CHAPTER 12-15
TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA: GEOMETROIDEA – NOCTUOIDEA

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CHAPTER 12-15 TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA: GEOMETROIDEA – NOCTUOIDEA

Figure 1. **Geometridae** larva eating ***Hypopterygium tamarisci***. Photo by Adaises Maciel da Silva, with permission.

GEOMETROIDEA

Geometridae – Geometrid Moths (Inch Worms)

The **Geometridae** get their name from their larvae, popularly known as inch worms (Figure 2). The method of movement has suggested that the larvae are measuring the earth. This family has cryptic coloration as larvae (Figure 2) (Bodner *et al*. 2010). In the montane rainforest of southern Ecuador, the brown, green, and gray tones help them to blend with the montane rainforest. For example, ***Phyllodonta semicava*** (see Figure 3) and ***Cargolia arana*** (Figure 4-Figure 5) resemble the mossy bark where they live.

Figure 2. **Geometridae** larva "inching" along the stem. Photo by Jérôme Albre, with permission.

Figure 3. ***Phyllodonta*** sp. adult; some species resemble the mossy bark where they rest. Photo by Daniel H. Janzen, through Creative Commons.

Figure 4. ***Cargolia arana*** larva, resembling mossy banks where it lives. Photo by Wilmer Simbaña and Luis Salgaje, through Creative Commons.

Figure 5. ***Cargolia arana*** adult with cryptic coloration. Photo by James Sullivan, with online permission.

In tropical montane rainforests of Brazil, larvae in the **Geometridae** are the culprits that feed on the mosses ***Hypopterygium tamarisci*** (Figure 7-Figure 14) and ***Lopidium concinnum*** (Figure 15), especially at the beginning of the rainy season (September to December) (Maciel-Silva & dos Santos 2011). Using an index of damage (ID) in 2007 and 2008, Maciel-Silva and dos Santos found that ***H. tamarisci*** had higher damage (68%, 35%) than ***L. concinnum*** (38%, 23%) in these two years (Figure 6), but they were unable to separate that of the geometrid from that of a cohabiting snail. Furthermore, these rates were lower than those for tracheophytes. They found no correlation of herbivory with phenols, proteins, or the ratio between these (Figure 6).

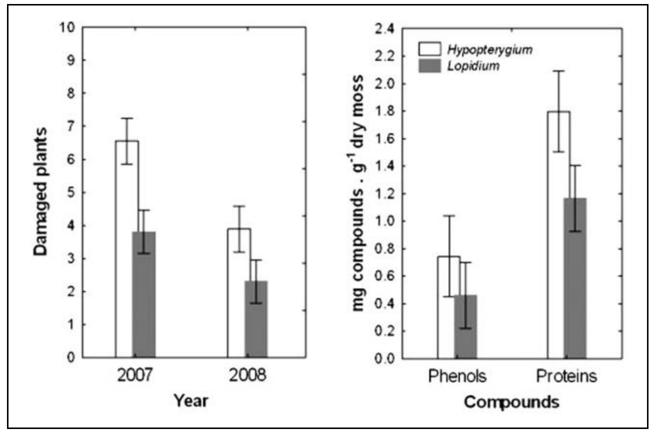

Figure 6. **Charopidae** (snail) and **Geometridae** damage to mosses in 10 colonies of plants. Modified from Adaises Maciel-Silva and Nivea Dias dos Santos.

Figure 7. Field damage to ***Hypopterygium tamarisci*** by larvae of the **Geometridae**. Photo by Adaises Maciel-Silva and Nivea Dias dos Santos, with permission.

Figure 8. Field damage to ***Hypopterygium tamarisci*** by larvae of the **Geometridae**. Photo courtesy of Adaises Maciel-Silva and Nivea Dias dos Santos, with permission.

Figure 9. Damage to leaves (circled) of ***Hypopterygium tamarisci*** by a **Geometridae** larva in the laboratory over about 50 days. Photo courtesy of Adaises Maciel da Silva.

Figure 10. **Geometridae** on its host plant, ***Hypopterygium tamarisci***. Photo courtesy of Adaises Maciel da Silva.

Figure 11. **Geometridae** on the host plant ***Hypopterygium tamarisci***. Photo courtesy of Adaises Maciel da Silva.

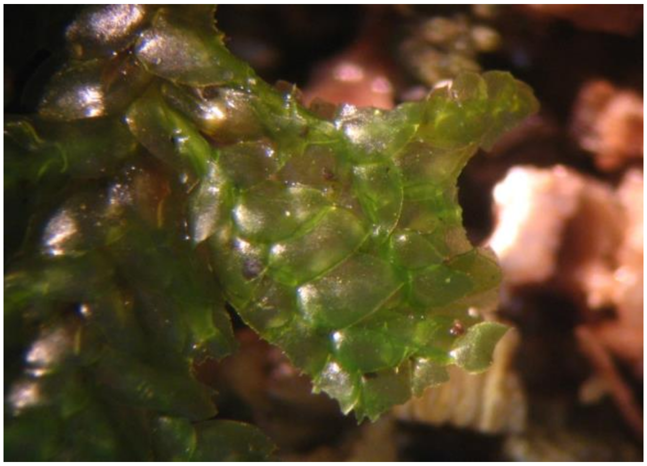

Figure 12. ***Hypopterygium tamarisci*** herbivory by **Geometridae** larvae. Photo courtesy of Adaises Maciel da Silva.

Figure 13. ***Hypopterygium tamarisci*** herbivory by **Geometridae**. Photo courtesy of Adaises Maciel da Silva.

Figure 14. Larva of **Geometridae** feeding on ***Hypopterygium tamarisci***. Photo by Adaises Maciel-Silva and Nivea Dias dos Santos, with permission.

