CHAPTER 12-14
TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA: TORTRICOIDEA – PAPILIONOIDEA

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Figure 1. Larva of **Lepidoptera (Crambidae?)** on the moss ***Syntrichia***. Photo courtesy of Wynne Miles.

TORTRICOIDEA

Tortricidae – Tortrix Moths, Leaf-roller Moths

This family has larvae that live among bryophytes on tree trunks. A male ***Pammene albuginana*** (Figure 2) was reared from mosses collected from decaying beechwood in Ireland (Bond & O'Connor 2012). Buchanan White (1971) reported ***Eana penziana*** (Figure 3) from among mosses near Perth, Australia, where it spins its feeding web (Buchanan White 1971). It is also known from Europe and the Near East where it apparently feeds on tracheophyte roots (Wall 2016).

Figure 2. ***Pammene albuginana*** adult, a species that can survive on mosses in its larval stage. Photo by Patrick Clement, with permission.

Figure 3. ***Eana penziana*** adult. Larvae of this species spin feeding webs on mosses in Australia. Photo by Kurt Kulac, through Creative Commons.

Another sometimes bryophyte user is ***Cnephasia pasiuana*** (Figure 4) – a cereal leafroller in Europe. The young, 1 mm long larvae of this species crawl about on the bark for about 2 days, then hide in bark crevices or among mosses (Ulenberg 2015). They then weave a small white cocoon (**hibernaculum**). They spend the summer there and continue there into a winter dormancy.

Figure 4. ***Cnephasia pasiuana*** adult, a species whose larvae hide in bark crevices and among mosses. Photo by James K. Lindsey, with permission.

Celypha aurofasciana (Figure 5) lives in galleries on trunk-dwelling mosses and liverworts, but is also suspected of eating rotting wood in the UK (Meyrick 1895; Cryer 2016).

Figure 5. ***Celypha aurofasciana*** adult; larvae make galleries on mosses and liverworts on tree trunks. Photo by Phil Boggis, with permission.

Mosses may contribute to providing suitable breeding grounds for ***Merophylas*** sp., in Danseys Pass, New Zealand (Patrick 1982). These moths fly from March to May, but the females have short wings. Two females were found on mosses in wet locations, suggesting that the mosses may be suitable egg-laying sites, or that both the moths and bryophytes like the same habitats.

PYRALOIDEA

Crambidae – Grass Moth; Sod Worms

Members of this family are often included in the **Pyralidae**. I have separated them here because the crambids seem to have a relationship with bryophytes that is seldom seen in the remaining **Pyralidae**.

Members of this family construct silken tunnels on their food plants (grasses and mosses) and reside there in relative safety as they feed (Shield 1856). The subfamily **Scopariinae** is listed in The Peterson Field Guide to Moths of Northeastern North America (Beadle & Leckie 2012) as the moss-eating Crambidae. These include ***Scoparia*** and ***Eudonia***. Munroe (1972) has found species of ***Eudonia*** (*e.g.* Figure 8-Figure 12), ***Scoparia*** (*e.g.* Figure 25-Figure 28), and ***Cosipara*** (Figure 6) adults among the mosses in forests of Vancouver, Canada.

Figure 6. ***Cosipara*** adult, a genus whose adults frequent forest mosses in Vancouver, Canada. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

I was introduced to this family when Will Haines (pers. comm. 17 February 2012) sent me a picture of ***Eudonia*** (Figure 7) from Hawaii. Over 60 species of this genus occur in Hawaii, many of which feed on mosses. This one came along with some mossy rocks that Haines collected for his terrarium. Loren Russell (pers. comm.) likewise suggested that this genus feeds on mosses in the forests of Vancouver. This suggestions is based on reports of the genus in the area (Munroe 1972) and Russell's own observations of adults in the genus in mossy habitats there.

Figure 7. ***Eudonia*** sp. caterpillar eating moss in Hawaii. Photo courtesy of Will Haines, with permission.

Eudonia meristis (Figure 8), an endemic in Hawaii, feeds on mosses (Wikipedia 2015a). In Europe, northwest Africa, and Asia, larvae such as ***Eudonia lacustrata*** (Figure 9-Figure 10) feed on mosses, usually on walls or tree trunks (Doremi 2016b). In eastern North America, ***Eudonia strigalis*** (Figure 11) larvae are moss eaters (Beadle & Leckie 2012).

Figure 8. ***Eudonia meristis*** adult, a Hawaiian species whose larvae feed on mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 9. ***Eudonia lacustrata*** larva on moss, where it feeds on walls and trees. Photo © Bob Heckford, with permission.

Figure 10. ***Eudonia lacustrata*** adult, a species whose larvae feed on mosses. Photo by James K. Lindsey, with permission.

Figure 11. ***Eudonia strigalis*** adult, a moth species whose larvae feed on mosses in eastern North America. Photo by Elizabeth, through Creative Commons.

Hoare (2011) suggested that ***Eudonia steropaea*** (Figure 12) feeds on the moss ***Campylopus*** (Figure 13) in New Zealand. To these ***Eudonia*** species, Patrick *et al.* (2011) added larvae of ***Eudonia aspidota*** (Figure 14), ***E. dinodes*** (Figure 15), and ***E. minualis*** (Figure 16) as having moss hosts in New Zealand; ***Eudonia philerga*** (Figure 17) lives in and presumably eats moss on wood. These researchers even added a new species of ***Eudonia*** feeding on mosses on coastal rocks.

Figure 12. ***Eudonia steropaea*** adult, a species whose larvae most likely feed on the moss ***Campylopus***. Photo by Donald Hobern, through Creative Commons.

Figure 13. ***Campylopus introflexus***, home and likely food for ***Eudonia steropaea***. Photo by J. C. Schou, through Creative Commons.

