CHAPTER 12-13
TERRESTRIAL INSECTS:
HOLOMETABOLA – LEPIDOPTERA:
MICROPTERIGOIDEA - GELECHIOIDEA

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Figure 1. Upper altitude limit of *Sabatinca chrysargyra* (Micropterigidae). Photo by George Gibbs, with permission.

MICROPTERIGOIDEA

Micropterigidae – Mandibulate Archaic Moths

As flowers rapidly expanded into numerous colors, sizes, and shapes, so did the Lepidoptera (see Powell et al. 1999). But these new flowers fed the adults, not the larvae.

This family is an ancient group, so it is not surprising that there are bryophyte specialists among them. Among these is the rarely collected *Epimartyria* sp. in the moth family Micropterigidae (Loren Russell pers. comm. Jan. 2008). The *Epimartyria* (Figure 11-Figure 16) larvae feed on *Conocephalum conicum* (Figure 2) and other liverworts in mountain springs, as well as on *Pellia neesiana* (Figure 3-Figure 4), the leafy liverworts *Scapania bolanderi* (Figure 5), and the *Calypogeia-Riccardia* association on logs, and once on *Porella navicularis* (Figure 6), an epiphyte.

Figure 2. *Conocephalum conicum*, home and food source for members of *Epimartyria*. Photo by Janice Glime.
Figure 3. *Pellia neesiana* showing the habitat that is home and food for *Epimartyria* larvae. Photo by C. & C. Johnson, with permission.

Figure 4. *Pellia neesiana* with antheridia, home and food for *Epimartyria* larvae. Photo by C. & C. Johnson, with permission.

Figure 5. *Scapania bolanderi*, home and food for species of *Epimartyria*. Photo by Matt Goff, with permission.

In the lab, *Epimartyria* sp. survived feeding on *Riccardia latifrons* (Figure 7) and the leafy liverworts *Calypogeia fissa* (Figure 8), *Jungermannia obovata* (Figure 9), and *J. rubra* (Figure 10) (Loren Russell pers. comm. Jan. 2008). Russell found them to be most abundant in wet seepage zones with abundant *Pellia neesiana* and *Conocephalum conicum*.

Figure 6. *Porella navicularis*, home and food for species of *Epimartyria*. Photo by Tonya Yoder, through Creative Commons.

Figure 7. *Riccardia latifrons*, food for species of *Epimartyria*. Photo by Kristian Peters (Korseby Online), with permission.

Figure 8. *Calypogeia fissa*, food for species of *Epimartyria*. Photo by David T. Holyoak, with permission.
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Figure 9. Jungermannia obovata, food for species of Epimartyria. Photo by Hermann Schachner, through Creative Commons.

Figure 10. Jungermannia rubra with perianth, food for species of Epimartyria. Photo by Ken-ichi Ueda, through Creative Commons.

In northeastern USA and Canada, Epimartyria auricrinella (Figure 11) lives in shaded locations of wet, swampy woods, boggy ditches, and streamsides where leafy liverworts are abundant (Gibbs 2010). One of its food plants is the leafy liverwort Bazzania trilobata (Figure 12-Figure 13) (Davis & Landry 2012). Epimartyria bimaculella (Figure 14), in the northwestern USA and Canada (Gibbs 2010), likewise feeds on leafy liverworts, including Lepidozia (Figure 15) (Davis & Landry 2012). Davis and Landry (2012) successfully reared them in the lab from larvae that were provided with only the leafy liverwort Jungermannia obovata (Figure 9). The larvae have a plastron mechanism (see Chapter 11-10) that permits them to survive short periods of flooding.

Figure 11. Epimartyria auricrinella adult, a species whose larvae live among and eat moist leafy liverworts. Photo by Jim Varg, through Creative Commons.

Figure 12. Bazzania trilobata on a log where Epimartyria auricrinella was found. Photo by D. R. Davis and J.-F. Landry, through Creative Commons.

Figure 13. Bazzania trilobata, home and food of Epimartyria auricrinella. Photo by Michael Lüth, with permission.
In 1989, Gibbs considered the Micropterigidae and Mnesarchaeidae to be similar in their habitats and seasonal requirements, often occurring together in New Zealand. But the Micropterigidae have a distribution around the Pacific rim, whereas the Mnesarchaeidae are endemic to New Zealand. Gibbs also considered the larvae of both families to live in the “periphyton layer” of their bryophytic habitat. In this often moist layer the larvae can find algae, bacteria, and fungi that provide suitable food.

The basal lineage of Lepidoptera – many as members of the Micropterigidae – continued their habit of feeding on cryptogams as larvae (Powell et al. 1999; Hashimoto 2006). Powell and coworkers pointed out that in East Asia there are about 25 endemic species that exclusively eat the thallose liverwort Conocephalum conicum (Figure 2). Nevertheless, the worldwide distribution of this family is patchy (Imada et al. 2011a). Its greatest species diversity is in Japan and Taiwan (greater than 25 spp.), New Caledonia (greater than 20 spp.), New Zealand (20 spp.), and Madagascar (ca 15 spp.) (Gibbs 2010). The Micropterigidae of Japan represent the largest radiation of herbivorous insects known from a single host taxon (Imada et al. 2011a).

Epimartyria pardella (Figure 16) is one such example of the dispersal limitations. This species lives in northern California to northern Oregon, USA (Tuskes & Smith 1984). Its flight is very sporadic, and on those occasions when it does fly, it fails to go more than 21 cm! These moths are day-active as adults and associate closely with liverworts [Conocephalum (Figure 2) and Pellia (Figure 3-Figure 4)]. They frequent canyon walls and stream sides. When they are protected from the wind, they often perch on the upper surfaces of fern fronds, but always near liverworts. When it is windy or dry, they remain among the moist bryophytes such as Hookeria lucens (Figure 17), Atrichum undulatum (Figure 18), and Conocephalum conicum (Figure 2). But unlike the Japanese members of this family, larvae of this species prefer the thallose Pellia for food. Young larvae are active both day and night, but older larvae become night active. They typically do not damage the margin of the thallus. Instead, they feed on the underside of the thallus, removing it but not chewing through the upper surface.
The poor dispersal ability of this group with its limited flying ability has created localized populations where the liverwort is available, creating geographic isolation that has resulted in this high diversity of endemic *Conocephalum* (Figure 2, Figure 19) specialists. In fact, larvae of the modern species in this family feed on either detritus or bryophytes (Kristensen 1999; Powell & Opler 2009).