Figure 15. ***Lopidium concinnum***, food for some larvae of **Geometridae**. Photo by Leon Perrie, through Creative Commons.

Orthonama obstipata (=*Camptogramma fluviata*; Figure 16) is not a moss feeder as far as I can tell, but it does "retire" among mosses or just below the soil surface (Hellins 1871). One must wonder if the mosses are an important component of its niche. It constructs a cocoon that is weak, thin, and made of silk. Mosses may help to buffer the temperature and maintain moisture.

Figure 16. ***Orthonama obstipata*** adult, a species that "retires" among mosses, or in the soil just below them. Photo by Ben Sale, through Creative Commons.

Helastia mutabilis (Figure 17) larvae feed on mosses in eastern Otago, New Zealand (Patrick 2016). The larva of ***Helastia mutabilis*** feeds on the moss ***Racomitrium*** (Figure 18) in the local area of Otago, thus far the only known host plant for it.

Figure 17. ***Helastia mutabilis*** adult, a species whose larvae feed on mosses in New Zealand. Photo by Donald Hobern, through Creative Commons.

Figure 18. ***Racomitrium lanuginosum***. ***Helastia mutabilis*** larvae feed on members of this genus. Photo by Juan Larrain, through Creative Commons.

Perizoma taeniatum (=*Martania taeniata*; Figure 19) is one of the macro-moths that most likely feeds on mosses as larvae (Pescott *et al*. 2015). Pescott and coworkers expressed concern that air pollution is harming the lichens and bryophytes and may lead to the demise of those that feed on them.

Figure 19. ***Perizoma taeniatum*** adult, a species whose larvae apparently feed on mosses and may be harmed by loss of mosses and lichens due to air pollution. Photo by M. Virtala, through Creative Commons.

Eupithecia austeraria (Figure 20) pupae occur among mosses on stumps, close to the moisture of the rotting wood (Shield 1856). ***Eupithecia irriguata*** (Figure 21) spends its pupal winters under bark and mosses (Dietz 1871). Krampl (1994) reported ***Eupithecia thalictrata*** (Figure 22) pupation in cocoons, usually in dry mosses near the base of its host plants. The pupae overwinter and adults emerge that spring.

Figure 20. ***Eupithecia austeraria*** adult, a species that pupates among mosses on stumps. Photo from Wikiwand.

Figure 21. ***Eupithecia irriguata*** adult, a species that overwinters as a pupa under bark and mosses. Photo by Marko Mutanen, through Creative Commons.

Figure 22. ***Eupithecia thalictrata*** adult, a species that pupates in dry mosses. Photo by Püngeler, through Public Domain.

Scotorythra paludicola (Figure 23) larvae don't eat mosses – they eat leaves and phyllodes of *Acacia koa* (Haines *et al.* 2013) and other members of the Fabaceae (Barton & Haines 2013). But the adults do use the mosses. The females lay their eggs in bark crevices and in mosses on the trunks of host trees, providing them with cover during development while keeping them close to their host leaves.

Figure 23. ***Scotorythra paludicola*** larva, a species that begins its life among mosses on *Acacia koa* where females lay eggs on tree trunks. The larvae then move to the leaves and phyllodes to feed. Photo by Forest Starr and Kim Starr, through Creative Commons.

Hyposidra talaca (Figure 24-Figure 25) lives in the tea plantations of northeastern India (Sinu *et al*. 2013). The species is a pest there, and the tree bark and its moss cover offer protection for the eggs of this species. This is one of the moths that oviposits in different places from the ones where it feeds (Wiklund 1977; Tammaru *et al*. 1995). Similarly, the Bruce spanworm (***Operophtera bruceata***; Figure 26-Figure 27) infests tree leaves, but the eggs are often laid among mosses growing at the bases of these trees (Ives 1984).

Figure 24. ***Hyposidra talaca*** larva, a pest in tea plantations. The female deposits eggs where they are hidden by mosses. Photo by Vaikoovery, through Creative Commons.

Figure 25. ***Hyposidra talaca*** adult, a pest in tea plantations. It deposits eggs where they are hidden by mosses. Photo by Sterling Sheehy, through Creative Commons.

Figure 26. ***Operophtera bruceata*** larva (Bruce spanworm) that begins it life among mosses at the base of host trees. Photo by E. Bradford Walker, through Creative Commons.

Figure 27. ***Operophtera bruceata*** adult. Females lay their eggs among mosses at the base of trees. Photo by Cody Hough, through Creative Commons.

Not all bryophyte associates are drab browns and grays. ***Milionia isodoxa***, although not a bryophyte dweller, does make use of them and is quite colorful. The adults of ***Milionia isodoxa*** (Figure 28) in Papua New Guinea illustrate the method that seems typical for obtaining water among many **Lepidoptera** (Wylie 1982). These moths probe and feed at moist sand and mud and in soil of puddle margins. Occasionally they obtain their water from mosses on rocks or on stream debris, but they do not drink from the free water itself.

Figure 28. ***Milionia isodoxa*** adult, a species that drinks from the moist mosses on rocks or along streams. Photo by David Polluck, through Creative Commons.

Camouflage is important, and even adults may rest where they are not easily seen. In New Zealand, ***Declana griseata*** (Figure 29) larvae feed on mistletoe that grows as a parasite in the trees, but as adults these moths rest on the mossy trunks of trees in the vicinity, blending with the color patterns there (Patrick & Dugdale 1997).