Figure 14. ***Eudonia aspidota*** adult, a species whose larvae live on mosses in New Zealand. Photo by Jon Sullivan, through Creative Commons.

Figure 15. ***Eudonia dinodes*** adult, a species whose larvae feed on mosses in New Zealand. Photo by Steve Kerr, through Creative Commons.

Figure 16. ***Eudonia minualis*** adult, a species that lives among and eats mosses in New Zealand. Photo by Phil Bendle, through Creative Commons.

Figure 17. ***Eudonia philerga*** adult, a species whose larvae eat mosses on logs in New Zealand. Photo by Donald Hobern, through Creative Commons.

Shield (1856) described ***Eudonia murana*** (Figure 18-Figure 19) as a species that occupies mosses on walls in the British Isles, spinning their webs among these plants.

Figure 18. ***Eudonia murana*** larva on moss. Photo © Bob Heckford, with permission.

Figure 19. ***Eudonia murana*** adult, a species whose larvae live among mosses on walls in the British Isles. Photo by Chris Johnson, with permission.

Heckford (2009) found one larva of ***Eudonia pallida*** (Figure 20-Figure 22) on the moss ***Calliergonella cuspidata*** (Figure 23) in Cornwall, England. It had spun a small silken ball covered in **frass** (insect feces). In captivity, the larva constructed a silken gallery along the moss stems and was reluctant to leave it. Wegner and Kayser (2006) reported four larvae of the species with similar silken tunnels on the moss ***Pleurozium schreberi*** (Figure 24). These were enclosed in a strong cocoon made of moss fragments; their frass was usually attached. These larvae laid eggs on the mosses in the lab.

Figure 20. ***Eudonia pallida*** early instar larva on moss. Photo by Heckford, with permission.

Figure 21. ***Eudonia pallida*** last instar larva on moss. Photo by Bob Heckford, with permission.

Figure 22. ***Eudonia pallida*** larva in cocoon on moss. Photo by Bob Heckford, with permission.

Figure 23. ***Calliergonella cuspidata***, home for ***Eudonia pallida*** larvae. Photo by David T. Holyoak, with permission.

Figure 24. ***Pleurozium schreberi***, home for ***Eudonia pallida*** larvae. Photo by Malcolm Storey, Discover Life, through Creative Commons.

Included among the moss eaters in eastern North America are larvae of ***Scoparia biplagialis*** (Figure 25) and ***S. basalis*** (Figure 26) (Beadle & Leckie 2012).

Figure 25. ***Scoparia biplagialis*** adult, a species of larval moss eaters in eastern North America. Photo by Andy Reago and Chrissy McClarren, through Creative Commons.

Figure 26. ***Scoparia basalis*** adult, a species whose larvae eat mosses in eastern North America. Photo by Andy Reago and Chrissy McClarren, through Creative Commons.

Stainton (1871) likewise considered ***Scoparia*** larvae to be moss eaters, citing a number of species that live among mosses in Europe. Larvae of ***Scoparia basistrigalis*** (Figure 27) feed on moss (Heckford & Sterling 2005). Heckford (2011) made it clear that not all members of ***Scoparia*** are moss eaters. Rather, based on experiments by Thurnall (1907, 1908) we know that at least ***S. pyralella*** (= *S. dubitalis*; Figure 28) feeds on roots of ***Rumex acetosella*** (Figure 29), and possibly other roots.

Figure 27. ***Scoparia basistrigalis*** adult, a moth whose larvae are parasitized by **Braconidae** and that feeds on mosses. Photo by J. C. Schou through Biopix.com, with permission.

Figure 28. ***Scoparia pyralella*** adult, a species of ***Scoparia*** whose larvae do not feed on mosses. Photo by Hectonichus, through Creative Commons.

Figure 29. ***Rumex acetosella***, host for ***Scoparia pyralella*** larvae in Europe. Photo by Forest and Kim Starr, through Creative Commons.

Paroplitis wesmaeli is a European species of **Braconidae**, a parasitic wasp that has larval **Lepidoptera** as hosts (Yu *et al*. 2012). Two of the **Lepidoptera** host larvae, ***Scoparia basistrigalis*** (**Crambidae**; Figure 27) and ***Bryotropha umbrosella*** (**Gelechiidae**; see Figure 30), feed on mosses (Heckford & Sterling 2005; Hantmoth 2012), the latter while living in a silken tube.

Figure 30. ***Bryotropha boreella*** larva on moss ***Rhytidiadelphus squarrosus***. Photo © Bob Heckford, with permission.

In New Zealand, ***Scoparia minusculalis*** (Figure 31) uses mosses as host plants (Patrick *et al*. 2011). But mosses are not the only food for the Crambidae. Cowley (1988) found that in Waikato hill country (New Zealand) the **Scopariinae** larvae were abundant in mossy regions but consumed most of the pasture grasses. When they laid their eggs, they chose both grasses and moss stems, laying to depths of 10 mm just below the ground level. The larvae that hatched constructed silk **hibernacula** (cocoons). To these they attached fine soil particles and mosses. If mosses were prolific, the larvae constructed their retreats at the bases of moss plants. The large larvae cut whole blades of grass or stems of mosses and dragged them into their burrows for food. These mosses and grasses were clipped near the burrow so that eventually the burrows were surrounded by an area that was entirely clipped. This clearing resulted in weed invasion, hence affecting the vegetation. Cowley found that all the Waikato hill country species of the **Scopariinae** were able to survive on mosses alone in the lab.

Figure 31. ***Scoparia minusculalis*** adult with epiphylls on a leaf. Photo by Maurice, through Creative Commons.

