lüth, with permission.

Melaphis

The sumac gall aphid *Melaphis rhois* (Pemphigidae; Figure 85-Figure 89) is one of these moss aphids in the USA, alternating between mosses and sumac [*Rhus glabra* (Figure 90) and *R. typhina* (Figure 91)] (Moran 1989; Hebert *et al.* 1991; Pike *et al.* 2012).



Figure 85. *Melaphis rhois* galls on sumac (*Rhus*) in the US. This species shifts its habitat to bryophytes when conditions on the leaves are not favorable. Photo from Department Agriculture, Conservation, and Forestry, Augusta, Maine, through Public Domain.



Figure 86. *Melaphis rhois* nymphs in gall, a stage that exists on the sumac host. Photo by Claude Pilon, with permission.



Figure 87. *Melaphis rhois* young nymph, a stage that may be found among mosses. Photo by Claude Pilon, with permission.



Figure 90. *Rhus glabra* with flowers, primary host of *Melaphis rhois*. Photo from Superior National Forest, through Creative Commons.



Figure 88. *Melaphis rhois* adult, a moss and sumac inhabitant. Photo by Claude Pilon, with permission.



Figure 91. *Rhus typhina*, primary host of *Melaphis rhois*. Photo through Creative Commons.



Figure 89. *Melaphis rhois* adult, a species that lives on sumac and uses mosses as alternate hosts for winter and egg laying. Photo by Claude Pilon, with permission.

Moran (1992), an avid aphidologist, was walking in the Santa Catalina Mountains, Arizona, USA, when she discovered 5-cm galls (Figure 85-Figure 86) on a stand of smooth sumac (*Rhus glabra*; Figure 90). Further inspection revealed the sumac gall aphid, *Melaphis rhois* (0.8-1.2 mm; Figure 85-Figure 89). Upon further research, she discovered that this aphid was known from New York and that A. C. Baker had suspected that the tiny aphids he found among mosses in West Virginia, USA, might be the unknown spring migrant stage of *Melaphis rhois*. A return trip to the mountains enabled Moran to gather mosses and find that they indeed were inhabited by tiny aphids. She also transferred aphids from the sumac to the mosses and these produced morphs exactly matching those identified by Baker in West Virginia. After spending the summer inside the gall, where the single female reproduces asexually to make daughters, and they in turn her granddaughters, the granddaughters leave the gall in autumn as the sumac leaves begin dying and winter approaches. The granddaughters must find appropriate mosses where they deposit tiny aphid offspring. There the tiny daughters (great grandchildren of the original gall-maker) feed, develop, and reproduce. Their own waxy secretions protect them from desiccation. In spring of the first – or the second – year these females produce not only females but also males. Within a week they mate, females

deposit their eggs once more on the sumac, and the mating generation dies.

This species depends on the mosses for food (Baker 1919; Heie 1980; Moran 1989; Hebert *et al.* 1991). Pike *et al.* (2012) list a number of mosses that serve as hosts for *M. rhois*: *Rhytidiadelphus loreus* (Figure 52), *Leucolepis acanthoneura* (Figure 92), *Claopodium crispifolium* (Figure 93), *Eurhynchium praelongum* (Figure 94), and *Dicranum scoparium* (Figure 113).



Figure 92. *Leucolepis acanthoneura*, home of *Melaphis rhois*. Photo by Matt Goff <<http://www.sitkanature.org/>>, with permission.



Figure 93. *Claopodium crispifolium*, winter home of *Melaphis rhois*. Photo by Matt Goff <www.sitkanature.org/>, with permission.



Figure 94. *Eurhynchium praelongum*, home for *Melaphis rhois* when sumac leaves are unsuitable. Photo by Blanka Shaw, with permission.

Clydesmithia (Pemphigidae)

Clydesmithia canadensis (1.5-2.7 mm; Figure 95) includes a number of species among its moss hosts and is associated with mosses in Alaska (Pike *et al.* 2012). These moss alternate hosts are summarized in a table in Pike *et al.* (2012) and include such species as *Climacium dendroides* (Figure 96) and *Rhizomnium magnifolium* (Figure 97) that have not been mentioned here for other aphids.



Figure 95. *Clydesmithia canadensis* nymph, a species that is associated with a number of moss species. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 96. *Climacium dendroides*, one of the bryophyte hosts for *Clydesmithia canadensis* (Figure 95). Photo by Michael Lüth, with permission.



Figure 97. *Rhizomnium magnifolium*, an alternate host for *Clydesmithia canadensis* (Figure 95). Photo by Janice Glime.



Figure 100. *Pemphigus spirothecae* gall, member of a genus that uses mosses as alternate hosts. Photo by Georg Slickers, through Creative Commons.

***Pemphigus* (Pemphigidae)**

There seem to be few reports of European gall makers that use mosses as alternate hosts. In the UK, *Pemphigus trehernei* (1.3-2.4; see Figure 98-Figure 100) reproduces only by **parthenogenesis** (reproduction from an unfertilized egg), using roots of grasses and moss mats for oviposition (Alexander 2008). Norzikulov (1964) reported *Pemphigus hydrophilus* (1.9-2.2 mm) from *Cratoneuron filicinum* (Figure 101) and possibly also *Hygrohypnum luridum* (Figure 102) in Russia.

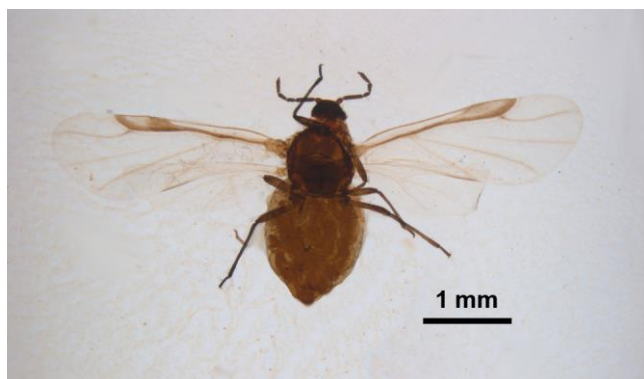


Figure 98. *Pemphigus bursarius*, a gall maker in a genus that uses mosses as alternate hosts. Photo from Pest and Diseases Image Library, through Creative Commons.



Figure 101. *Cratoneuron filicinum*, home for *Pemphigus hydrophilus*. Photo by J. C. Schou, with permission.



Figure 99. *Pemphigus bursarius* showing detail of antenna. Photo from Pest and Diseases Image Library, Bugwood.org, through Creative Commons.