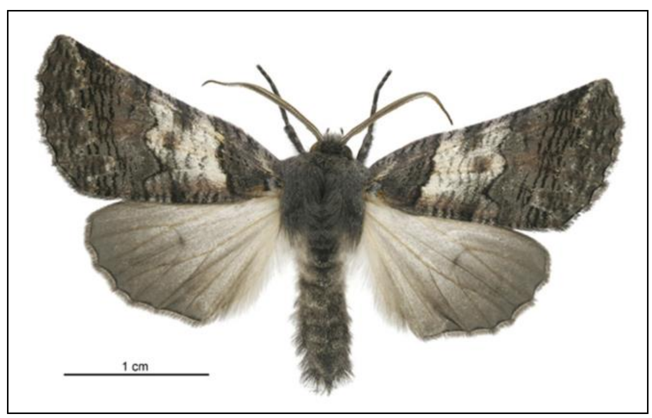

Figure 29. ***Declana griseata*** male adult, a species that rests on mossy tree trunks. Photo by Landcare Research, Manaaki Whenua, with permission.

Shaking a carefully removed clump of epiphytic moss may reveal the cocoon of ***Odontopera bidentata*** (Figure 30) attached to the tree trunk and looking like "dark whitey-brown paper with a few pieces of moss attached to it" (Shield 1856). The larvae are good mimics of lichens on a twig (Figure 31).

Figure 30. ***Odontopera bidentata*** adult showing its cryptic coloration for resting on bark. Photo by Donald Hobern, through Creative Commons.

Figure 31. ***Odontopera bidentata*** larva, a species that builds a cocoon on tree trunks, attaching mosses to it. This one is a lichen mimic. Photo by Kimmo Silvonen, with permission.

Hydriomena impluviata (syn=*Ypsipetes impluviaria*; Figure 32) pupates in mosses and Shield (1856) describes the method to look for them. He warns that one must remove the moss carefully from its bark substrate, starting at the moss tips and holding it on both sides. A sample the size of one's hand should be removed, then shaken to dislodge the black pupae. The moss should be kept intact as a sheet. Unfortunately, this method is quite destructive of the mosses.

Figure 32. ***Hydriomena impluviata*** adult, a species that pupates among mosses. Photo by Fvlamoen, through Creative Commons.

Erannis jacobsoni (Figure 33) larvae defoliate the trees in the spruce-fir forests of Russia (Турова & Юрченко 1996). Outbreaks of this species are primarily in the "green-moss" types of these forests, suggesting that the mosses may be important in their life cycle, perhaps as a place for laying eggs. For example, Kinghorn (1952) found that the western hemlock looper lays eggs among mosses and that oviposition increases when the density of the mosses is greater. On the trees, having mosses grow to higher positions increases the correlation between egg density and height on tree. Kinghorn suggested that moss density might be the strongest single factor influencing the place where eggs were deposited.

Figure 33. ***Erannis jacobsoni*** larva, a species that defoliates trees in spruce-fir forests with abundant moss ground cover. Photo by Vladimir Petko, through Creative Commons.

The western hemlock looper, ***Lambdina fiscellaria lugubrosa*** (Figure 34), along the western coast of North America lays most of its eggs in mosses on tree trunks, branches, and logs (Hopping 1934; Carolin *et al*. 1864; Shore 1990). But in the forests of the interior, their preferred oviposition sites are on the pendant lichen ***Alectoria*** spp. (Figure 35) (Thomson 1958). ***Lambdina fiscellaria fiscellaria*** (Figure 36) usually lays its eggs singly, but sometimes these are in groups of 2 or 3 (Carroll 1956). These are typically placed on mosses and lichens on the tree trunk or under old bark scales, but also on mosses covering stumps and logs.

Figure 34. ***Lambdina fiscellaria lugubrosa*** (western hemlock looper) larva, a species that often lays its eggs in mosses. Photo by Jerald E. Dewey, through Creative Commons.

Figure 35. ***Alectoria sarmentosa***, one of the preferred oviposition sites for ***Lambdina fiscellaria lugubrosa*** (Figure 34). Photo by Jason Hollinger, through Creative Commons.

Figure 36. ***Lambdina fiscellaria fiscellaria*** larva. Photo from Pennsylvania Department of Conservation and Natural Resources, through Creative Commons.

Shepherd and Gray (1972) bemoaned the difficulty of counting the eggs (Figure 37) of the hemlock looper (***Lambdina fiscellaria lugubrosa***; Figure 34) that were attached to mosses. Finding it both tedious and inaccurate, they devised a more consistent method for this process. They treated moss samples with 0.5% NaOH for 1 minute to release the eggs. These were then washed and filtered out of the moss sample. A solution of 15% NaCl helps to separate other debris from the sample by flotation. Using this method, they were able to obtain density estimates with two standard errors.

Figure 37. ***Lambdina fiscellaria*** eggs on fir. Photo from Natural Resources Canada, Canadian Forest Service, with online permission.

Otvos and Bryant (1972) likewise tested methods for assessing the eggs present on mosses and bark. They tried a range of bleach solutions and found that a 2% bleach solution bath for 45 minutes would release eggs of ***Lambdina fiscellaria*** (Figure 38) eggs without deleterious effects.

Figure 38. ***Lambdina fiscellaria*** adult, the hemlock looper. Photo by D. Gordon E. Robertson, through Creative Commons.

Dobesberger (1989) developed a management plan for ***Lambdina fiscellaria fiscellaria*** (Figure 36). Dobesberger determined that only six midcrown branches were adequate to obtain an average sample number. More eggs were present on the midcrown area of the balsam fir, ***Abies balsamea*** (Figure 39), than on other substrates including ground mosses – mostly ***Hylocomium splendens*** (Figure 40), ***Pleurozium schreberi*** (Figure 41), and ***Ptilium crista-castrensis*** (Figure 42), as well as loose bark of paper birch and lichens in the crown (mostly *Usnea longissima*; Figure 43).

Figure 39. ***Abies balsamea***, most common egg-laying site for ***Lambdina fiscellaria fiscellaria*** (Figure 36). Photo by DVS, through Creative Commons.