Heckford (2009) provides us with a rare view of the details of moss use by the **Lepidoptera**. When ***Scoparia ambigualis*** (Figure 32-Figure 33) larvae were reared in the lab with only the moss ***Polytrichum commune*** (Figure 34) for food and home, these first instar larvae spun fine silken strands in the leaf axils. Heckford interpreted these silken nets as cushions because the larvae curled up on them when they were not feeding. These are not very hairy larvae, but nevertheless, Heckford suggested that this net cushion may permit the larvae to get support for their bodies without crushing their hairs.

Figure 32. ***Scoparia ambigualis*** larva on moss. Note the spun cushion under it and the frass around it. Photo © Bob Heckford, with permission.

Figure 33. ***Scoparia ambigualis*** adult, a species whose larvae spin "cushions" in the leaf axils of ***Polytrichum commune***. Photo by James K. Lindsey, with permission.

Figure 34. ***Polytrichum commune***, home and food for ***Scoparia ambigualis*** larvae. Photo by Michael Lüth, with permission.

These ***Scoparia ambigualis*** (Figure 32-Figure 33) larvae ate only moss leaves in this lab observation (Heckford 2009). Their feces (**frass**) were pale greenish or yellowish for young larvae. In later instars these became reddish brown. Then Heckford added the mosses ***Rhytidiadelphus loreus*** (Figure 35) and ***Dicranum scoparium*** (Figure 36), as well as fragments of fern fronds of ***Pteridium aquilinum*** (Figure 37), to the choices for the larvae. Larvae occur on all three of these species in Devon, England. The larvae fed on all the mosses, but none ate the fern fragments.

Figure 35. ***Rhytidiadelphus squarrosus***, a food choice of ***Scoparia ambigualis*** larvae. Photo by Michael Lüth, with permission.

Figure 36. ***Dicranum scoparium***, one of the food choices of ***Scoparia ambigualis*** larvae. Photo by Michael Lüth, with permission.

Figure 37. ***Pteridium aquilinum***, a food choice that was refused by ***Scoparia ambigualis*** larvae. Photo by Sanja, through Creative Commons.

Patrick *et al*. (2011) reports ***Gadira acerella*** (Figure 38) and ***Glaucocharis elaina*** (Figure 39) in moss on rocks in New Zealand, whereas ***Helastia corcularia*** (**Geometridae**; Figure 40-Figure 41) lives on moss and herbs there – an unusual non-specialist strategy. Gaskin (1971) also reported ***Glaucocharis elaina*** on mosses, including ***Funaria*** (Figure 42). Hudson (1928) reared ***G. microdora*** (Figure 43) and ***G. metallifera*** (Figure 44-Figure 45) on bryophytes.

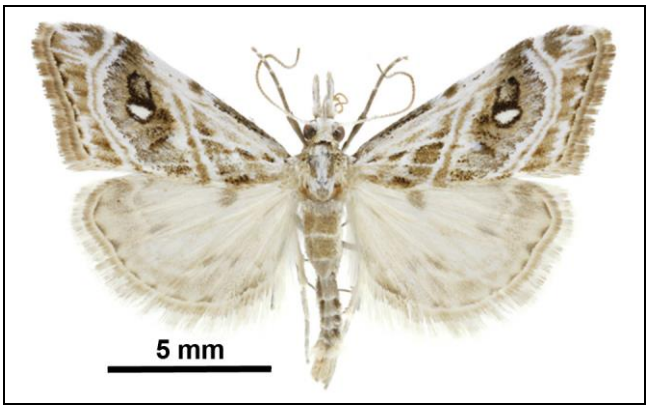

Figure 38. ***Gadira acerella*** adult. Larvae of this species live among mosses on rocks in New Zealand. Photo from Landcare Research, Manaaki Whenua, with online permission.

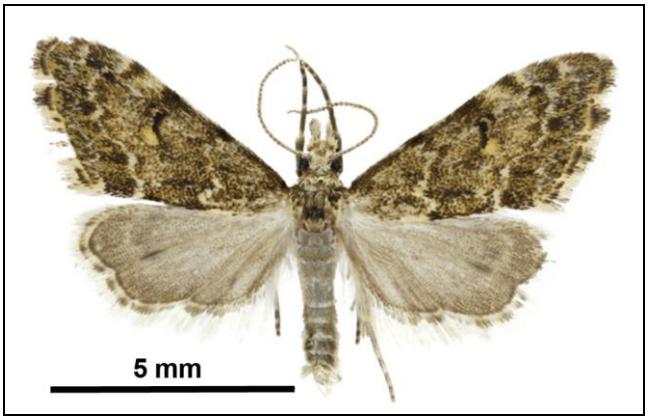

Figure 39. ***Glaucocharis elaina*** adult. Larvae of this species live among mosses on rocks in New Zealand. Photo from Landcare Research, Manaaki Whenua, with online permission.

Figure 40. ***Helastia corcularia*** female adult, a species whose larvae eat both mosses and herbs. Photo by Phil Bendle, with permission through John Grehan.

Figure 41. ***Helastia corcularia*** male adult, a species whose larvae eat both mosses and herbs. Photo by Phil Bendle, with permission through John Grehan.

Figure 42. ***Funaria hygrometrica*** leaves, food for larvae of ***Helastia corcularia***. Photo through Creative Commons.