The Micropterigidae in Japan illustrate the species radiation of this family, and it goes beyond *Epimartyria*. In the Japanese archipelago, 17 species of *Micropterigidae* are present (Hashimoto 2006). These species are typical of moist riverine environments, a habitat suitable for lush growths of bryophytes and ferns. Kobayashi and Ando (1981) demonstrated that both larvae and eggs of *Neomicropteryx nipponensis* (Figure 19-Figure 21) are easily harmed by drought stress. Four [*Palaeomicroides* (Figure 21), *Neomicropteryx*, *Kurokopteryx* (Figure 22), *Issikiomartyria* (Figure 23)] of these five genera feed exclusively on *Conocephalum conicum* (Figure 2) (Yasuda 1962; Imada *et al.* 2011a). This is in habitats where as many as 14 other bryophyte species commonly co-occur. It is interesting that despite their specificity on this species, these larvae do not discriminate (Imada *et al.* 2011b) among the three cryptospecies (Akiyama & Hiraoka 1994; Miwa *et al.* 2009) of *C. conicum*. Only *Paramartyria* (Figure 24) uses several liverworts as food: *Makinoa crispa* (Figure 25), *Heteroscyphus coalitus* (Figure 26), and *Conocephalum conicum*.

Figure 18. *Atrichum undulatum* with capsules, habitat for *Epimartyria pardella*. Photo by Mejdlowiki, through Creative Commons.

Figure 19. *Neomicropteryx nipponensis* larva feeding on *Conocephalum conicum*. Note the darkened necrotic areas where the outer cells have been removed. Photo by Yume Imada, with permission.

Figure 20. *Neomicropteryx nipponensis* adult, a species whose larvae eat *Conocephalum conicum*. Photo by Yume Imada, with permission.

Figure 21. *Palaeomicroides obscurella* adult, a species whose larvae feed exclusively on *Conocephalum conicum*. Photo from BIO Photography Group, Biodiversity Institute, Ontario, through Creative Commons.

Figure 22. *Kurokopteryx dolichocerata* adult, a genus whose larvae feed exclusively on *Conocephalum conicum*. Here the adult is resting on that liverwort. Photo by Yume Imada, with permission.
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Figure 23. *Issikiomartyria* sp. adult, a genus whose larvae feed exclusively on *Conocephalum conicum*. Photo by Yume Imada, through Creative Commons.

Figure 24. *Paramartyria semifasciella* adult, in a genus that feeds on several species of thallose liverworts. Photo by Yume Imada, through Creative Commons.

Figure 25. *Makinoa crispata*, food for larvae of *Paramartyria*. Photo through Creative Commons.

Figure 26. *Heteroscyphus coalitus*, food for larvae of *Paramartyria*. Photo by Jiadong Yang, through Creative Commons.

Figure 27. *Sabatinca quadrijuga* eggs. This species is a leafy liverwort inhabitant and feeder. Photo by George Gibbs, with permission.

Sea of Japan. *Kurokopteryx* (Figure 22) occurs only in south central Japan, facing the northwest Pacific Ocean. Yet their diets are the same, representing the "largest radiation of herbivorous insects that does not accompany any apparent niche differentiation" (Powell *et al*. 1999). These five genera (*Palaeomicroides* (Figure 21), *Neomicropteryx* (Figure 19-Figure 20), *Kurokopteryx* (Figure 22), *Issikiomartyria* (Figure 23), *Paramartyria* (Figure 24)) of larvae feed on the thalli of *Conocephalum conicum* (Figure 2) by grazing the surface, with no apparent differences in feeding mode among these micropterigid species (Imada *et al*. 2011a).

These genera are spatially separated (allopatric) (Imada *et al*. 2011a). Among these, *Issikiomartyria* (Figure 23) occurs only in the snow-rich area facing the Sea of Japan. *Kurokopteryx* (Figure 22) occurs only in south central Japan, facing the northwest Pacific Ocean. Yet their diets are the same, representing the "largest radiation of herbivorous insects that does not accompany any apparent niche differentiation" (Powell *et al*. 1999). These five genera (*Palaeomicroides* (Figure 21), *Neomicropteryx* (Figure 19-Figure 20), *Kurokopteryx* (Figure 22), *Issikiomartyria* (Figure 23), *Paramartyria* (Figure 24)) of larvae feed on the thalli of *Conocephalum conicum* (Figure 2) by grazing the surface, with no apparent differences in feeding mode among these micropterigid species (Imada *et al*. 2011a).

In Japan and New Caledonia, the larvae of the endemic *Sabatinca* live (Harris 2012) and feed on bryophytes (Figure 1) (Yasuda 1962; Holloway 1993). *Sabatinca* larvae have cryptic coloration that is greenish with large setae that help to camouflage them among the liverworts (Tillyard 1922). On Mt. Cargill, N. Z., *Sabatinca quadrijuga* (Figure 27-Figure 28) lives on leafy liverworts as larvae (Harris 2015). Most of the adults of *Sabatinca* are day-active and feed mostly on fern spores, but they also eat club moss (Lycopodiaceae) spores or pollen from sedges and other flowers (Gibbs & Lees 2014). The adult still has an affinity for bryophytes, however. It "hops" around on the mosses on rocks (flying close to the ground), but only when the sun is shining (Harris 2015).
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Figure 28. *Sabatinca quadrijuga* adult, a species that lives among and eats liverworts as larvae and hops around on mosses as an adult. Photo by George Gibbs, with permission.

*Sabatinca caustica* (Figure 29-Figure 31) illustrates the bryophytic adaptations of this genus. The hunched-backed caterpillars (Figure 29) are camouflaged by their pigments (Gibbs & Lees 2014). Like all members of *Sabatinca*, they feed on leafy liverworts and are known as exposed feeders because they feed on the surface.