Figure 102. *Hygrohypnum luridum* home for *Pemphigus hydrophilus* in Europe. Photo by Michael Lüth, with permission.

Other Aphididae that Live Among Mosses

Decorosiphon corynothrix (1.4-1.9 mm; Aphididae; Figure 103) lives on basal parts of *Polytrichum* spp. (Figure 17) growing in damp, shady situations and on *Atrichum undulatum* (Figure 104) (The Aphids 2015).

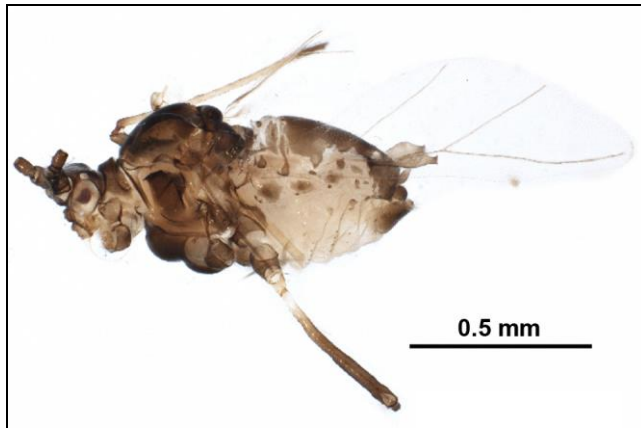


Figure 103. *Decorosiphon corynothrix*, a species that lives on the basal parts of *Polytrichum* spp. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 104. *Atrichum undulatum*, home to *Decorosiphon corynothrix*. Photo by Janice Glime.

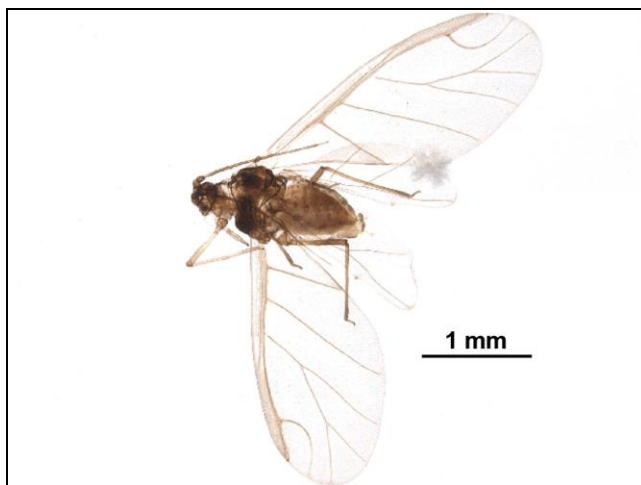


Figure 105. *Jacksonia papillata*, an aphid that often spends time among mosses. Photo through BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Jacksonia papillata (Aphididae; Figure 105) often occurs among mosses (Müller 1973). This is consistent with the mossy habitats of its primary hosts. Müller suspects that it sometimes feeds on mosses. *Pachypappa rosettei* (0.84-1.41 mm; Aphididae or Pemphigidae; Figure 106), *Pachypappa sacculi* (Figure 107), *Prociphilus*

xylostei (~3 mm; Aphididae; Figure 108-Figure 109), and *Thecabius populimonilis* (only once; Aphididae; Figure 110-Figure 111) also occur on mosses (Pike *et al.* 2012). *Prociphilus xylostei* is a strange-looking insect that secretes copious wax to cover and camouflage itself, making it look more like a fungus than an insect.



Figure 106. *Pachypappa rosettei*, a moss inhabitant. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 107. *Pachypappa sacculi*, a moss inhabitant. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

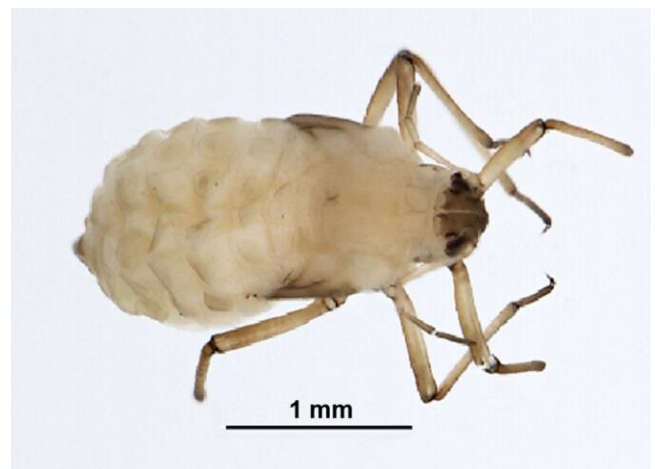


Figure 108. *Prociphilus xylostei* nymph, a moss dweller. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 109. *Prociphilus xylostei* adult, a moss dweller that secretes wax that serves to camouflage it. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 110. *Thecabius populimonilis*, a moss inhabitant. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Pseudacaudella rubida (0.7-1.0 mm; Figure 111- Figure 112) lives on the moss genera *Calliergonella* (Figure 54), *Climacium* (Figure 96), *Dicranum* (Figure 113), *Hylocomium* (Figure 61), *Mnium* (probably *Plagiomnium*; Figure 33-Figure 34, Figure 43-Figure 44), *Pleurozium* (Figure 114), *Polytrichum* (Figure 17), *Pseudoscleropodium* (Figure 62), and *Thuidium* (Figure 31) (The Aphids 2015).

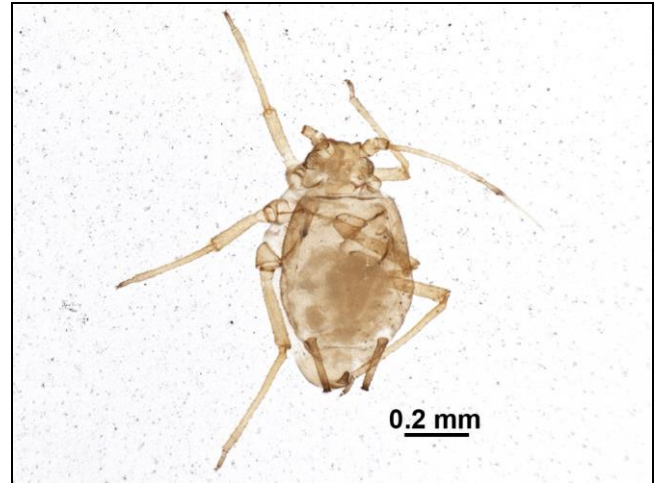


Figure 111. *Pseudacaudella rubida* nymph, a species that lives in a variety of mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