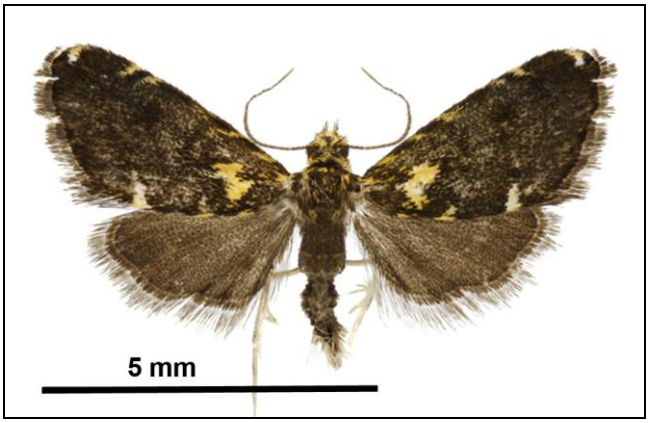

Figure 43. ***Glaucocharis microdora*** adult male, a species that has been reared on bryophytes. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

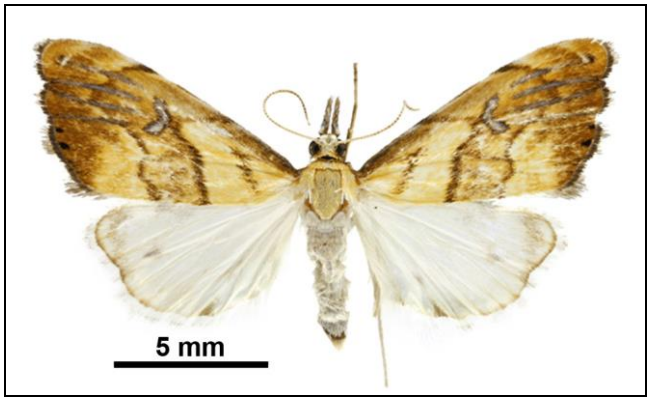

Figure 44. ***Glaucocharis metallifera*** adult female, a species that has been reared on bryophytes. Photo from Landcare Research, NZ, with permission for non-commercial educational use.

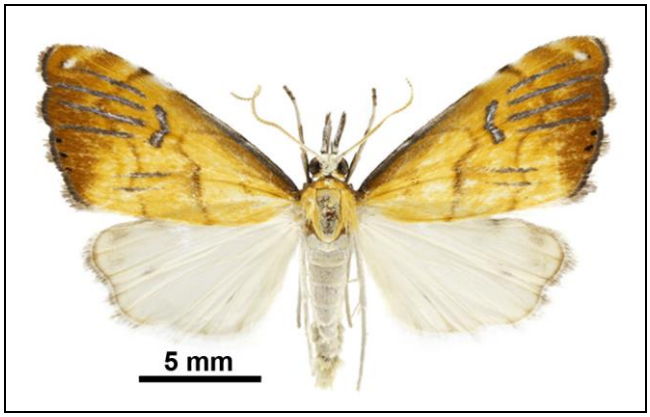

Figure 45. ***Glaucocharis metallifera*** adult male, a species that has been reared on bryophytes. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

Beever and Dugdale (1994) observed severe damage to a colony of the moss ***Dawsonia superba*** (Figure 46) on a stream bank on the southern slopes of Mt Ruapehu, North Island, NZ. This damage was later determined to be the work of the moth larva ***Glaucocharis epiphaea*** (Figure 47). Its feeding resulted in chewing off terminal portions of many leaves. They left the shoots with heavy encrustations of refuge tunnels made with silk, leaf fragments, and frass from the larvae. Leaves were severely chewed, with only 1-5 mm of green lamina remaining and the shoot apex completely destroyed. Beever (Beever & Dugdale 1994) also reared ***G. bipunctella*** (Figure 48) on liverwort cushions from a forest remnant.

Figure 46. ***Dawsonia superba***, home for larvae of ***Glaucocharis epiphaea*** (Figure 47). Photo by Phil Bendle, with permission from John Grehan.

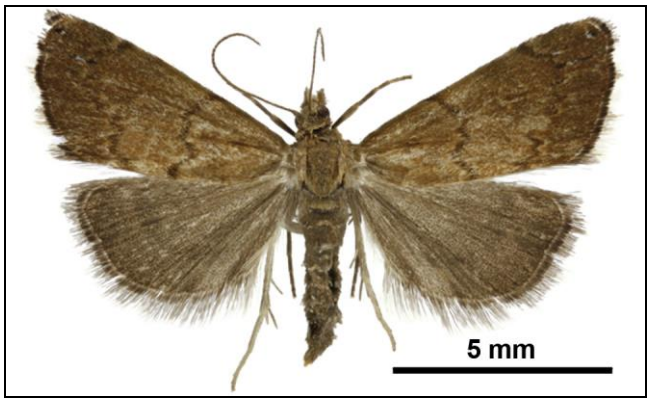

Figure 47. ***Glaucocharis epiphaea*** adult female, a species whose larvae consume ***Dawsonia superba*** in New Zealand. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

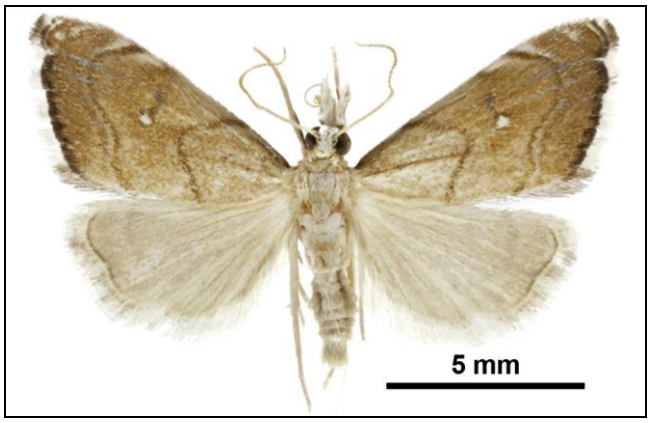

Figure 48. ***Glaucocharis bipunctella*** adult male. Larvae of this species develop successfully on liverworts. Photo from Landcare Research, NZ, with online permission for non-commercial educational use.

Beever and Dugdale (1994) followed these observations by collecting larvae of ***Glaucocharis epiphaea*** (Figure 47) in September and rearing them to adults on shoots of ***Polytrichadelphus magellanicus*** (Figure 49). ***Glaucocharis epiphaea*** is an endemic that lives in the montane rainforests and alpine seepage areas in New Zealand.