Figure 29. *Sabatinca caustica* larva, illustrating bryophytic adaptations. Note the hunched back, bryophytic coloring, and projections that resemble bryophyte leaves. Photo by George Gibbs, with permission.

Figure 30. *Sabatinca caustica* adult, a species whose larvae eat leafy liverworts. Photo by George Gibbs, with permission.

Figure 31. Habitat with mosses and liverworts where one can find *Sabatinca caustica*. Photo by George Gibbs, with permission.

Gibbs (2014) described four new species of *Sabatinca* in New Zealand. All 19 of the New Zealand species are confirmed liverwort feeders. The life cycle of this genus is typically annual. Larvae grow throughout the winter and the pupal stage is short. The larvae exhibit cryptic coloration (Figure 32), but the adults instead often have brilliant iridescent colors (Figure 33, Figure 36, Figure 38). Nevertheless, the adult coloration helps to conceal these small moths in the spotty light of their wooded and streamside habitats. *Sabatinca callichora* (Figure 32-Figure 33) and *S. doroxena* (Figure 35-Figure 36), and a number of other *Sabatinca* species, exhibit on the upper forewing (at rest) a black patch with several brilliant white spots in it (Figure 33, Figure 36). Gibbs speculated that these might serve as mimics of one of their main predators, a jumping spider in the *Salticidae* (Figure 34).

Figure 32. *Sabatinca callichora* larva showing adaptations to the bryophyte habitat, shown here on a leafy liverwort. Photo by George Gibbs, with permission.
Figure 33. *Sabatinca calliarcha* adult showing black area with white spots on wings. Photo by George Gibbs, with permission.

Figure 34. *Maratus volans* (*Salticidae*) showing color patterns and black spots (eyes) that seem to be mimicked by some species of *Sabatinca*. Photo by Jurgen Otto, with permission.

Gibbs (2014) was able to name specific larval hosts, mostly leafy liverworts, for a number of the New Zealand *Sabatinca* (Table 1). Larvae of *Sabatinca* on *Plagiochila* not only feed there, but they roll the leaves or otherwise use them to form a cocoon (David Glenny, pers. comm.; Figure 45).

Table 1. Larval hosts for some of the New Zealand members of *Sabatinca*, based on Gibbs (2014).

<table>
<thead>
<tr>
<th>Species</th>
<th>Larval Hosts</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. aurella</em></td>
<td>Figure 37-38 <em>Heteroscyphus normalis</em> possibly <em>Plagiochila intertexta</em></td>
</tr>
<tr>
<td><em>S. bimacula</em></td>
<td>Figure 40 <em>Bazzania involuta</em></td>
</tr>
<tr>
<td><em>S. chalcophanes</em></td>
<td>Figure 41 <em>Hymenophyton flabellatum</em> variety of foliose liverworts</td>
</tr>
<tr>
<td><em>S. doroxena</em></td>
<td>Figure 35-36 <em>Heteroscyphus normalis</em></td>
</tr>
<tr>
<td><em>S. heighwayi</em></td>
<td>Figure 45-47 <em>Plagiochila circumcincta</em></td>
</tr>
<tr>
<td><em>S. weheka</em></td>
<td>Figure 49-50 <em>Plagiochila deltoidea</em></td>
</tr>
</tbody>
</table>

Figure 35. *Sabatinca doroxena* larva, a recently described liverwort feeder from streamsides in New Zealand. Photo by George Gibbs, with permission.

Figure 36. *Sabatinca doroxena* adults copulating, a recently described liverwort dweller from streamsides in New Zealand. Photo by George Gibbs, with permission.
Figure 37. *Sabatinca aurella* larva on a leafy liverwort. Photo by George Gibbs, with permission.

Figure 38. *Sabatinca aurella* adult, a species whose larvae feed on *Heteroscyphus normalis*. Photo by George Gibbs, with permission.

Figure 39. *Heteroscyphus* cf. *normalis*, a leafy liverwort eaten by *Sabatinca aurella* larvae. Photo by Andrew Hodgson, with permission.

Figure 40. *Sabatinca bimacula* larva, a species that lives on *Bazzania involuta*. Photo by George Gibbs, with permission.

Figure 41. *Sabatinca chalcophanes* adult, a liverwort feeder as larvae. Photo by Neville Hudson, through Public Domain.

Figure 42. *Hymenophyton flabellatum*, home and food for *Sabatinca chalcophanes*. Photo by Niels Klazenga, with permission.
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Figure 43. *Sabatinca* habitat where one can find *S. aurantissima* (Figure 44), *S. aurella*, *S. aemula*, *S. chalcophanes*. Photo by George Gibbs, with permission.

Figure 44. *Sabatinca aurantissima* larva, an inhabitant of bryophytes. Photo by George Gibbs, with permission.

Figure 45. Pupa of *Sabatinca heighwayi* showing leaves of *Plagiochila cf. fasciculata*. Photo by George Gibbs, with permission.

Figure 46. Pupa of *Sabatinca heighwayi* removed from its cocoon. Photo by George Gibbs, with permission.

Figure 47. *Sabatinca heighwayi* male adult, a species whose larvae feed on *Plagiochila circumcincta*. Photo by George Gibbs, with permission.

Figure 48. *Sabatinca* habitat with *Plagiochila circumcincta*, host of *S. heighwei*. Photo by George Gibbs, with permission.

Figure 49. *Sabatinca weheka* larva, a species that feeds on *Plagiochila deltoidea*. Photo by George Gibbs, with permission.

Figure 50. *Sabatinca weheka* male adult, a species whose larvae feed on *Plagiochila deltoidea*. Photo by George Gibbs, with permission.
But not all members of the *Micropterigidae* are bryophyte feeders. Some are not able to eat bryophytes and choose other food sources (Lorenz 1961; Luff 1964). Instead, these larvae eat fungi, detritus, and flowering plant green leaves (Kristensen 1998). For example, *Micropterix calthella* (Figure 55) and *M. aruncella* (Figure 56-Figure 57) ate the flowering plant *Stellaria* spp. in the lab and refused both mosses and liverworts (Carter & Dugdale 1982). But Shield (1856) recorded them from mosses and Meyrick (1895) found that both live on wet mosses in the British Isles, claiming that the genus feeds on mosses. Likewise, Chapman (1894) found that they eat mosses. Later, Coutin (2004b) stated that the larvae of *M. calthella* feed on mosses and liverworts. Perhaps they are choosy about the mosses they eat.
Gibbs (1983) noted that in Australia the evolution of the Micropterigidae is paralleled by the evolution of the eastern Australian rainforests. In other locations, particularly in New Caledonia, the developing lineages seem to mirror the development or disappearance of different land masses.