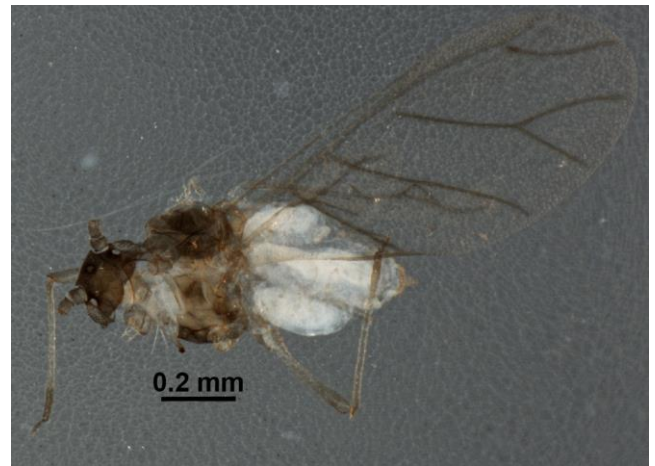


Figure 112. *Pseudacaudella rubida* adult. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 113. *Dicranum scoparium* with developing capsules, a moss that hosts *Pseudacaudella rubida*. Photo by Janice Glime.



Figure 114. *Pleurozium schreberi*, secondary host for *Pseudacaudella rubida*. Photo by Michael Lüth, with permission.

Attractants?

Do aphids help mosses attract more aphids? *Nurudea shiraii* (Aphididae) uses *Hypnum plumaeforme* (Figure 115) as a food plant (Lou & Chen 2000). *Thuidium cymbifolium* (Figure 31) is the host plant of *Schlechtendalia elongallis* (Pemphigidae). Lou and Chen found that these two mosses and the host moss *Brachythecium buchananii* (Figure 1) produce such aliphatic compounds as alcohols, aldehydes, ketones, and esters. They suggested that production of these compounds might be induced by the damage caused by their inhabiting aphids. They further suggested that these compounds might help the aphids locate their host plants. This sounds like an interesting hypothesis in need of testing.



Figure 115. *Hypnum plumaeforme*, food for *Nurudea shiraii*, produces aliphatic compounds that might help aphids to locate these mosses. Photo by Janice Glime.

Why Alternate Hosts?

Moran (1989) speculated on the evolutionary pressures that would cause such a host alternation as mosses and woody plants to evolve. Since this strategy is present in both the Chinese species and the North American ones, she postulated that both had their origins in Alaska and were separated when forced southward before the land bridge across the Bering Strait separated. Moran (1989) had already found fossil evidence of a 48-million-year-old aphid (*Melaphis rhois*; Figure 85-Figure 88) – host plant association with a similar moss/sumac alternation in

Alaska, apparently established prior to the southward retreat of sumac. Unlike the alternation seen in China and North America, in England and Scandinavia the aphid has lost its alternate host behavior and lives entirely on mosses, but has sacrificed all sexual behavior. This type of response is also known in the whitefly parasitoid *Encarsia formosa* (Hymenoptera) (Birkett *et al.* 2003), but both the production of aliphatic compounds by the moss and the insect response to these need to be verified as a consequence of moss herbivory.

Adelgidae – Woolly Conifer Aphids

The Adelgidae made their claim to fame by destroying forests, especially in the Appalachian Mountains, USA. Their connection with bryophytes is indirect, but can be strong. The woolly adelgids (*Adelges tsugae*; 1.5-mm; Figure 116-Figure 118) have had a major impact on the eastern hemlock (*Tsuga canadensis*; Figure 119-Figure 120) in the Appalachian Mountains, as far south as the Smoky Mountains (Jackson & Bellemare 2014). This disturbance has caused a decline in the leafy liverwort *Bazzania trilobata* (Figure 121) because the dying hemlocks open the canopy and the habitat becomes drier. This is accompanied by more deciduous litter (resulting from invasion of black birch – *Betula lenta*), greater light exposure, and higher temperatures.



Figure 116. *Adelges tsugae* on host eastern hemlock (*Tsuga canadensis*). Photo from Connecticut Agricultural Experiment Station Archive, USA, through Creative Commons.



Figure 117. *Adelges tsugae*, a destroyer of eastern hemlock forests. Photo by Shimat Joseph, University of Georgia, through Creative Commons.



Figure 118. *Adelges tsugae* eggs. Photo by Shimat Joseph, University of Georgia, through Creative Commons.



Figure 119. Dead hemlocks (*Tsuga canadensis*) in South Carolina resulting from *Adelges tsugae* infestations. Photo by Steve Norman, U.S. Forest Service, through Public Domain.

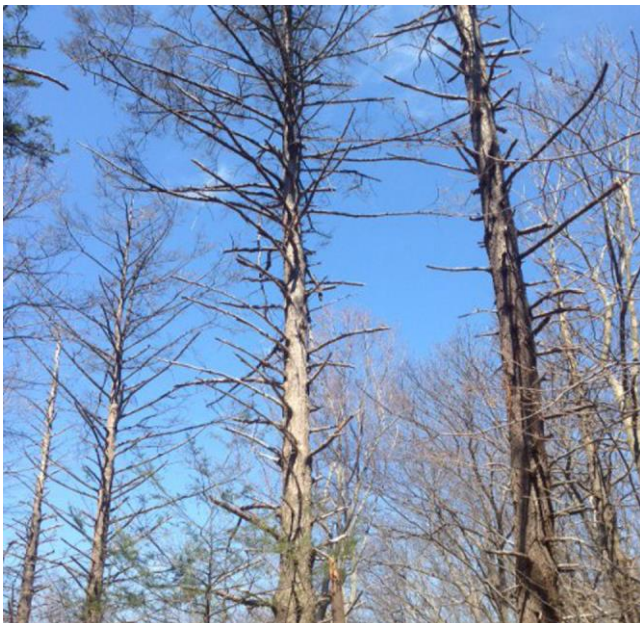


Figure 120. *Tsuga canadensis* showing open canopy after attack by *Adelges tsugae*. Photo by Matthew Willis, through Creative Commons.



Figure 121. *Bazzania trilobata*, a leafy liverwort that is disappearing where hemlocks have been killed by *Adelges tsugae*. Photo by Janice Glime.

Quite the opposite story can be told about one moss in the southern Appalachian Mountains of North Carolina. There, in high elevation locations, the moss *Leptodontium viticulosoides* (Figure 122-Figure 123) had become rather rare (Zander 1980). But prior to 1980 it began spreading. This spread is attributed to *Adelges piceae bouvieri* (Figure 124, Figure 125, Figure 128). In this case, the adelgid aphid causes the bark of the **endemic** (growing in a limited area) Fraser fir (*Abies fraseri*; Figure 126-Figure 128) tree to peel, creating habitat suitable for the moss.