Figure 49. ***Polytrichadelpus magellanicus***, food for ***Glaucocharis epiphaea***, with capsules. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Members of the **Acentropinae** make cases or tunnels (Yen 2016). Many are aquatic and feed on aquatic plants, including mosses. However terrestrial larvae live in portable cases or make tunnels under mosses or lichens. The pupa of the ***Paracymoriza nigra*** (Figure 50) group rests in a chamber-like cocoon under mosses. Larvae of ***Nymphicula morimotoi*** (Figure 51) in the Philippines occur along streams on stones and rocks with rich growths of liverworts in the **Jungermanniaceae** (Yoshiyasu 1997). Females of ***Nymphicula morimotoi*** in the laboratory laid eggs one by one between the leaves of the liverwort. The hatchlings spin fine soil particles around themselves to construct small cases.

Figure 50. ***Paracymoriza nigra*** adult, a species that pupates in a cocoon under mosses. Photo through Creative Commons.

Figure 51. ***Nymphicula queenslandica*** adult. ***Nymphicula morimotoi*** larvae in the Philippines live among liverworts in the **Jungermanniaceae** on rocks along streams. Photo from Photography Group, BIO-CSIRO, through Creative Commons.

In Australia, ***Pyrausta cingulata*** (syn=***Ennychia cingulalis***; Figure 52-Figure 53) lives among mosses and spins its web in them (Buchanan White 1971). This behavior was known more than a century ago in Europe, where its retreat is among mosses and dead leaves (Heyden 1861). It can be located by the large heaps of frass nearby.

Figure 52. ***Pyrausta cingulata*** larva, a species that lives among mosses and spins its web there. Photo by Bob Heckford, with permission.

Figure 53. ***Pyrausta cingulata*** adult, a species that lives among mosses and spins its web there. Photo by Tiroler Landesmuseen, through Creative Commons.

Crambus tristellus (see Figure 54) occurs in damp locations along ditches where it makes silken galleries on mosses (Shield 1856). Other former members of ***Crambus*** (Figure 54) that dwell among mosses have been reclassified into a variety of genera. Buckler (1901) reported that members of ***Crambus*** feed among stems and roots of grasses or on moss (Stainton 1852), but these bryophages may now belong to other genera.

Figure 54. ***Crambus pascuella*** male adult. ***Crambus tristellus*** makes silken galleries on mosses in damp locations. Photo by Jérôme Albre, with permission.

Catoptria falsella (syn=*Crambus falsellus*; Figure 55) is a wall dweller (Doremi 2016a). The larva builds a silk tube that helps to hide it while it is feeding, typically on mosses, and especially on the moss ***Tortula muralis*** (Figure 56). This is the ultimate site for its pupation. Shield (1856) found larvae of ***Catoptria falsella*** in the unique habitat of mosses on thatch of a barn. This species primarily hides among mosses on walls, stones, and rocks in the daytime, feeding at night on mosses, including ***Tortula muralis***, ***Syntrichia ruralis*** (Figure 57), ***Barbula*** (Figure 58), and ***Brachythecium rutabulum*** (Figure 59) (Wikipedia 2014). South (1890) reported ***Catoptria verellus*** (syn=*Crambus verellus*; Figure 60) among mosses on tree trunks, particularly older plum, apple, and poplar trees. The species also occurs in fir woods with moss-covered ground.

Figure 55. ***Catoptria falsella*** adults – wall dwellers, showing two color phases. Larvae typically feed on mosses, including ***Tortula muralis***. Photos by Donald Hobern, through Creative Commons.

Figure 56. ***Tortula muralis*** with capsules on wall, food for ***Catoptria falsella***. Photo by Mike, through Creative Commons.

Figure 57. ***Syntrichia ruralis***, food for the nighttime feeder ***Catoptria falsella***. Photo by Hermann Schachner, through Creative Commons.

Figure 58. ***Barbula unguiculata***. Some members of this genus provide food for the nighttime feeder, ***Catoptria falsella***. Photo by James K. Lindsey, with permission.

Figure 59. ***Brachythecium rutabulum***, nighttime food for ***Catoptria falsella***, with capsules. Photo by J. C. Schou <www.biopix.com>, with permission.

Figure 60. ***Catoptria verellus*** adult, a species whose larvae live on moss-covered tree trunks and moss-covered ground. Photo by Donald Hobern, with permission.

Chrysoteuchia culmella (=*Crambus hortuellus*; Figure 61) larvae build silken galleries on the ground under mosses (Shield 1856). Where it is damp along ditches, one can also find larvae of ***Agriphila straminella*** (syn=*Crambus culmellus*; Figure 62) with their silken galleries. The larvae mature there and spend their pupation there.

Figure 61. ***Chrysoteuchia culmella*** adult. Their larvae build their silken galleries under ground mosses. Photo through Wikimedia Commons.

Figure 62. ***Agriphila straminella*** adult; the larvae occur along damp ditches, including among mosses. Photo by André Karwath, through Creative Commons.

Huggins (2011) listed ***Oxyelophila callista*** (Figure 63) as a species of moss shredders, but these are aquatic mosses.

Figure 63. ***Oxyelophila callista*** adult; larvae are shredders of aquatic mosses. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Some evidence that **Crambidae** live among mosses is indirect (Russell 1979). Their head capsules have been found numerous times in mosses on logs and deciduous tree trunks. Webbing and fecal pellets occur among damaged mosses. Based on this evidence, it appears that ***Hypnum circinale*** (Figure 64) and ***Tetraphis pellucida*** (Figure 65) are most likely eaten by larvae of **Crambidae** (formerly placed in **Pyralidae**).

Figure 64. ***Hypnum circinale***, food for larvae of the **Crambidae**, with capsules. Photo by Matt Goff, with permission.