MNESARCHAEOIDEA

Mnesarchaeidae – New Zealand Primitive Moths

When the Micropterigidae emerged, the New Zealand endemic Mnesarchaeidae likewise was becoming established. Mnesarchaea acuta (Figure 58) can occur in large numbers on the damp moss-covered banks of streams in a variety of New Zealand forests and at a wide range of altitudes (Gibbs 1979). But it is the periphyton (algae and Cyanobacteria – Figure 59) layer on the mosses and liverworts that serves as their food. Their fecal matter indicates that they ingest pieces of both live and dead moss leaves, liverwort leaves and rhizoids, fern sporangia, fungal spores and hyphae, and filamentous algae. This is an unusually diverse diet for any lepidopteran. When the females are placed in vials with sufficient periphyton on mosses and liverworts, M. loxoscia (Figure 60) and M. acuta lay their eggs on the bryophytes. The suitable bryophytes live on rotting logs, tree trunks, and soil in the damp portions of the forests.

HEPIALOIDEA

Hepialidae – Ghost Moths

The Hepialidae can be considered indicators of the ancient fauna of New Zealand (Patrick 1988). Their larvae are common in bogs among the mosses. They have poor dispersal ability because the females generally either have short wings or are reluctant to fly. Even with mobile males, reproduction in a distant location is not possible. Grehan (1989) considered the mosses to be among the food sources for the Hepialidae larvae. Grehan suggested that this family was originally fungivorous (feeding on fungi) and that its change to primarily tracheophytes resulted from suppression of mycophagy. But in pastures and grassland species mosses may be important food sources, whereas liverworts seem to be ignored. Among these moss feeders is Korscheltellus gracilis (Figure 61-Figure 63) (Brower 1984). Larvae of this species feed above ground in thick mosses.
Figure 62. *Korscheltellus gracilis* host tree where larvae live under mosses. Photo by John Grehan, with permission.

Figure 63. *Korscheltellus gracilis* adult, a species that emerges from pupae on the forest floor. Photo by Matthew Priebe, with permission for educational purposes.

Larvae of *Korscheltellus gracilis* (Figure 61) typically take two years to mature, following an egg development of 16-19 days at 22°C. Pupation occurs on the forest floor in the second year. These require another month to develop before the adult (Figure 63) emerges. It is the larval stage that is of interest to us. These larvae are *polyphagous*—that is, they eat a variety of foods, including leaf litter, fungi, mosses, and below ground tissues of ferns and seed plants.

*Korscheltellus gracilis* (Figure 61-Figure 63) has an interesting mating behavior that may give insight into other members of the family. Using wind tunnel experiments, Kuenen *et al.* (1994) found that when light intensity was reduced to 11-25 lux after a 16-hour photophase of 450 lux, females initiated wing fanning. Males downwind of them began wing fanning, rapid walking, or both, and flew upwind toward the female soon afterwards. If the hind wings of the females were removed, the fanning activity of the females failed to evoke a male response. Hence, Kuenen and coworkers concluded that the hind wings emit a pheromone that elicits the male's mating behavior.

Figure 64. *Cladoxycanus minos* male adult, a bog inhabitant that lives in and feeds on cushion plants, including mosses. Photo by Landcare Research, Manaaki Whenua, with online permission.

Figure 65. *Sphagnum* habitat of *Heloxycanus patricki*. Photo by Hamish Patrick, with permission.

Figure 66. *Aoraia* (Figure 66-Figure 67) (Grehan 1989), *Oncopera brachyphylla* (Figure 68) (in Australia; Elder 1970), and *Eudalaca rufescens* (in South Africa; Joubert 1975), another chamber may be used as a storage room for cut plant material. For those living in bogs [*Cladoxycanus*...
(Figure 64) and *Heloxycanus* (Figure 74-Figure 75) the *Sphagnum* (Figure 65) surface absorbs radiant heat and larvae spend the daytime up in that warm chamber. These bog dwellers have larval shafts that reach or even penetrate the water surface (Grehan & Patrick 1984). *Cladoxycanus minos* (Figure 64) occurs in water as deep as 300 mm and eats *Sphagnum cristatum* (Figure 72) (Grehan & Patrick 1984). A similar construction is present for *Wiseana umbraculata* (Figure 70-Figure 71) (Dugdale 1994). This permits it to avoid submersion during high water levels; this species is only known from saturated mosses where it is in relatively close contact with the soil surface (Grehan & Patrick 1984).

![Oncopera brachyphylla](image)

Figure 68. *Oncopera brachyphylla* female adult, a species whose larvae excavate tunnels in the sedges (*Oreobolus pectinatus*) of bogs. Photo by John Grehan, with permission.

![Wiseana larva](image)

Figure 69. *Wiseana* larva, a genus that lives among mosses. Photo by Phil Bendle, with permission from John Grehan.

![Aoraia enysii](image)

Figure 66. *Aoraia enysii* female adult, member of a genus that makes side chambers in its tunnels in bogs. Photo by Birgit E. Rhode, Landcare Research, with permission for non-commercial educational use.

![Aoraia sp. tunnel under Oreobolus pectinatus](image)

Figure 67. *Aoraia* sp. tunnel under *Oreobolus pectinatus* in bog showing chambers where fecal pellets are deposited. Modified from Grehan 1989.

![Wiseana umbraculata](image)

Figure 70. *Wiseana umbraculata* female adult; larvae often live among mosses. Photo from Landcare Research, Manaaki Whenua, with online permission.
Figure 71. *Wiseana umbraculata* male adult; larvae often live among mosses. Photo from Landcare Research, Manaaki Whenua, with permission.