Figure 122. *Leptodontium viticulosoides*, a moss that is spreading in areas where bark of Fraser fir (*Abies fraseri*) is peeling due to infestations of *Adelges piceae*. Photo courtesy of Claudio Delgadillo Moya.



Figure 123. Close view of *Leptodontium viticulosoides*. Photo by Li Zhang, with permission.

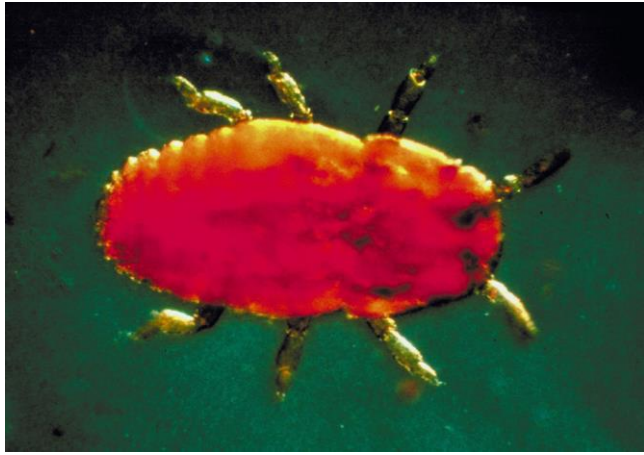


Figure 124. *Adelges piceae*, a species that causes the bark of the Fraser fir to peel, permitting the moss *Leptodontium viticulosoides* to become established. Photo by USDA Forest Service - Ashville Archive, through Creative Commons.

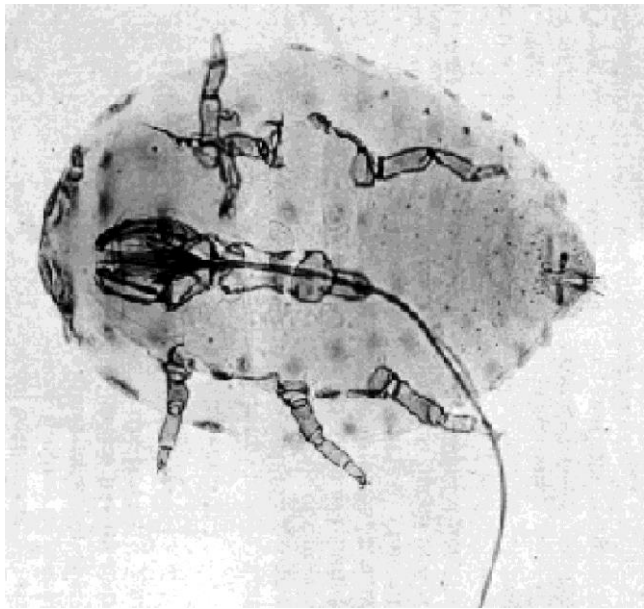


Figure 125. *Adelges piceae*, a species that damages Fraser Fir and opens habitat for the moss *Leptodontium viticulosoides*. Note the long proboscis. Photo from USDA, in Public Domain.



Figure 126. *Abies fraseri* in the Blue Ridge Mountains, USA. Photo by Gene, through Creative Commons.



Figure 127. *Abies fraseri*, home for *Adelges piceae* in the southern Appalachian Mountains, USA. Photo by Steve Baskouf <www.bioimages.vanderbilt.edu>, through Creative Commons.

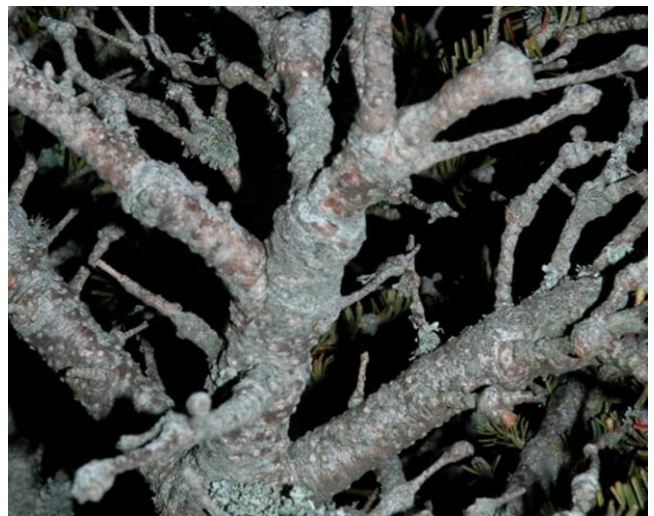


Figure 128. *Adelges piceae* on *Abies fraseri*. Photo by William M. Ciesla, Forest Health Management International, <Bugwood.org>, through Creative Commons.

In the Southern Appalachian Mountains, the hornwort *Megaceros aenigmaticus* suffered a decrease in sexual reproduction. Although this was partly due to its rarity and lack of contact between males and females, Villareal (2009) suggested that its survival is further threatened by habitat degradation due to the adelgid plague on the hemlocks that created its habitat.

SUBORDER COLEORRHYNCHA

(moss bugs or beetle bugs)

The **Coleorrhyncha**, with only one exception, are flightless. They have an extremely reduced **pharyngeal ring** muscle layer (muscles surrounding the pharynx, which is the first part of the foregut) (Spangenberg *et al.* 2013). Spangenberg and coworkers suggest that this reduction prevented any secondary shift in diet (these are bryophyte eaters), preventing them from using a broad range of food sources and consequently preventing radiation of the species into new locations and new species.

Peloriidiidae – Moss Bugs

The **Peloriidiidae** are cryptic species that frequent wet mosses, liverworts, and leaf litter (Spangenberg *et al.* 2013). They are small (2-4 mm), flattened, and cryptically-colored relict **Hemiptera** in the Southern Hemisphere (Evans 1982; Burckhardt 2009), resulting in their remaining undiscovered in Australia until 1932, although they were known elsewhere in the area (Monteith 2015). Cranston (2010) cites this family as one living among *Sphagnum* and liverworts (Austin *et al.* 2004; Cranston 2009). Evans (1941) considered the presence of moss in a habitat that is moist all year round to be a necessity.

One adaptation of bryophyte fauna that is often forgotten is vibration frequency of the "call." Hoch *et al.* (2006) considered the small size of the **Peloriidiidae** to necessitate vibrational signals for mates to locate each other. The low frequency of the signals suggests that they may be adapted to calling from their host of soft mosses. This signal is effective at short range and would therefore be effective to initiate courtship or signal disturbance.