Figure 65. ***Tetraphis pellucida*** with gemmae, a species most likely eaten by members of the **Crambidae**. Photo by Hermann Schachner, through Creative Commons.

Pyralidae – Snout Moths

There are few known bryophages remaining in this family in its more restricted definition. Fraenkel and Blewett (1947) suggested that some of this snubbery of the bryophytes may be due to the chemical composition. However, they failed to show that bryophytic linoleic acid was detrimental, and bryophyte arachidonic acid actually promotes growth of the larvae of ***Ephestia kuehniella*** (Figure 66-Figure 67).

Figure 66. ***Ephestia kuehniella*** larva, a species whose growth is promoted by arachidonic acid from bryophytes. Photo by Simon Hinkley and Ken Walker, Museum Victoria, through Creative Commons.

Figure 67. ***Ephestia kuehniella*** mating adults. Photo by Magne Flåten, through Creative Commons.

Synaphe punctalis (Figure 68) and ***S. angustalis*** (Figure 69) builds its scant webs among damp mosses on the ground (Meyrick 1895). In addition to these, in

Australia, ***Phycis subornatella*** lives among mosses and spins its web in it (Buchanan White 1971).

Figure 68. ***Synaphe punctalis*** adult, a species whose larvae build webs among damp ground mosses. Photo by Thorsten Denhard, through Creative Commons.

Figure 69. ***Synaphe angustalis*** adult, a species whose larvae build scant webs on damp mosses. Photo from ©entomart, through Creative Commons.

HESPERIOIDEA

Hesperiidae – Skippers

These lepidopteran differ from both moths and butterflies. They have short, fat bodies like moths, hooked antennae unlike the club antennae of butterflies or the feathery antennae of moths, and a unique rapid, skipping flight (Bartlett 2004; Wikipedia 2015c).

The skippers are generally not associated with mosses. However, ***Polites mardon*** (Figure 70-Figure 73) builds a larval shelter of silk with mosses, dry grass blades, litter, and dry frass serving to camouflage it (Henry & Beyer 2013). These are located at the bases of grasses near the soil surface.

Figure 70. ***Polites mardon*** larva, a species that incorporates pieces of mosses in its silk shelter. Photo by Jim P. Brock, with permission.

Figure 71. ***Polites mardon*** pupa, a species that incorporates pieces of mosses in its silk shelter. Photo by Jim P. Brock, with permission.

Figure 72. ***Polites mardon*** adult, a species whose larvae include mosses in their net. Photo by Lauren Sobkoviak, through Creative Commons.

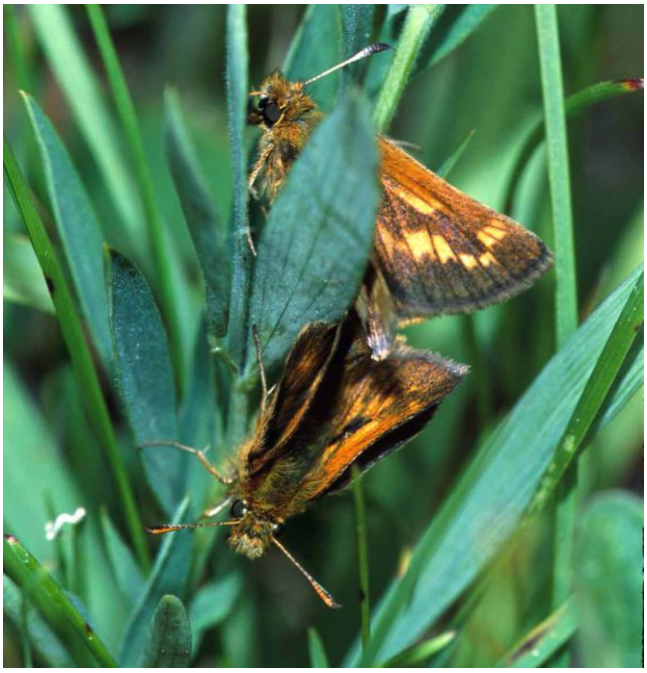

Figure 73. ***Polites mardon*** adult, a species that incorporates pieces of mosses in its silk shelter. Photo by William Leonard, with permission.

PAPILIONOIDEA

Lycaenidae – Blues, Coppers, Hairstreaks, Harvesters (Butterflies)

Some Lepidoptera seem to have switched from feeding on leaves to feeding on the **epiphylls** (Figure 74) on the leaves (Callaghan 1992). It appears that in this case, the bryophytes, mostly the leafy liverworts in **Lejeuneaceae**, were an important food source. In a Nigerian cola forest, ***Pentila picena cydaria*** (Figure 75) lays its eggs singly on live trees. Its substrate includes not only the woody stems, but also green lichens and mosses. These eggs are initially white, but within a day they become dark brown, making them less conspicuous.

Figure 74. **Lejeuneaceae** epiphylls on leaf, food for several **Lepidoptera**, including ***Pentila piceana cydaria***. Photo by Claudine Ah-Peng, with permission.

Figure 75. ***Pentila picena*** adult, a species whose larvae feed on epiphylls, including bryophytes. Adults include mosses among their oviposition sites. Photo by Sáfián Szabolcs, with permission.

Nymphalidae – Brush-footed Butterflies

Singer and Mallet (1986) expressed excitement at finding ***Euptychia insolata*** (Figure 76) alighting on "green" tree trunks in Costa Rica. As they continued observations, they found six green spherical eggs, then observed the female ovipositing on the epiphytic moss ***Neckeropsis undulata*** (Figure 77). This species landed on tree trunks with green bryophytes, searching for oviposition sites. The larvae of this butterfly are well camouflaged on the moss. They are "moss-shaped" and moss-colored. This appears to be the first record for butterfly larvae that feed on a moss (Singer *et al.* 1983; Singer & Mallet 1986), but they were unable to determine if they were restricted to this moss species. Singer and Mallet (1986) were able to raise 5 adults from 6 eggs by using ***Neckeropsis undulata*** as the only food source. The larvae of this species are "moss-shaped" and have cryptic coloration, rendering them safe on this moss.