Figure 72. *Sphagnum cristatum*, a species consumed by *Cladoxycanus minos* in New Zealand. Photo by Jan-Peter Frahm, with permission.

*Wiseana* (Figure 69-Figure 71) lives among litter and mosses and has a predator in the beetle family *Staphylinidae* (Eyles 1966). This beetle, *Thyreocephalus chloropterus* (Figure 73), attacks the *Wiseana* and sucks out its fluids. Some of the *Wiseana* larvae may be killed to protect the beetle eggs. Both live in a habitat with plant litter and mosses and are often associated with ants.

Figure 73. *Thyreocephalus chloropterus*, a beetle that attacks *Wiseana* larvae to suck out its fluids. Photo by Ken Walker, Living Atlas of Australia, through Creative Commons.

*Heloxycanus patricki* (Figure 74-Figure 75) is a New Zealand ghost moth that feeds on *Sphagnum* (Figure 74-Figure 75) (Hamish 2011). It is an endemic and is in danger of extinction as its habitat has become severely fragmented and further suffers from collection for horticulture. Its adults disappear in even-numbered years, presumably indicating that the larvae require two years to develop.

Figure 74. *Heloxycanus patricki* adult on *Sphagnum*, its larval food source. Photo by Hamish Patrick, with permission.

Figure 75. *Heloxycanus patricki* adult on *Sphagnum*. Photo by Hamish Patrick, with permission.

Many of the bryophyte-dwelling larvae in *Hepialidae* spin a web in which they feed or pupate, or both (Figure 76). The larvae of the borer *Aenetus virescens* (Figure 77-Figure 81) live on trees (Grehan 1983). The larva enters its host by positioning itself axially with its head uppermost. It then places silk threads over itself, fastening them to the bark to form a roughly oval web that covers the larva. The larva is still visible through the cover at this stage. Sometimes the larva does this from within a depression so that the cover is nearly flat with the substrate surface. Once this cover is completed, the larva removes the mosses and lichens growing on the surface and places these particles inside the web. This task completed, the larva begins construction of the feeding tunnel by excavating the bark and wood tissue under the top part of the web. These fragments likewise are placed within the net cover, creating
a cover that completely hides the larva inside. This chamber becomes filled with wood chips, causing the larva to make an inner silk lining to form a bag-like cavity extending from the entrance to the tunnel. Fecal pellets are placed in the lower third of the cover. *Aenetus virescens* larvae (Figure 77, Figure 79) feed primarily on the fruiting bodies of eight species of wood-inhabiting fungi (Grehan 1984).

Figure 76. Insect pupa inside its web, Kyushu, Japan. Photo by Janice Glime

Figure 77. *Aenetus virescens* first instar feeding on fungus. Photo by John Grehan, with permission.

Figure 78. *Aenetus virescens* new tunnel under moss. Photo by John Grehan, with permission.

Figure 79. *Aenetus virescens* tunnel in *Nothofagus*. Photo by John Grehan, with permission.

Figure 80. *Aenetus virescens* litter of frass pellets. Photo by John Grehan, with permission.

Figure 81. *Aenetus virescens* adult emerging. Photo by Nga Manu Images NZ, through Creative Commons.
Aoraia macropis (Figure 82) has been collected from mosses (Dugdale 1994), including those larvae that build shafts in Sphagnum (Figure 64) peat (Grehan 1989). Females of this species are brachypterous (short-winged), but males are able to fly. This arrangement suggests limited dispersal and brachyptery seems to be a common characteristic for bryophyte-dwelling insects. The genus is endemic to New Zealand.

Figure 82. Aoraia macropis male adult, a moss dweller that builds shafts in Sphagnum. Photo by Birgit E. Rhode, Landcare Research, for non-commercial educational use.

Phymatopus hecta (Figure 83) was originally reported as a feeder on dandelion (Taraxacum) (Stainton 1857). But Sterling and Heckford (2005) found the final three larval instars feed on the moss Mnium hornum (Figure 85-Figure 86) at the bases of oak trees. Later, Heckford and Stella Beavan found a larva that had spun its silken web over Mnium hornum in an open woodland (Grehan 2016). The larva lived in a tunnel in the soil, but it fed on the moss. They also succeeded in rearing the third instar larvae to adulthood with only Mnium hornum as a food source. Nevertheless, multiple records indicate that it is also a root feeder.

Figure 83. Phymatopus hecta larva amid mosses and litter in Ashurst Wood, Hampshire, U.K. This species feeds on Mnium hornum in the final larval instars. Photo © Stella Beavan and Bob Heckford, with permission.

Figure 84. Phymatopus hecta adult, a larval moss feeder. Photo by Stanislav Krejčík, through Creative Commons.

Figure 85. Mnium hornum on tree base, home for Phymatopus hecta larvae. Photo by Ján Jaďuď. PERMISSION PENDING.

Figure 86. Mnium hornum, home for Phymatopus hecta larvae. Photo by Tim Waters, through Creative Commons.
Palaeosetidae – Miniature Ghost Moths

Although their small size would suggest that bryophytes could make a suitable home for these ghost moths, few actually are known to live there. Heppner et al. (1995) has collected both males and females of Ogygioses caliginosa (Figure 87) that were congregating on mossy banks of streams where the mosses were kept wet. The larvae in the lab were provided a variety of food plants, but only the mosses appeared to be eaten. Surely there are other bryophyte associates in this family awaiting our discovery.

TINEOIDEA

Psychidae – Bagworm Moths, Case Moths

These moths construct cases or bags as larvae (Figure 88-Figure 89). These larvae are mobile, although they may attach when at rest. The bag is later used for pupation and at that time is attached to its substrate.

Although the case moths usually occur with lichens and algal films, some feed on grass and a few feed on mosses. For example, Dugdale (1987) recommends beating low shrubs and branches covered by bryophytes in order to collect more larvae of Grypotheca (Figure 90). Sapphire McFish (Bryonet 31 March 2016) reports accidentally collecting some of the case moth larvae in Tasmania. These were on mossy buttresses and logs in a wet forest gully. The larvae stuck 2-3 mosses in their cases in about the same proportions as the mosses appeared in the area. Among these was Thuidiopsis sparsa.
Dr. Peter B. McQuillan of the University of Tasmania described a larva that may be a species of *Narycia* (Figure 94-Figure 95). This larva makes an "untidy case" near the ground. This seems to be an advantage in providing camouflage. The larvae include grasses and mosses and other small plants in their diet.