The history of the **Peloriidiidae** is an interesting one. *Peloriidum* (Figure 129) had been collected from Tierra del Fuego in 1892, *Xenophyes* (Figure 131) from New Zealand in 1920, and *Hemiodoecus* (Figure 135) from Tasmania in 1904 (Monteith 2015). But in total, only six specimens had been collected to represent these three genera! All came from dripping wet *Nothofagus* forests (Figure 130). In 1932, Hacker described *Hemiodoecus veitchi* from the Antarctic Beech forest of Lamington National Park, Queensland, Australia. This name was later changed to honor both Hacker and his mentor – *Hackeriella veitchi*. In 1971, a further discovery by Bob Taylor resulted in the description of *Rhacophysa taylori* (Burckhardt 2009) from dripping mosses near Cairns, Queensland, a wet area receiving 8 m of rainfall per year.

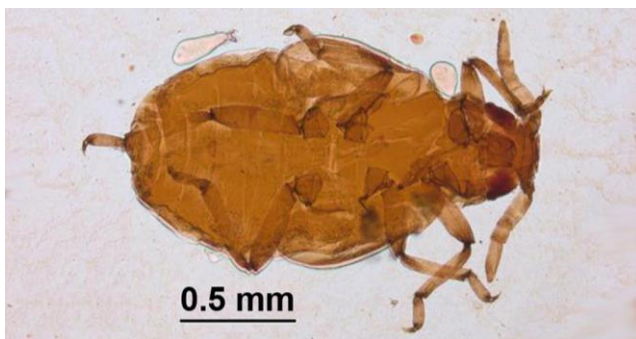


Figure 129. *Pemphigus bursarius*, member of a moss-dwelling genus. Photo from Pest and Diseases Image Library, Bugwood.org, through Creative Commons.

Despite having only 21 species known in 1982 (Evans 1982), the **Peloriidiidae** have been reported from bryophytes many times compared to other **Hemiptera**. These frequent reports, nevertheless, most likely grossly under-represent their presence because of their cryptic habits and small size (Burckhardt *et al.* 2011). Adequate sampling requires sifting of the mosses and forest litter with a sieve. They also tend to occur in remote locations that are hard to reach.

Moss bugs are known from fossils, occurring on mosses in the wet, cool *Nothofagus* (beech) forests (Figure 130) in the Southern Hemisphere (Bechly & Szewo 2007). Today they are most common in the *Nothofagus* forests of southern South America, Australia, Tasmania, New Caledonia, Lord Howe Island, and New Zealand, where they live in damp mosses on decaying mossy trunks and twigs of the *Nothofagus*. In addition to eating the leafy mosses, they may feed on moss rhizoids, wood-decaying fungi, or lichens.



Figure 130. *Nothofagus* beech forest with a dense bryophyte ground cover, Eglinton Valley, NZ. Photo from Department of Conservation of NZ, through Creative Commons.

Drake and Salmon (1948) first reported *Xenophyes cascus* (2.48-3.10 mm; Figure 131) from New Zealand in 1948, identifying it from damp moss. *Xenophyes cascus* is currently distributed in temperate forests and fens in the Southern Hemisphere (Australia, New Zealand, New Caledonia, Chile, Argentina) (Grozeva *et al.* 2014). They also occur on the moss *Notoligotrichum crispulum* (Figure 132) in heavily forested areas where *Weinmannia racemosa* (Figure 133) is dominant (Carter 1950). These are both moss dwellers and moss feeders. Burckhardt *et al.* (2011) reported New Zealand moss dwellers to include *Xenophyes cascus* from moss on an old log, the broadleaf-taraire dominant *Xenophyes adelphus* (2.35-2.63 mm) by sifting mosses from cloud forests and the mosses and liverworts on tree trunks and branches, *Xenophyes goniomus* (2.68-3.10 mm) and *Xenophyes kinlochensis* (2.80-3.23 mm) from mosses, *Xenophyes metoponcus* (2.35-2.55 mm) from mosses in mixed podocarp/broadleaf forest, and *Xenophyes rhachilophus* (2.18-2.95 mm; Figure 134) from mosses under beech trees, sifted mosses, and mosses on a wet bank.

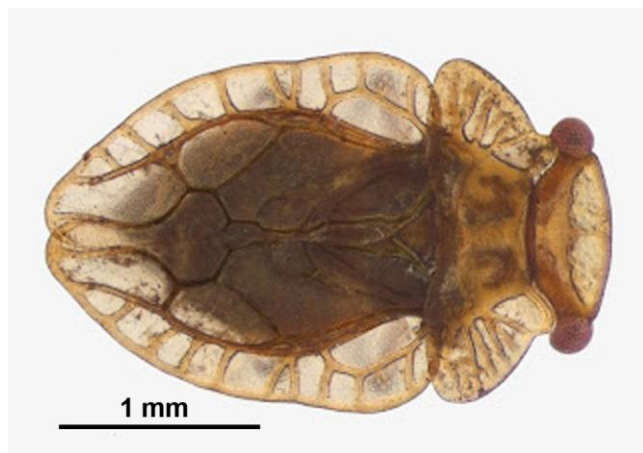


Figure 131. *Xenophyes cascus*, an inhabitant of *Notoligotrichum crispulum* in New Zealand. Photo by Birgit E. Rhodes in Larivière *et al.* 2011, with permission.



Figure 134. *Xenophyes rhachilophus*, a species that occurs among mosses under beech trees in New Zealand. Photo by S. E. Thorpe, through Creative Commons.



Figure 132. *Notoligotrichum crispulum* with capsules, home of *Xenophyes cascus* (Figure 131) in New Zealand and elsewhere. Photo by David Tng <<http://www.davidtng.com/>>, with permission.



Figure 133. *Weinmannia racemosa*, home for the moss *Notoligotrichum crispulum* and inhabiting *Xenophyes cascus*. Phil Bendle, through Creative Commons.

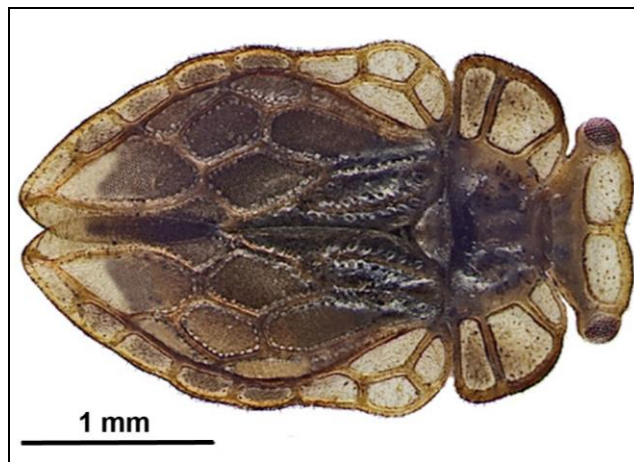


Figure 135. *Hemiodoecus leai*, a species most likely introduced into New Zealand with frozen fish eggs packed in mosses. Photo by Marie-Claude Larivière <www.nzhemiptera.com/>, with permission.