Figure 76. ***Euptychia insolata*** adult, a butterfly that oviposits on epiphytic mosses on tree trunks and its larvae eat there. Photo by Will & Gill Carter, with permission.

Figure 77. ***Neckeropsis undulata***, oviposition site for ***Euptychia insolata***. Photo by Bobby Hattaway, from <www.discoverlife.org>, through Creative Commons.

Hamm (2015) expressed surprise that members of ***Euptychia*** have switched from feeding on grasses to feeding on low-nutrient plants like ***Selaginella*** (a fern ally; Figure 78) and mosses (Scriber & Slansky 1981). On the other hand, Egorov (2007) concluded that the epiphytic mosses had sufficient nitrogen due to contributions from epiphytic **Cyanobacteria** (Figure 79) and the slow growth of the mosses. Furthermore, in experiments with ***E. westwoodi*** (Figure 80), Hamm (2015) found that the larvae would not eat grasses (*Lasiacis ruscifolia*, a preferred food of close relatives) when those were the only choice, losing weight and ultimately dying. Those fed with ***Selaginella*** ate and developed normally.

Figure 78. ***Selaginella***, a fern ally that ressembles a moss, has low nutrients, and serves as food for some species of ***Eutypchia***. Photo by Tim Waters, through Creative Commons.

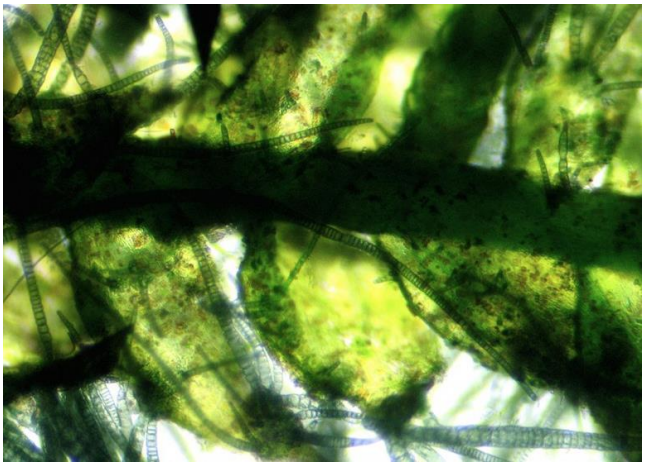

Figure 79. **Cyanobacteria** on a moss, a source of nitrogen for feeders on epiphytic bryophytes. Photo by Nat Tarbox, through Creative Commons.

Figure 80. ***Euptychia westwoodi*** adult, a species that will not eat grasses as larvae. Photo by Daniel H. Janzen, through Creative Commons.

The genus ***Euptychia*** occurs elsewhere in South America. Pulido *et al*. (2011) describe it as living in the mountain foothills and montane forests of the Andes in Colombia and Peru. Neild *et al*. (2014) described a new species from the Amazon Basin and the Guianas, describing the genus as occurring throughout the Neotropical region. This is a small butterfly and seems to generally have singular hosts among fern allies and mosses. Singer and Mallet (1986) predicted that we will eventually find that many South American **Euptychiines** feed on "lower" plants.

But not all members of ***Euptychia*** are bryophages. Beccaloni *et al*. (2008) reported that ***Euptychia hilara*** feeds on a member of **Poaceae** (grasses).

Bryophytes are often among a group of convenient locations for pupation. This is the case for the White Mountain Arctic butterfly (***Oeneis melissa semidea***; Figure 81) (Lucking 2000). Its larvae are night-active feeders, spending their day between or under rocks (Scudder 1874, 1889; Gradish & Otis 2015). Pupation, however, uses safe sites under rocks, moss, or soil. Male adults perch in areas with considerable Bigelow's sedge, the probable substrate for oviposition and food plant for the larvae (Scudder 1891, 1901).

Figure 81. ***Oeneis melissa semidea*** (White Mountain Arctic) adult, a species whose pupae often occur under mosses. Photo by Kent McFarland, through Creative Commons.

Some adult **Lepidoptera** provide very interesting mimics. The moth in Figure 82 resembles a leaf with epiphyllous liverworts (Figure 74). Is there some advantage to adding the liverworts? The leaf itself is brown, suggesting it may be high in tannins and not very palatable. Do the liverworts further discourage carnivory? Might the Lejeuneaceae they seem to mimic have secondary compounds that discourage "herbivory" (in this case on a fake)? Or do they just blend with leaves, hence avoiding larger carnivores such as birds?

Figure 82. Moth mimicking a leaf with epiphyllous bryophytes, especially liverworts, in Malaysia. Photo courtesy of Tamás Pócs.

The bog fritillary, ***Boloria eunomia*** (Figure 83-Figure 87), is of special concern in Wisconsin, USA (WDNR 2009). Its habitat is in classical acid bogs (Wikipedia 2011), a habitat that is diminishing. Schtickzelle and Baguette (2004) warn that glacial relict species such as this one are increasingly more vulnerable as their fragmented habitat becomes more and more rare. Typically, the ***Sphagnum*** (Figure 88) mosses provide the right conditions for the host plants. Natives of Scotland have been concerned about the conversion of the classic bog at Aucheninnes Moss to a landfill (Buglife 2011). This is the location of the small pearl-bordered fritillary ***Boloria selene*** (Figure 89-Figure 92), a species of conservation concern, and the only site in Scotland for the sorrel pigmy moth ***Enteucha acetosae*** (Figure 93). A third species there, ***Coenonympha tullia*** (Figure 94-Figure 97), is listed as vulnerable in Europe. These moss-dominated bog habitats house many insects that are in danger of disappearing as these bogs disappear.