Figure 40. ***Hylocomium splendens***, lesser egg-laying site for ***Lambdina fiscellaria fiscellaria*** (Figure 36). Photo by Andrew Spink, with permission.

Figure 41. ***Pleurozium schreberi*** occasional egg-laying site for ***Lambdina fiscellaria fiscellaria*** (Figure 36). Photo by Michael Lüth, with permission.

Figure 42. ***Ptilium crista-castrensis***, lesser egg-laying site for ***Lambdina fiscellaria fiscellaria*** (Figure 36). Photo by Li Zhang, with permission.

Figure 43. ***Usnea*** sp., one of the substrates for egg laying of ***Lambdina fiscellaria fiscellaria***. Photo by T.cegy, through Creative Commons.

Eggs of ***Lambdina fiscellaria lugubrosa*** (Figure 34) in coastal forests of British Columbia, Canada, could be sampled at 6-7 m intervals from the ground level to the top of tree trunks by sampling the mosses (Richmond 1947). When defoliation averaged 82%, the egg count was 226 healthy eggs per 30 cm square of moss from ground level to the top of the tree at 27 m elevation. But at 427 m, the mean defoliation dropped to 10% and the egg count to 0.3 eggs per 30 cm square of moss.

But why are the entomologists so interested in counting eggs of this species on mosses? Feeding on the leaves by the hemlock looper can devastate a hemlock forest in only one year, fir trees in 2-3 (USDA 2016). Hébert *et al.* (2003) found that the outbreaks of ***Lambdina fiscellaria*** (Figure 38) have a sudden rapid increase and patchy distribution across wide areas. This means that predicting where control is needed can be difficult. To be prepared, it is necessary to conduct egg surveys, a tedious and expensive process. But Hébert and coworkers found a simpler means. They used white polyurethane foam substrates with the Luminoc insect trap and a portable light trap. These oviposition traps were highly efficient for sampling eggs and the results were highly correlated with those of extracting eggs from mosses on 1-m branches.

Otvos and Bryant (1972) pointed out the importance of assessing ***Lambdina fiscellaria*** eggs (Figure 37), present September to June, as a means to help them prepare for potentially devastating years. The larvae that cause the damage are present for only two weeks before the damage becomes serious. By counting eggs, managers can assess and prepare for the upcoming year. These larvae are able to cause great damage not by fully consuming leaves, but by nibbling the ends of leaves, causing rapid and permanent desiccation (USDA 2016).

But all is not well for the eggs of the eastern hemlock looper (***Lambdina fiscellaria fiscellaria***; Figure 36). A pest on the balsam fir, ***Abies balsamea*** (Figure 39), the eggs (Figure 37) of this species are subject to parasitism (Otvos 1977). Otvos experimented with these in the lab using eggs collected on the peat moss ***Sphagnum*** spp. (Figure 44), the lichen (*Usnea* sp.; Figure 43) and on birch bark (*Betula* spp.; Figure 45). Otvos found that the percentage of mortality for overwintering eggs is inversely related to the difference between the mean winter temperature and normal winter temperature. Mortality from parasites was about the same for eggs collected in autumn and spring.

Figure 44. ***Sphagnum magellanicum*** and ***Sphagnum fimbriatum***, egg laying sites for ***Lambdina fiscellaria fiscellaria***. Photo from NY Botanical Garden, through Public Domain.

Figure 45. Birch (*Betula*) bark where ***Lambdina fiscellaria fiscellaria*** deposits eggs. Photo by Sue Sweeney, through Creative Commons.

The hemlock looper also uses mosses for pupation. ***Lambdina fiscellaria somniaria*** (Figure 46-Figure 48) uses both mosses and bark crevices on the lower branches and tree trunks as well as debris on the ground near the host trees, providing them with protection during this stage (Willhite 2013). In Alaska, when it is time for pupation, the full-fed larvae of ***Lambdina fiscellaria*** extend a silken thread and descend from the conifer needles to the ground where they pupate under mosses or bark scales or in crevices of rotting tree stumps (Torgersen & Baker). In 14-20 days the adult emerges.

Figure 46. ***Lambdina fiscellaria somniaria*** (hemlock looper) larva, a species that uses mosses for pupation. Photo from USFS, through Public Domain.

Figure 47. ***Lambdina fiscellaria somniaria*** larva in moss. Photo from USFS, through Public Domain.

Figure 48. ***Lambdina fiscellaria somniaria*** pupa in moss. Photo from USFS, through Public Domain.

LASIOCAMPOIDEA

Lasiocampidae – Snout Moths

Norman (1871) noted that ***Macrothylacia rubi*** (as ***Lasiocampa rubi***; Figure 49-Figure 50) larvae swarm on mosses in autumn in Morayshire, Scotland. These larvae are known to the ophthalmologists because their hairs cause conjunctivitis of the eye.

Figure 49. ***Macrothylacia rubi*** female adult. In Scotland, larvae of this species swarm on mosses in autumn. Photo by Jérôme Albre, with permission.

Figure 50. ***Macrothylacia rubi*** female adult. Larvae of this species swarm on mosses in autumn in Scotland. Photo by Jérôme Albre, with permission.

Some of the interactions get complicated. ***Bracca*** sp. occurs on the ground where moss and leaf litter are common in their habitat between tree buttresses (Brown 2006). What makes this interesting is that the ***Bracca*** sp. mimics the coral snake (*Hemibungarus calligaster*) in the Philippines. These two species share this habitat.

NOCTUOIDEA

Arctiidae – Tiger Moths *etc*.

You may be familiar with this family through the woolly bear caterpillar. Few members of the family seem to be bryophyte dwellers. Nevertheless, I have already noted that the subfamily **Lithosiinae** eat bryophyte capsules (Liu 1989 in Fang & Zhu 2012). Yuanfu (1989) concluded that the large number of species and individuals in this family that occur in the tropical mountain rainforest of Hainan Island can "be explained" by the large number of mosses and lichens here.