Figure 136. *Ptychomnion aciculare*, home for *Hemiodoecus leai* (Figure 135). Photo by Andy Hodgson, with permission.



Figure 139. *Bartramia* sp., home and food for *Hemiodoecus leai* (Figure 135). Photo by Andy Hodgson, with permission.



Figure 137. *Weymouthia cochlearifolia*, home for *Hemiodoecus leai* (Figure 135). Photo by Juan Larrain, with permission.



Figure 138. *Weymouthia mollis*, home for *Hemiodoecus leai* (Figure 135). Photo by Juan Larrain, with permission.



Figure 140. *Oiophysa ablusa*, a New Zealand bryophyte dweller on a leafy liverwort. Photo by E. Wachmann through M.-C. Larivière, with permission.

The genera *Oiophysa* (2.19-2.98 mm; Figure 140) and *Xenophysella* (2.34-3.00 mm) are among the moss dwellers in New Zealand (Larivière *et al.* 2011). These include *Oiophysa ablusa* (3 mm; Figure 140), *O. cumberi* (2.5 mm; Figure 141), *O. distincta* (2.6 mm), *O. pendergrasti* (2.5 mm), *Xenophysella greensladeae* (2.48-3.0 mm), and *X. stewartensis* (2.34-2.63 mm; Figure 142). *Xenophysella greensladeae* has two 3-lobed **bacteriomes** where bacteria are maintained. Larivière and coworkers presumed that as environmental conditions become drier the **Peloriidiidae** would move deeper into the moss layers where there is greater humidity, remaining there until the surface becomes more suitable.

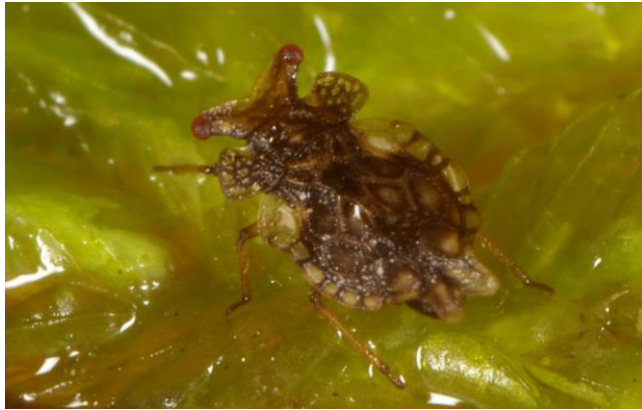


Figure 141. *Oiophysa cumberi*, a New Zealand bryophyte dweller on a moss. Photo by George Gibbs, with permission.

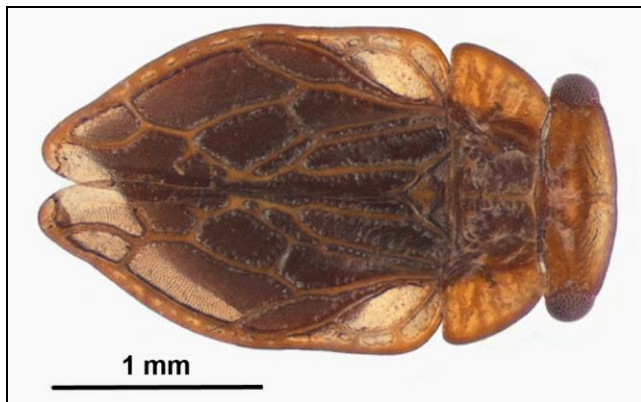


Figure 142. *Xenophysella stewartensis*, a New Zealand moss dweller. Photo by Birgit E. Rhodes in Larivière *et al.* 2011, with permission.

Oiophysa distincta (2.44-2.98 mm) is considered a living fossil relict in native New Zealand forests, where it lives among wet mosses in the temperate and Antarctic rainforests (Figure 143) (Harris 2011; Grozeva *et al.* 2014). Today other *Peloridiidae* likewise occur in damp mosses, frequenting the decaying mossy trunks and branches of *Nothofagus* (Figure 130), where they feed on wood-decaying fungi, lichens, and moss rhizoids (Bechly & Szwedo 2007).



Figure 143. Rainforest, Fiordland National Park, New Zealand, mossy home for *Oiophysa distincta*. Photo by Christiaan Briggs, through Creative Commons.

On Lord Howe Island, *Howeria kingsmilli* (3.0-3.1 mm) occurs on the long pendent moss *Spiridens vieillardii* (Figure 144) and on the leafy liverwort *Porella elegantula* (Figure 145-Figure 146) (Evans 1967).



Figure 144. *Spiridens vieillardii* with capsules, a pendent moss that houses *Howeria kingsmilli*. Photo by Louis Thouvenot, with permission.



Figure 145. *Porella elegantula*, a leafy liverwort that is home to *Howeria kingsmilli*. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.



Figure 146. *Porella elegantula* showing its underside. This pendent leafy liverwort is home to *Howeria kingsmilli*. Photo by Jan-Peter Frahm, with permission.

In Australia, *Hemiodoecellus fidelis*, like *Hemiodoecus leai* (Figure 135) in New Zealand, lives in

damp moss where its movement is limited by its short legs and limited space for movement (Robinson 2003).

In Australia, *Hackeriella veitchi* (3.0-3.3 mm; Figure 147) inhabits the pendent moss *Papillaria crocea* (Figure 148) (Helmsing & China 1937; Carter 1950; Spangenberg *et al.* 2013). On the other hand, a much later visit to the area failed to reveal any individuals of this species on the *P. crocea* (Spangenberg *et al.* 2013). Nevertheless, new locations have been found, making this the most readily available member of the family. *Hackeriella veitchi* is unique among the **Peloridiidae** in being able to jump. This is accomplished without any apparent morphological adaptation, but rather by suddenly rotating the hind **femora** (third segments of legs) on the **coxae** (bases of legs) (Burrows *et al.* 2007).



Figure 147. *Hackeriella veitchi*, an inhabitant of a pendent moss in Australia. Photo by J. Deckert, with permission.