**Tineidae – Fungus Moths**

*Tinea* (Figure 96-Figure 97) is a stone mason caterpillar. The larvae cement together grains of stone, including small fragments of mosses and lichens (Rennie 1857; Zagulyayev 1970). This encasement is carried around much like the cases of the caddisflies.

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**Figure 91.** *Canephora hirsuta* larva in case. This species eats bryophytes. Photo through Creative Commons.

**Figure 92.** *Canephora hirsuta* larva head, the head of a moss eater. Photo by Donald Hobern, through Creative Commons.

**Figure 93.** *Canephora hirsuta* adult, a species with larvae that feed on mosses. Photo by Jeroen Voogd <info@butterflies-moths.com>, with permission.

**Figure 94.** *Narycia duplicella* larva with a case adorned with lichens. Photo by Patrick Clement, with permission.

**Figure 95.** *Narycia duplicella* larva with grey lichens adorning its case, blending with the grey lichens on the substrate. Photo by Jeroen Voogd <info@butterflies-moths.com>, with permission.

**Figure 96.** *Tinea pellionella* larva in case that earned it the name of stone mason. Photo from ©entomart, through Creative Commons.

**Figure 97.** *Tinea pellionella* larva with grey lichens adorning its case, blending with the grey lichens on the substrate. Photo by Jeroen Voogd <info@butterflies-moths.com>, with permission.
Klok and Chown (1997) looked at temperature tolerance in a member of this family. Using *Pringleophaga marioni* (Figure 98), they found that this moth had a tolerance range from -0.6°C to 38.7°C, a range it might encounter on any day in its larval life in the sub-Antarctic Marion Island. These larvae are able to supercool to -5.0°C, with 100% of the caterpillars surviving freezing to -6.5°C. Their high temperature survival, however, was poor at 35°C and above. Larvae of this species have no osmoregulatory ability. Klok and Chown suggest that they are able to survive by living in damp situations.

*Pringleophaga marioni* (Figure 98) is a decomposer (Sinclair et al. 2004). It often nests in old albatross nests (Haupt et al. 2014). Haupt et al. suggested that the moths might select habitats that meet their thermal requirements. They choose newly abandoned nests of the Wandering Albatross (*Diomedea exulans*) more frequently than other habitats. But nests are short-lived, so other resources seem to be important. The researchers looked for possible chemosensory and thermal cues among choices in the laboratory, but they found no significant difference in larval preferences for newly abandoned nest material over old nests, the common mire moss *Sanionia uncinata* (Figure 99-Figure 100), or no choice. Larvae commonly occur in this mire moss species (Burger 1978). Although the larvae preferred lower temperatures (5°C) over higher ones (15°C), the researchers concluded that temperature and chemical cues were not the basis for the choice of substrate materials. Furthermore, the caterpillars apparently do not seek the materials that compose the nests, but rather avoid high temperatures.

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**Figure 97.** *Tinea pellionella* adult; larvae sometimes incorporate bryophytes in their cases. Photo from ©entomart, through Creative Commons.

**Figure 98.** *Pringleophaga marioni* adult, a sub-Antarctic species that tolerates temperatures to -6.5°C as larvae. Note reduced wings that seem to characterize many moss dwellers. Photo by Steven L. Chown, through Creative Commons.

**Figure 99.** *Pringleophaga marioni* (Figure 98) choice of bird nest material vs the moss *Sanionia uncinata* (Figure 100) for their nests. Adapted from Haupt et al. 2014.

**Figure 100.** *Sanionia uncinata* with capsules, nest material for *Pringleophaga marioni*. Photo by David T. Holyoak, with permission.

**GELECHIOIDEA**

**Gelechiidae – Twirler Moths**

This is one of the largest families of *Microlepidoptera* (Powell 1980). They are common in north temperate zones and use mosses and liverworts as their larval food.
However, the family includes leaf and needle miners, gall makers, and scavengers. Of these 2% of the records of food are from mosses (18 records). Fewer than 2% of the larvae have multiple host plant species.

The Gelechiidae are characterized by being concealed while feeding. Some accomplish this by feeding within tracheophyte leaf tissue. The bryophyte feeders seem to accomplish this by hiding under bark or bryophytes, or by creating their own cover (e.g. *Bryotropha umbrosella* – Figure 101) by making silken tubes or tents (Fernández-Triana et al. 2013). Unfortunately, these do not protect them from the parasite *Shireplitis* spp. (Hymenoptera: Braconidae; Figure 102) that uses this caterpillar as a host (Fernández-Triana et al. 2013).

**Figure 101.** *Bryotropha umbrosella* adult, a larval moss dweller that is subject to parasitism by Braconidae. Photo by Janet Graham, through Creative Commons.

**Figure 102.** *Shireplitis bilboi* adult, member of a genus that is parasitic on *Bryotropha umbrosella*. Photo through Creative Commons.

Kullberg and coworkers (2013) were able to report that *Bryotropha galbanella* (Figure 103) lives on mosses. In Europe, this species lives on the mosses *Dicranum scoparium* (Figure 104) and *Homalothecium lutescens* (Figure 105) as its food source (Rutten & Karsholt 2004). In 1856, Shield reported *Bryotropha desertella* (Figure 106-Figure 107) and *B. umbrosella* (= *B. mundella*; Figure 101) from among bryophytes on sandhills in Europe.

**Figure 103.** *Bryotropha galbanella* adult, a species whose larvae live among mosses and eat them. Photo by Roy Leverton, with permission.

**Figure 104.** *Dicranum scoparium*, home and food for *Bryotropha galbanella*. Photo by Dale Vitt, with permission.

**Figure 105.** *Homalothecium lutescens*, home and food for *Bryotropha galbanella*. Photo by Michael Lüth, with permission.

Gelechiidae in the Holarctic (Rutten & Karsholt 2004). The genus *Bryotropha* is among the relatively few Lepidoptera known to feed on bryophytes, especially mosses (Heckford & Sterling 2002, 2003; Rutten & Karsholt 2004).