The larvae of ***Cybosia mesomella*** (Figure 51-Figure 52) (sometimes placed in **Erebidae**) consume liverwort leaves, particularly the genus ***Jungermannia*** (Figure 53), as well as lichens (Coutin 2004). Some of the larvae of the lichen moths (**Lithosiinae**) (*e.g.* ***Hypoprepia miniata***; Figure 54-Figure 55) feed on mosses as well as algae and lichens (Rawlins 1984; Anonymous 2011). Members of this subfamily normally feed on cryptogams such as algae, lichens, and bryophytes, eating only the photosynthetic partner in the lichens (Simonson 2016).

Figure 51. ***Cybosia mesomella*** larva, a species that eats the leafy liverwort ***Jungermannia***. Photo by Wolfgang Wagner, with permission.

Figure 52. ***Cybosia mesomella*** adult, a species that eats leafy liverworts as larvae. Photo by Stanislav Krejčik, through Creative Commons.

Figure 53. ***Jungermannia leiantha*** with perianths, a genus that is a food source for ***Cybosia mesomella***. Photo by Hermann Schachner, through Creative Commons.

Figure 54. ***Hypoprepia miniata*** larva, a species that feeds on both mosses and lichens. Its coloration hides it well among mosses. Photo by M. J. Hatfield, through Creative Commons.

Figure 55. ***Hypoprepia miniata*** adult. Photo by Tom Peterson, Fermilab, through Public Domain.

In northern Europe ***Nudaria mundana*** (Figure 56) larvae feed on both lichens and liverworts growing on rocks (Forster & Wohlfahrt 1960).

Figure 56. ***Nudaria mundana*** adult; larvae feed on lichens and liverworts on rocks. Photo by James K. Lindsey, with permission.

Erebidae

Many of the bryophyte-feeding species have been removed from **Arctiidae** and placed in **Erebidae**, whereas other systematists keep them in **Arctiidae**. I have chosen to list them under **Erebidae** because the majority of bryophyte feeders are grouped here. My usual source for nomenclature, Encyclopedia Online, is inconsistent in its placement of them.

Atolmis rubricollis (Figure 57-Figure 59) is one of these species. Its larvae feed on mosses and lichens growing on the trunks of trees (epiphytes) (Shield 1856; Dincă 2005). Hence, it is not surprising that the pupae occur under moss, but on decaying trees. ***Atolmis rubricollis*** is a tiny, inconspicuous moth that makes its winter cocoon in mosses and litter (Coutin 2004).

Figure 57. ***Atolmis rubricollis*** larva, a stage that eats mosses and makes cocoons there on trees. Photo by Harald Süpfle, through Creative Commons.

Figure 58. ***Atolmis rubricollis*** pupa on moss where it spends its winter. Photo by Harald Süpfle, through Creative Commons.

Figure 59. ***Atolmis rubricollis*** adult, emergent from a pupa that overwinters in mosses and litter. Photo by Sanja565658, through Creative Commons.

Larvae of both ***Miltochrista miniata*** (Figure 60-Figure 62) and ***Lithosia quadra*** (Figure 63-Figure 64) are bryophyte and lichen feeders in Romania (Dincă 2005). Likewise, ***Dysauxes ancilla*** (Figure 65-Figure 67) and the genus ***Eilema*** include bryophytes in their larval diet there, including ***E. lurideola*** (Figure 68-Figure 70), ***E. complana*** (Figure 71-Figure 72), ***E. pseudocomplana*** (Figure 73), and ***Eilema sororcula*** (Figure 74-Figure 76). In addition to these, Wagner (2016b) adds ***E. morosina*** (Figure 77-Figure 80) as a species that includes mosses in its diet in Europe.

Figure 60. ***Miltochrista miniata*** eggs on rotting wood, a species whose larvae include mosses among their food. Photo by Wolfgang Wagner, with permission.

Figure 61. ***Miltochrista miniata*** larva on moss, one of its food sources. Photo by Wolfgang Wagner, with permission.

Figure 62. ***Miltochrista miniata*** adult, a species whose larvae feed on bryophytes. Photo by Stanislav Krejčík, through Creative Commons.

Figure 63. ***Lithosia quadra*** larva, a species that includes mosses and lichens in its diet. Photo by Wolfgang Wagner, with permission.

Figure 64. ***Lithosia quadra*** adult, a species whose larvae feed on bryophytes. Photo by František Šaržík, through Creative Commons.

Figure 65. ***Dysauxes ancilla*** larva, a species that includes mosses in its diet. Photo by Wolfgang Wagner, with permission.

Figure 66. ***Dysauxes ancilla*** habitat. Photo by Wolfgang Wagner, with permission.