Figure 148. *Papillaria crocea* in cloud forest where it can provide a home for *Hackeriella veitchi*. Photo by Peter Woodard, through Creative Commons.

Burkhardt and Agosti (1991) reported *Peloridora kuscheli* (2.8-3.3 mm; Figure 149), *P. minuta* (~2.6 mm), and *P. holdgatei* (~2.6 mm) from mosses in the *Nothofagus* forests (Figure 130) in Chile. Other Chilean moss dwellers include *Pantinia darwini* (3.2-3.9 mm; Figure 150) and *Pantinia* sp. and several unidentified early instar nymphs.



Figure 149. *Peloridora kuscheli*, an inhabitant of mosses in the *Nothofagus* forests of Chile. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 150. *Pantinia darwini*, a moss dweller in *Nothofagus* forests (Figure 130) in Chile. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Shcherbakov (2014) found that some of the **Peloridiidae** are restricted to one or only a few bryophyte species (**mono-** or **oligophagous**). For example, *Peloridium hammoniorum* (3.8-5.2 mm; Figure 151) in Fuegia in Southern Patagonia was found only on *Pohlia cruda* (Figure 152) (China 1962; Cekalovic 1986), *Polytrichum strictum* (Figure 153) (Estévez & Remes Lenicov 1990), and *Polytrichadelphus magellanicus* (Figure 154) (Shcherbakov 2014), and it is known to eat mosses (Larivière *et al.* 2011; Shcherbakov 2014). [The host *Polytrichum strictum* was not reported previously from that region (Larrain 2007) and may be a misidentification.] The recently described species *Peloridium pomponorum* (3.4-4.1 mm) is only known from *Sphagnum magellanicum* (Figure 156) and *S. cf. recurvum* (Figure 157), both in open areas (Shcherbakov 2014).



Figure 151. *Peloridium hammoniorum* on *Polytrichadelphus magellanicus*. Photo by Roman Rakitov, with permission.



Figure 154. *Polytrichadelphus magellanicus*, home of *Peloridium hammoniorum* in Fuegia in Southern Patagonia. Photo by David Tng <www.davidtng.com>, with permission.



Figure 152. *Pohlia cruda*, a moss where *Peloridium hammoniorum* lives in Southern Patagonia. Photo by Martin Hutten, with permission.



Figure 155. *Peloridium pomponorum* on *Sphagnum magellanicum*. Photo by Roman Rakitov, with permission.



Figure 153. *Polytrichum strictum*, a peatland species where *Peloridium hammoniorum* might live in Southern Patagonia. Photo by Janice Glime.



Figure 156. *Sphagnum magellanicum*, a home for *Peloridium pomponorum*. Photo by Janice Glime.



Figure 157. *Sphagnum recurvum*, a home for *Peloridium pomponorum*. Photo by Jan-Peter Frahm, with permission.

Symbiotic Bacteria

One of the factors that may permit the **Peloriidiidae** to eat mosses is their associated symbiotic bacteria. The **Coleorrhyncha**, including the **Peloriidiidae**, is one of the oldest lineages of **Hemiptera**. Kuechler *et al.* (2013) analyzed **Peloriidiidae** bacterial symbionts from 15 representatives from South America, Australia, Tasmania, and New Zealand. These proved to be an unknown group of **Gammaproteobacteria**, which they named *Candidatus Evansia muelleri*. These bacteria develop at the posterior pole of a developing oocyte and thus are transmitted from parent to offspring before birth. A second bacterium was usually associated with the Malpighian tubules, an endosymbiont in the genus *Rickettsia* (Figure 158).

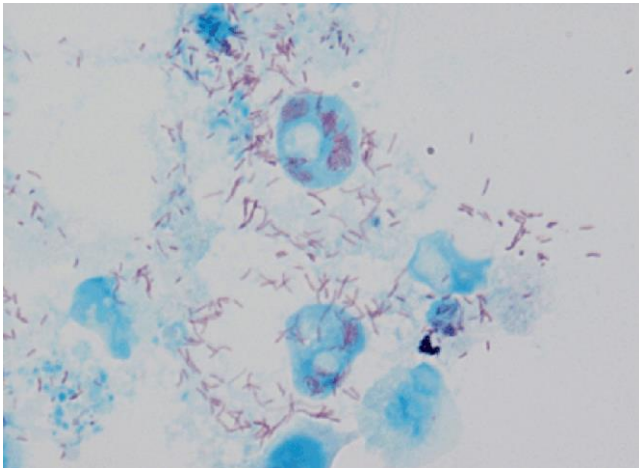


Figure 158. *Rickettsia conorii*, a possible symbiont of **Peloriidiidae** that permits it to digest mosses. Photo by Clarisse Rovey, Philippe Brouqui, & Didier Raoult, through Creative Commons.

ORDER THYSANOPTERA – Thrips

The thrips are tiny, slender insects with fringed wings (Greek *thysanos* = fringe) (Thrips 2015). They feed by sucking cell contents of plants or animals. Their tiny size (<1mm) gives them an ideal fit among bryophytes, but only one sub-tribe among the 6,000 species lives there (Mound

1989). Curiously, the word "thrips" is both singular and plural.

Although an insect most people do not often notice, these insects (**Thysanoptera**) can be associated with mosses (Mound 1989). Bhatti (1979) found two new species in a new genus of thrips (**Thripidae**) living among mosses in West Africa. Mound (1970) reported *Nesothrips lativentris* from this family among mosses on the Solomon Islands.

The Old World genera of *Bournierothrips* and *Muscithrips* are bryophyte dwellers. In fact, *Bournierothrips* seems to be restricted to mosses (Bournier 1979). A recent new genus, *Solanithrips*, was described from Mexico as an inhabitant of *Solanum* (Johansen 1997). This genus is closely related to the two Old World bryophyte-dwelling genera, so it is possible that it too may just use bryophytes when the *Solanum* is seasonally unavailable. Other members of **Thysanoptera** are known from bryophytes (and lichens) in Mexico (Mojica Guzman & Johansen 1990).

In their study of New Zealand **Thysanoptera**, Mound and Walker (1982) found records of a number of species of **Thripidae** in association with mosses: *Anaphothrips obscurus* (1.5 mm), *Anaphothrips woodi*, *Aptinothrips rufus* (1.5mm; Figure 159-Figure 160), *Aptinothrips stylifer* (~1.5 mm; Figure 161), *Ceratohrips frici* (Figure 162), *Lomatohrips paryphis*, *Pseudanaphothrips achaetus*, *Thrips australis*, *T. nigropilosus*, *T. obscuratus*, *T. tabaci* (Figure 163). At least some species, including *Ceratohrips frici*, are attracted to their primary hosts by colors (Teulon & Penman 1992). *Ceratohrips frici* is attracted to white and yellow traps. The associations of all these thrips with a number of flowering plants suggest that the mosses were most likely a refuge and not a food source (Mound & Walker 1982).