Figure 83. ***Boloria eunomia*** first instar caterpillar, a bog species. Photo by Gilles San Martin, through Creative Commons.

Figure 84. ***Boloria eunomia*** last instar, a bog species. Photo by James K. Lindsey, with permission.

Figure 85. ***Boloria eunomia*** adult, a bog dweller. Photo by Gilles San Martin, through Creative Commons.

Figure 86. ***Boloria eunomia***, a bog dweller. Photo by Gilles San Martin, through Creative Commons.

Figure 89. ***Boloria selene tollandensis*** 5th instar larva, a bog dweller. Photo by Todd Stout, with permission.

Figure 87. ***Boloria eunomia*** egg, a bog species. Photo by Gilles San Martin, through Creative Commons.

Figure 90. ***Boloria selene tollandensis*** pupa, a bog species. Photo by Todd Stout, with permission.

Figure 88. ***Sphagnum capillifolium***, one of the bog mosses that provide suitable homes for ***Boloria eunomia***. Photo by Michael Lüth, with permission.

Figure 91. ***Boloria selene*** adult, a bog dweller. Photo by Kristian Peters, through Creative Commons.

Figure 92. ***Boloria selene*** adult, a bog dweller. Photo by James K. Lindsey, with permission.

Figure 93. ***Enteucha acetosae*** adult, a rare bog dweller. Photo by Patrick Clement, with permission.

Figure 94. ***Coenonympha tullia*** egg, a vulnerable bog species. Photo by Wolfgang Wagner, with permission.

Figure 95. ***Coenonympha tullia*** larva on moss. Its colors permit it to blend with mosses in bogs. Photo by Wolfgang Wagner, with permission.

Figure 96. ***Coenonympha tullia*** pupa, a bog species. Photo by Wolfgang Wagner, with permission.

Figure 97. ***Coenonympha tullia*** adult, a bog species. Photo by Ryan Hodnett, through Creative Commons.

Some members of this family are so well adapted to living among mosses that their cryptic form and coloration has earned them the name of moss caterpillars. At least some of these unusual caterpillars are in the Western Hemisphere genus ***Adelpha*** (Figure 98-Figure 103). The earliest record of these seems to be that of Moss (1933) for ***Adelpha melona leucocoma*** larvae that resemble a moss. In Costa Rica, ***Adelpha serpa celerio*** resembles mosses on a twig (DeVries 1987). Wilmott (2003) cited several species in ***Adlepha*** that mimicked mosses, including ***Adelpha leucophthalma leucophthalma*** larvae that resemble moss-covered twigs. There seem to be multiple forms of these mimics, and those forms may contribute to their occurrences in different habitats, potentially leading to separation as species.

Figure 98. ***Adelpha serpa celerio***, moss-mimicking caterpillar in Panama, blending with its habitat. Photo by Arthur Anker, with permission

Figure 99. ***Adelpha serpa celerio***, showing the byrophyte-like appendages of this moss-mimicking caterpillar in Panama. Photo by Arthur Anker, with permission.

Figure 100. ***Adelpha serpa celerio*** spinning its web on a leaf. Photo by Arthur Anker, with permission.

Figure 101. ***Adelpha*** (?) larva from Brazil, showing head and appendages. Photo by Troy Bartlett, through Creative Commons.

Figure 102. ***Adelpha*** (?) larva looking like moss on a twig. Photo by Troy Bartlett, through Creative Commons.

Figure 103. ***Adelpha fessonia*** adult, a member of the moss caterpillar genus showing the differences in coloration from its cryptic larva. Photo by Thomas Bresson, through Creative Commons.

Rionidae – Tropical Butterflies

This small family of butterflies does not seem to have a common name.

The species ***Sarota gyas*** (Figure 104) in the tropics can be found on leaves of tracheophytes, but Mota *et al*. (2014) pointed out that these are not the real hosts. Instead, the larvae are there to feed on the **epiphylls** (Figure 74) – the non-nitrogen-fixing epiphylls (DeVries 1988). In one case, larvae on a member of the Urticaceae fed on leafy liverwort epiphylls in the **Lejeuneaceae** (Figure 74). Apparently the host tree is unimportant for either oviposition or larval feeding. These larvae have long setae that provide defense and they are camouflaged among the epiphylls.

Figure 104. ***Sarota gyas*** adult, a species whose larvae live on leaves of tracheophytes where they feed on epiphylls (Figure 74). Photo by Harold Greeney, through Creative Commons.

Summary

The **Tortricidae** include a few bryophyte associates, particularly those on tree trunks. The **Crambidae**, on the other hand, construct silken tunnels on mosses and grasses where they feed in safety. The subfamily **Scopariinae** is known as the moss-eating **Crambidae**. This family has been separated from the **Pyralidae** and few bryophyte associates remain in the **Pyralidae**. The **Hesperiidae** are skippers and seem to have only one member (***Polites mardon***) that associates with mosses. The **Lycaenidae** feed on the **epiphylls** on leaves, particularly the leafy liverworts in the **Lejeuneaceae**. In the **Nymphalidae**, ***Euptychia insolata*** adults are cryptically colored to be able to alight on moss-covered tree trunks without being obvious. These are butterflies and among the ones that feed on mosses. They may use the mosses as a source of nitrogen derived from their epiphytic **Cyanobacteria**. ***Adelpha***, in the **Nymphalidae** also exhibits moss mimicry. Members of this family are common bog dwellers. The **Rionidae** has one member, ***Sarota gyas***, that feeds on epiphylls such as members of the **Lejeuneaceae**, in particular to obtain nitrogen from the associated nitrogen fixers.

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