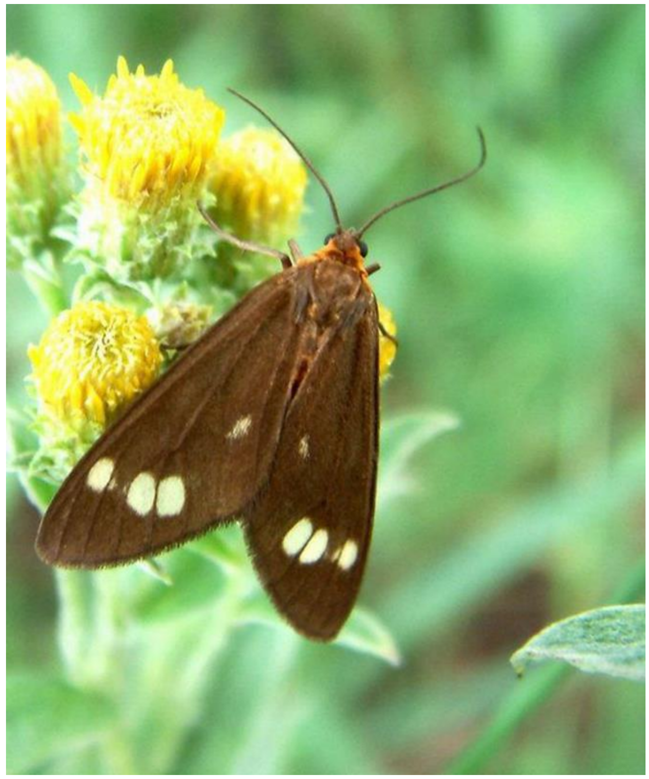

Figure 67. ***Dysauxes ancilla*** adult, a species whose larvae include mosses in their diet. Photo by Ondřej Zicha, through Creative Commons.

Figure 68. ***Eilema lurideola*** larva, a moss and lichen feeder. Photo by Wolfgang Wagner, with permission.

Figure 69. ***Eilema lurideola*** pupa, a species that includes bryophytes in its larval diet. Photo by Wolfgang Wagner, with permission.

Figure 70. ***Eilema lurideola***, a species whose larvae feed on a variety of plants, including mosses. Photo by Kurt Kulac, through Creative Commons.

Figure 71. ***Eilema complana*** larva on moss, one of its food items. Photo by Tristan Bantok, with permission.

Figure 72. ***Eilema complana*** adult, a species with a broad larval diet that includes mosses. Photo by Ondřej Zicha, through Creative Commons.

Figure 73. ***Eilema pseudocomplana*** adult, a species whose larvae include mosses in the diet. Photo by Matthew Gandy, with permission.

Figure 74. ***Eilema sororcula*** larva, a species with a broad diet that includes mosses and lichens. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 75. ***Eilema sororcula*** larval head, a species having a broad diet that includes mosses and lichens. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 76. ***Eilema sororcula*** adult, a species whose larvae include mosses in their diet. Photo by Miroslav Fiala, through Creative Commons.

Figure 77. ***Eilema morosina*** larva, a moss eater. Photo by Wolfgang Wagner, with permission.

Figure 78. ***Eilema morosina*** larval habitat. Photo by Wolfgang Wagner, with permission.

Figure 79. ***Eilema morosina*** pupa. Photo by Wolfgang Wagner, with permission.

Figure 80. ***Eilema morosina*** adult, a species whose broad larval diet includes mosses. Photo by Wolfgang Wagner, with permission.

Hypercompe scribonia (syn. = *Ecpantheria deflorata*; Figure 81-Figure 82) actually eats the thallose liverwort, ***Conocephalum conicum*** in western Indiana, USA (Figure 83) (Spencer *et al*. 1984). It normally feeds on two species of *Plantago* (Figure 84), a seed plant, and Spencer and coworkers suggest that the surface is similar to that of the liverwort and the two plants grow intermixed, possibly causing the shift despite major differences in chemistry. They noted this liverwort feeding behavior in the autumn, which suggests the possibility that the chemical shift may be a means of preparing for winter. Nevertheless, they raised several larvae to adults in the lab, using ***C. conicum*** as the only food source.

Figure 81. ***Hypercompe scribonia*** larva, a herbivore on ***Conocephalum conicum***. Photo by Micha L. Rieser, through Creative Commons.

Figure 82. ***Hypercompe scribonia*** adult, a species whose larvae consume the liverwort ***Conocephalum conicum***. Photo by R. A. Nonenmacher, through Creative Commons.

Figure 83. ***Conocephalum conicum***, a food source for ***Hypercompe scribonia***. Photo by Hermann Schachner, through Creative Commons.

Figure 84. ***Plantago major***, a genus that is normal food for ***Hypercompe scribonia***. Photo by Olivier Pichard, through Creative Commons.

The secondary compounds of ***Conocephalum conicum*** (Figure 83) are well known. This liverwort is rich in mono- and sesquiterpenoids (Asakawa *et al.* 1976; Markham & Porter 1978; Spencer 1979). We also know that some terpenoids from liverworts inhibit Lepidoptera feeding (Wada & Munakata 1971). *Plantago* (Figure 84), on the other hand, is rich in iridoid glycosides (Jensen *et al*. 1975). It is possible that whatever permits the larvae to feed on the toxic glycosides also permits them to feed on the terpenoids in liverworts.

The **Lithosiini** have been known from several studies as bryophyte feeders (Forbes 1960; Holloway 1988; Aba 2013). Moreno *et al*. (2014) summarized feeding in the family by stating that the members of the tribe **Arctiini** feed on a wide range of plant species whereas the **Lithosiini** specialize on lichens, algae, and bryophytes (Wagner 2009).

Several species of Tribe **Lithosiini** resemble **Microlepidoptera** as adults (Coutin 2004). Furthermore, the larvae consume liverworts. Larvae of ***Thumatha senex*** (Figure 85) likewise consume liverwort leaves, particularly the genus ***Jungermannia*** (Figure 53), as well as lichens. Manley (2009) treated ***Thumatha senex*** as a nighttime cryptogam feeder that includes mosses in its diet (Macek *et al*. 2007; Manley 2009).

Figure 85. ***Thumatha senex*** adult, a liverwort and lichen consumer. Photo by James K. Lindsey, with permission

Lymantriidae – Tussock Moths

Lymantria dispar (Figure 86-Figure 87), the gypsy moth, spins threads over its retreat in a crack in the bark (Rennie 1857). Occasionally they may use a curtain of moss such as ***Hypnum*** (Figure 88) growing there instead of spinning these threads.

Figure 86. ***Lymantria dispar*** (gypsy moth) male adult. Larvae of this species sometimes use mosses instead of spinning threads over their retreat on bark. Photo by Jérôme Albre, with permission.