Kullberg et al. (2013) lamented that we know little about the role of mosses for the many Lepidoptera species living in the Arctic tundra of European Russia. Yet *Bryotropha* (e.g. Figure 101-Figure 103; originally considered part of Gelechia) is one of the most common
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In the Netherlands, one can often collect large numbers of adults of these drab *Bryotropha* moths (e.g. Figure 108, Figure 111-Figure 113, Figure 115-Figure 116) (Rutten 1999). Most of them occur in open heaths and dunes, some in forests or urban areas. But all are thought to feed on mosses as larvae. *Bryotropha basaltinella* (Figure 108) feeds on mosses, especially *Syntrichia ruralis* (Figure 109), on walls and thatched roofs (Britain – Meyrick 1895; Netherlands – Rutten 1999).

*Bryotropha affinis* (Figure 110-Figure 111), *B. senectella* (Figure 112-Figure 113), and *B. domestica* (Figure 114-Figure 115) larvae feed on mosses on walls, but they make a silken gallery in which to live and move about, affording them cover and camouflage (Meyrick 1928; Rutten 1999). But for the Netherlands, Rutten was only able to list "possible" food plants for *B. similis* (Figure 116): *Hypnum cupressiforme* (Figure 117), *Brachythecium rutabulum* (Figure 118), *Syntrichia ruralis* (Figure 109), *S. montana* (Figure 119), *Grimmia pulvinata* (Figure 120), *Rosulabryum capillare* (Figure 121), and *Bryum caespititium* (Figure 122) (see also Stainton 1871). Only *Bryotropha basaltinella* has a preference for urban areas, the location of most of the walls covered with mosses. Rutten reminds us that it is easier to locate the larvae on wall mosses and that in non-urban areas the adults are abundant in dry areas with no mosses.
Figure 111. *Bryotropha affinis* adult, a moss dweller in its larval state. Photo by Patrick Clement, with permission.

Figure 112. *Bryotropha senectella* adult, gray form, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Patrick Clement, with permission.

Figure 113. *Bryotropha senectella* adult, brown form, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Patrick Clement, with permission.

Figure 114. *Bryotropha domestica* larva, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo through Public Domain.

Figure 115. *Bryotropha domestica* adult, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Patrick Clement, with permission.

Figure 116. *Bryotropha similis* adult, a species whose larvae make their silken feeding tunnels on mosses on walls. Photo by Janet Graham, through Creative Commons.

Figure 117. *Hypnum cupressiforme*, home and food for *Bryotropha similis*. Photo by J. C. Schou, Biopix, with permission.
Figure 118. *Brachythecium rutabulum* with capsules, home and food for *Bryotropha similis*. Photo by J. C. Schou <www.biopix.com>, with permission.

Figure 119. *Syntrichia montana*, home and food for *Bryotropha similis*. Photo by Michael Lüth, with permission.

Figure 120. *Grimmia pulvinata* on wall, home and food for *Bryotropha similis*. Photo by J. C. Schou, Biopix, through Creative Commons.

Figure 121. *Rosulabryum capillare* with capsules, home and food for *Bryotropha similis*. Photo through Creative Commons.

Figure 122. *Bryum caespiticium*, home and food for *Bryotropha similis*, with capsules. Photo by Michael Lüth, with permission.

In Europe, the silken feeding tubes of *Bryotropha boreella* (Figure 123-Figure 125) occur on species such as *Hypnum jutlandicum* (Figure 126), *Rhytidiadelphus squarrosus* (Figure 127), and *Aulacomnium palustre* (Figure 128) (Palmer 2016). All of these species are also suitable for breeding *B. boreella*.

Figure 123. *Bryotropha boreella* larva in its silken feeding tube on *Rhytidiadelphus squarrosus*. Photo by R. J. Heckford, with permission.
Figure 124. *Bryotropha boreella* pupa among mosses. Photo by R. J. Heckford, with permission.

Figure 125. *Bryotropha boreella* adult on *Sphagnum*. Photo by Stephen Palmer, with permission.

Figure 126. *Hypnum jutlandicum* with capsules, a moss where *Bryotropha boreella* builds silken feeding tubes. Photo by J. C. Schou, with permission.

Figure 127. *Rhytidiadelphus squarrosus*, a moss where *Bryotropha boreella* builds silken feeding tubes. Photo by Michael Lüth, with permission.

Figure 128. *Aulacomnium palustre*, a moss where *Bryotropha boreella* builds silken feeding tubes. Photo by Kristian Peters, with permission.

*Bryotropha terrella* (Figure 129-Figure 130) in the British Isles feeds on the moss *Rhytidiadelphus squarrosus* (Figure 127) and the grass *Agrostis capillaris* (Palmer & Palmer 2016b). But elsewhere in Europe it is also known from the mosses *Syntrichia ruralis* (=*S. ruraliformis*; Figure 109), *Hypnum jutlandicum* (Figure 126), and *Calliergonella cuspidata* (Figure 131). Early instars construct a tough, opaque silken tube low among moss or grass, the upper end reaching near the moss surface. The tube is covered with chewed moss fragments and bits of grass. But in the final instar, the larva makes a flimsy, transparent gallery with no attached plant material.
Larvae of *Bryotropha politella* (Figure 132), also from the British Isles, feeds on *Rhytidiadelphus squarrosus* (Figure 127) (Palmer & Palmer 2016a). But these larvae also can occur under the moss *Schistidium* (Figure 133), although its food relationship to that species is not known (Heckford & Sterling 2003).

In the USA and Canada, the genus *Bryotropha* is less common. *Bryotropha gemella* (Figure 134) sometimes occurs on mosses (Rutten & Karsholt 2004). The bryophage *Bryotropha galbanelia* is also known from Alaska.

Figure 129. *Bryotropha terrella* larva, a species that includes mosses in its feeding tube until its last instar, shown here on *Rhytidiadelphus squarrosus*. Photo by R. J. Heckford, with permission.

Figure 130. *Bryotropha terrella* adult, a species whose larvae live among mosses or at the base of grasses. Photo by Steve Palmer, with permission.