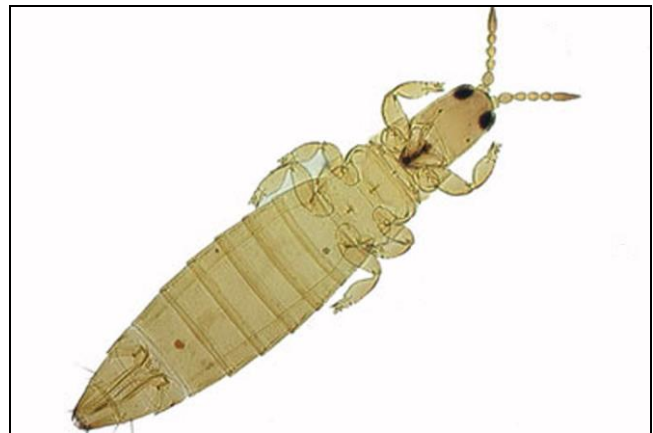


Figure 159. *Aptinothrips rufus*, a moss associate in New Zealand. Photo by John W. Dooley, through Creative Commons.



Figure 160. *Aptinothrips rufus*, a moss associate and flowering plant eater in New Zealand. Photo through Creative Commons.



Figure 161. *Aptinothrips stylifer*, a moss associate in New Zealand. Photo through Creative Commons.



Figure 162. *Ceratothrips frici*, a New Zealand moss dweller. Photo by John W. Dooley, USDA APHIS PPQ, through Public Domain.



Figure 163. *Thrips tabaci*, a flowering plant associate that also spends time among mosses. Photo by Alton N. Sparks, through Creative Commons.

Johansen *et al.* (1983) discussed the New World (Eastern Mexico and Costa Rica) *Wegenerithrips* (0.738–1.16 mm; **Thripidae**), a genus with nine species at the time, as a bryophyte feeder. This is a genus thus far known only from females (Taylor 2013). Most likely more of these bryophyte feeders remain unknown.

Mound (1989) reported that only one sub-tribe within **Thysanoptera** feeds on mosses, the **Williamsiella** (family **Phlaeothripidae**). This sub-tribe is comprised of two genera, *Lissothrips* and *Williamsiella*. These are mostly New World species. In addition to their small size, these genera seem further adapted to moss dwelling by

being wingless. And their ability to feed on mosses seems to be a highly derived character. One even bears the name *Lissothrips muscorum* (1.17 mm), a wingless female found among mosses in Illinois, USA, and only known from mosses (Rhode 1955). Chiasson (1986) reported it from *Sphagnum* and moss litter, and it feeds on mosses. An early record of **Phlaeothripidae** among mosses is that of *Liothrips ocellatus* (Figure 164) in Illinois, USA (Hood 1908).



Figure 164. *Liothrips ocellatus*, one of the early known moss dwellers among the thrips. Photo through Creative Commons of Snipeview.

But it may not always be the moss that gives them their nutrition. In Australia and New Zealand species of these two genera have a blue-green gut, suggesting they may eat the associated **Cyanobacteria** (Mound & Tree 2015). The fact that these genera are understudied is indicated by the new finds: two species of *Lissothrips* were recorded from Australia for the first time in 2015, as well as six new species; *Williamsiella* was recorded from Australia for the first time with a new species.

Bryophytes may actually play an important role for leaf-inhabiting thrips. When the weather becomes cool and wet, these leaf dwellers seem to disappear from the landscape (Mound & Walker 1982). But if one uses a Berlese funnel to extract them from leaf litter and ground mosses, many will appear. The mosses serve as a refuge when leaves become inhospitable. Further evidence of bryophytes as a refuge comes from *Iridothrips mariae* (**Thripidae**). In Hungary, this species seeks mosses in the fall as a place to spend the winter (Jenser 2013).

Peck and Moldenke (1999) have been concerned with the invertebrates, especially insects, that are collected with harvestable mosses. Not only does this disturb the communities of origin, in some cases depriving birds, lizards, and other predators of a food source, but also it introduces these creatures to a new ecosystem where they may have no or few natural predators. They could easily become crop pests in some receiving ecosystems. Peck and Moldenke reported that the number of individuals of **Thysanoptera** per gram were greater in those moss samples collected at the bases of shrubs than in those from the tips of branches. They recommended prohibiting the harvesting of mosses from the shrub bases due to their importance in housing insect diversity.

Summary

Several previous orders have been combined into the **Hemiptera**, including leaf hoppers, plant hoppers, aphids, and moss bugs.

Some of the **Cicadellidae** are true **tyrphobionts** (bog dwellers). The **Delphacidae** includes moss eaters, especially on **Polytrichaceae**; few seem to be bog dwellers.

Other important moss-dwelling aphids include members of **Myzodium** and **Muscaphis**, both of which typically use mosses for overwintering and seasonal food. **Derbidae** and **Issidae** have moss dwellers, but little seems to be known about their habits. The latter uses a pair of gears to aid jumping in nymphs. Even less is known about **Eriococcidae** that live among mosses.

This classification includes several kinds of gall makers in the **Aphididae** that depend on bryophytes, especially **Mniaceae**, for part of the life cycle and winter food. For the Chinese gall maker *Schlechtendalia chinensis* and others, and even some North American gall makers, the bryophytes serve as an essential winter host, serving for both food and shelter and often oviposition sites. In the **Aphididae**, a family with a stylet for sucking plant juices, moss specialists have been used to trace the movement of fluids in the leptoids of mosses in the **Polytrichaceae**. Some of these moss inhabitants may respond to aliphatic compounds in the moss, but direct relationships remain to be tested.

Members of the genus *Adelges* (**Adelgidae**) have destroyed habitat for the leafy liverwort *Bazzania trilobata* and in other cases have opened new habitat for the moss *Leptodontium viticulosoides*.

The family **Peloriidiidae** is so common among mosses that the common name of "moss bugs" is applied. They seem to require that constantly moist environment, probably burrowing deeper as the moss dries. At least some members of the family may have bacteria that help in their digestion of the mosses.

Information on thrips (**Thysanoptera**) is limited, but several genera are represented among bryophytes, with the sub-tribe **Williamsiellina** feeding on mosses.

Acknowledgments

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