Figure 87. **Lymantridae** larva. ***Lymantria dispar*** sometimes uses mosses instead of spinning a cocoon. Photo by Jérôme Albre, with permission.

Figure 88. ***Hypnum cupressiforme*** with young sporophytes on bark. ***Hypnum*** is sometimes used to cover larvae of ***Lymantria dispar***. Photo by Dick Haaksma, with permission.

Noctuidae – Owlet Moths

Haines and Renwick (2009) summed up the paucity of bryophagous insects. They considered that three deterrents were responsible for their limited consumption: chemical defenses, low digestibility, and low nutrient content. They examined this phenomenon by testing pre and post-ingestive defenses of four species of mosses [***Bryum argenteum*** (Figure 89), ***Climacium americanum*** (Figure 90), ***Leucobryum glaucum*** (Figure 91), ***Sphagnum warnstorfii*** (Figure 92)]. Even when they had no other choice, larvae of ***Trichoplusia ni*** (cabbage looper; Figure 93-Figure 94) ate considerably more lettuce or wheat germ than they did any of the moss species. Post ingestive responses could only be evaluated in ***C. americanum*** because the larvae ate too little of the other species for evaluation. Digestibility, assimilation, and overall utilization efficiency did not differ between lettuce and ***C. americanum***. In disk choice experiments, ethanol extracts of ***Leucobryum glaucum*** were deterrent, explaining why this was the least consumed moss in the experiment and providing evidence of pre-ingestive mechanisms. The hypotheses of poor nutrient content and low digestibility were not supported in these experiments.

Figure 89. ***Bryum argenteum***, a moss avoided by ***Trichoplusia ni*** in feeding trials. Photo by Michael Becker, through Creative Commons.

Figure 90. ***Climacium americanum***, a moss avoided by ***Trichoplusia ni*** in feeding trials. Photo by Li Zhang, with permission.

Figure 91. ***Leucobryum glaucum***, a moss avoided by ***Trichoplusia ni*** in feeding trials. Photo by James K. Lindsey, with permission.

Figure 92. ***Sphagnum warnstorfii***, a moss avoided by ***Trichoplusia ni*** in feeding trials. Photo by Michael Lüth, with permission.

Figure 93. ***Trichoplusia ni*** larva, a species that avoids eating bryophytes. Photo by M. J. Hatfield, through Creative Commons.

Figure 94. ***Trichoplusia ni*** adult, a species whose larvae do not choose mosses even with no other choice. Photo by Barry Stewart, with permission.

Several species in Romania feed on mosses (Dincă 2005). These include ***Parascotia fuliginaria*** (Figure 95), ***Calymma communimacula*** (Figure 96)**,** ***Cryphia receptricula*** (Figure 97), and ***Cryphia raptricula*** (Figure 98). Wagner (2016a) also includes ***Cryphia muralis*** (Figure 99) and ***C. algae*** (Figure 100-Figure 102) among the moss feeders in Europe.

Figure 95. ***Parascotia fuliginaria*** adult, a species whose larvae include mosses in their diet. Photo by Biopix, through Creative Commons.

Figure 96. ***Calymma communimacula*** adult, a species whose larvae include mosses in their diet. Photo by Dumi, through Creative Commons.

Figure 97. ***Cryphia receptricula*** adult, a species whose larvae feed on mosses. Photo by Peter Huemer, through Creative Commons.

Figure 98. ***Cryphia raptricula*** adult, a species whose larvae eat mosses. Photo by Biopix, through Creative Commons.

Figure 99. ***Cryphia muralis*** larva, a species that includes mosses and lichens in its diet. Photo by Wolfgang Wagner, with permission.

Figure 100. ***Cryphia algae*** larva, a species that eats mosses, algae, and lichens. Photo by Wolfgang Wagner, need permission.

Figure 101. ***Cryphia algae*** larval habitat. Photo by Wolfgang Wagner, with permission.

Figure 102. ***Cryphia algae*** adult, a species whose larvae include mosses in their diet. Photo by Jérôme Albre, with permission.

Kimmo Silvonen (pers. comm. 1 March 2016) told me about ***Caradrina montana*** (Figure 103) in Europe. He found this larva on a rocky hill on a moss. It accepted the moss as food during rearing, but it may be a polyphagous species that eats a variety of plants. Among these, it feeds on alfalfa leaves in northwestern North America (McLeod 2005).

Figure 103. ***Caradrina montana*** larva, a species that can be reared on moss. Photo courtesy of Kimmo Silvonen.

The feeding of ***Agrotis*** sp. (Figure 104) on moss capsules (Figure 105-Figure 106) of ***Haplocladium microphyllum*** (Figure 107) is well documented. Fang and Zhu (2012) experimented to see what else they would eat and found they would feed to various degrees on capsules of ***Ditrichum pallidum*** (Figure 108), ***Funaria hygrometrica*** (Figure 109), ***Physcomitrium sphaericum*** (Figure 110), ***Pogonatum inflexum*** (Figure 111), and ***Trematodon longicollis*** (Figure 112). The latter two species were only sparsely grazed and caused a high mortality rate. Fang and Zhu suggested that the lipid content may be important in their selection.

Figure 104. ***Agrotis puta*** adult male, member of a genus in which larvae of at least some species feed on moss capsules. Photo by Jérôme Albre, with permission.