Figure 131. *Calliergonella cuspidata*, larval home of *Bryotropha terrella*. Photo by Michael Becker, through Creative Commons.

Figure 132. *Bryotropha politella* larva on moss. Photo © Bob Heckford, with permission.

Figure 133. *Schistidium apocarpum* with capsules, a moss genus that sometimes provides cover for *Bryotropha politella* larvae. Photo by Hermann Schachner, through Creative Commons.

Figure 134. *Bryotropha gemella* adult, a North American species that sometimes lives among mosses as larvae. Photo by Jeremy deWaard, through Creative Commons.
In Russia, Bidzilya and Li (2010) reported that *Agnippe echinuloides* (Figure 135) lives in moss bogs.

![Agnippe echinuloides adult, a bog species in Russia. Photo by Marko Mutanen, through Creative Commons.](image1)

**Figure 135.** *Agnippe echinuloides* adult, a bog species in Russia. Photo by Marko Mutanen, through Creative Commons.

*Monochroa tenebrella* (Figure 136) lives among mosses in Europe (Shield 1856). *Pseudotelphusa scalella* (Figure 137) larvae feed on mosses, lichens, and *Quercus robur* in Europe (Wikipedia 2015b).

Hoare (2011) found a new species of *Kiwaia* in northern New Zealand. Two specimens were found on the dominant moss *Campylopus introflexus* (Figure 138). Laboratory experiments verified that these larvae could grow to adulthood when only this moss was available as food. On the other hand, *K. jeanae* live on *Raoulia* (Asteraceae; Figure 139-Figure 140) mats, cushions that somewhat resemble a cushion of *Campylopus introflexus*, suggesting that the growth form may be important for moisture conservation.

![Monochroa tenebrella adult, a species whose larvae live among mosses. Photo by Patrick Clement, Gelechiid Recording Scheme, with permission.](image2)

**Figure 136.** *Monochroa tenebrella* adult, a species whose larvae live among mosses. Photo by Patrick Clement, Gelechiid Recording Scheme, with permission.

![Pseudotelphusa scalella adult, a species whose larvae live among mosses. Photo by Donald Hobern, through Creative Commons.](image3)

**Figure 137.** *Pseudotelphusa scalella* adult, a species whose larvae live among mosses. Photo by Donald Hobern, through Creative Commons.

![Campylopus introflexus, probably home for a species of *Kiwaia*. Photo by J. C. Schou, through Creative Commons.](image4)

**Figure 138.** *Campylopus introflexus*, probably home for a species of *Kiwaia*. Photo by J. C. Schou, through Creative Commons.

![Raoulia sp. in full flower, home for *Kiwaia jeanae*. Photo by Nicola Tilley, through Creative Commons.](image5)

**Figure 139.** *Raoulia* sp. in full flower, home for *Kiwaia jeanae*. Photo by Nicola Tilley, through Creative Commons.
Figure 140. *Raoulia* sp. cushion with a few flowers, home for *Kiwaia jeanae*. The cushion suggests a similarity to a moss cushion. Photo from the University of Basel, through Creative Commons.

But food is not the only use this family makes of mosses. The pupal stage of *Teleiodes luculella* (Figure 141-Figure 143) in the Maltese Islands overwinters (Patocka 1987). Sorhagen (1996) found that this stage can occur under mosses or bark (Zerafa 2009).

Figure 141. *Teleiodes luculella* larva, a species that overwinters as pupae under mosses on bark. Photo © Bob Heckford, with permission.

Figure 142. *Teleiodes luculella* adult, a species that overwinters as pupae under mosses and bark. Photo by Peter Clement, with permission.

Figure 143. *Teleiodes luculella* adult, a species that overwinters as pupae under mosses and bark. Photo by Trevor & Dily's Pendleton <www.eakringbirds.com>, with permission.

**Oecophoridae – Concealer Moths**

At least some of the *Oecophoridae* (concealer moths) prefer mossy habitats (Coutin 2004a). The larva of the rare *Aplota palpella* (Figure 144-Figure 145) lives among mosses on tree trunks; this species was recorded in England by Phil Sterling and Derek Hallett in Dorsett County for the first time since the 19th century! (Butterfly Conservation 2001). *Crassa tinctella* (Figure 146) develops from September to May among the arboreal plant bodies of mosses and lichens, which also serve as its food (Coutin 2004b).

Figure 144. *Aplota palpella* adult, a species whose larvae live among mosses on tree trunks. Photo by Peter Huemer, through Creative Commons.

Figure 145. *Aplota palpella* adult, a species whose larvae live among mosses on tree trunks. Photo by Graham Wenman, with permission.
appreciate help from Steve Palmer and John Grehan in getting me permission for some of the images. Bob Heckford sent me many images of larvae and George Gibbs provided many images and several references.

**Literature Cited**


**Summary**

The Microlepidae include the Micropterigidae and the *Mnesarchaeidae*, but it is really a group of small Lepidoptera without close phylogenetic ties. The Micropterigidae is a primitive family that specializes on liverworts, although some (e.g. *Epimartyria pardella*) eat mosses. The *Mnesarchaeidae* seem to prefer the periphyton living on the moss leaves and stems. The *Hepialidae* seem to ignore liverworts and feed mostly on mosses, but they are less likely to be specialists. Some include both bryophytes and tracheophytes or fungi in their diets. Bryophyte feeders seem to prefer bags. *Heloxycanus* prefers cushion plants – mosses or otherwise. Many of the bryophyte dwellers spin a web on the bryophytes for feeding or pupation.

In the Palaeosetidae, only one species is known as a moss dweller and moss feeder. The *Psychidae* construct "bags" and cases that sometimes include bryophytes. The *Tineidae* make stone cases and these may include small moss fragments. The Gelechiidae hide, while feeding in such places as interiors of tracheophyte leaves, under bark or bryophytes, or in silken tubes of their own making, and some eat mosses. In the Oecophoridae, mosses are eaten by at least a few members, typically epiphytes on trees.

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Figure 146. *Crassa tinctoria* adult, a species whose larvae develop among epiphytic bryophytes and lichens and use them for food. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.