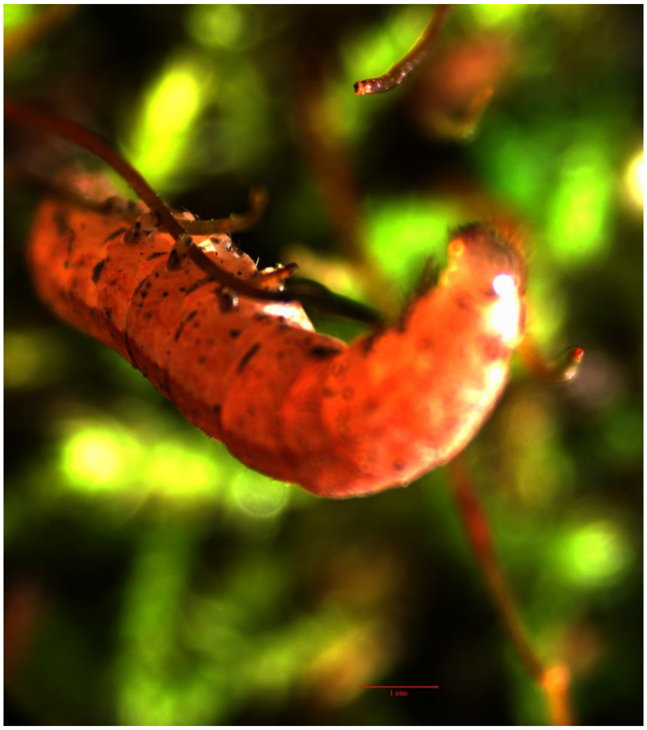

Figure 105. ***Agrotis*** eating capsules of ***Haplocladium microphyllum***. Photo by Rui-Liang Zhu, with permission.

Figure 106. ***Haplocladium microphyllum*** capsules missing due to feeding by ***Agrotis***. Photo by Rui-Liang Zhu, with permission.

Figure 107. ***Haplocladium microphyllum*** with capsules. Species of ***Agrotis*** feed on these capsules. Photo by Scott Zona, through Creative Commons.

Figure 108. ***Ditrichum pallidum*** with capsules that serve as food for ***Agrotis***. Photo by Bob Klips, with permission.

Figure 109. ***Funaria hygrometrica*** with capsules that serve as food for ***Agrotis***. Photo by Li Zhang, with permission.

Figure 110. ***Agrotis*** sp. eating a capsule of ***Physcomitrium sphaericum***. Photo by Rui-Liang Zhu, with permission.

Figure 111. ***Pogonatum inflexum*** with capsules that serve as food for ***Agrotis***. Photo through Creative Commons.

Figure 112. ***Trematodon longicollis*** capsules that serve as food for ***Agrotis***. Photo by Bobby Hattaway, through Creative Commons.

Agrotis sp. avoids the capsules of ***Pogonatum inflexum*** (Table 1; Fang & Zhu 2012). On the other hand, when only ***Haplocladium microphyllum*** was available as food, a late-instar larva consumed 190 capsules (Figure 113). Similar herbivory occurred on ***Physcomitrium sphaericum*** and ***Funaria hygrometrica*** (Figure 113) Fang and Zhu compared the phenolic content (Figure 114) and nutrient content (Figure 115) among several mosses. They found that These capsules contained significantly more lipids that the tracheophyte leaves from the same environment (Figure 115).

Table 1. 24-hour consumption of moss capsules in three samples of 30 capsules each by an individual ***Agrotis*** sp. in early, mid, and late instar stages. Based on Fang & Zhu 2012.

	instars				
	early		**mid**		**late**
Haplocladium microphyllum	30	–	30	–	30
Funaria hygrometrica	30	–	30	–	30
Physcomitrium sphaericum	30	–	30	–	30
Trematodon longicollis	30	–	30	–	28
Ditrichum pallidum	30	–	2	–	3
Pogonatum inflexum	5	–	4	–	7

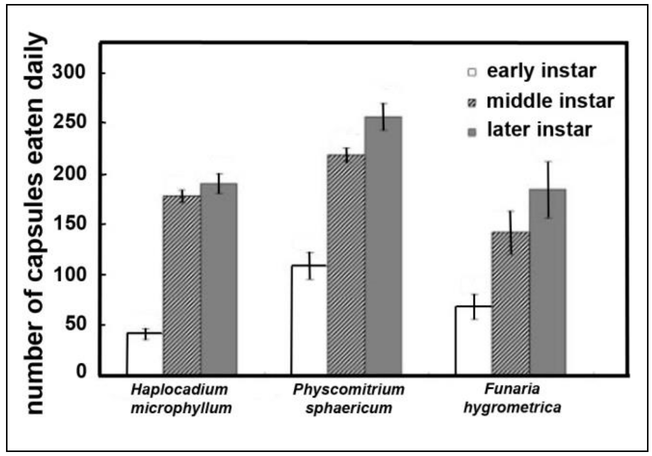

Figure 113. Number of moss capsules consumed in 24 hours by individuals of ***Agrotis*** sp. Based on Fang & Zhu 2012.

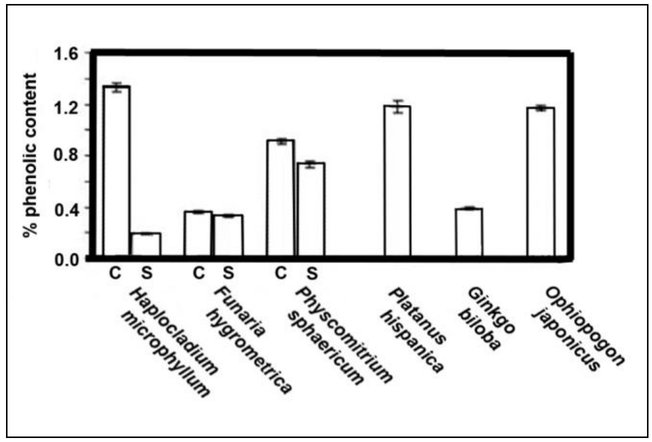

Figure 114. Phenolic content of capsules of three mosses compared to that of three tracheophytes. Based on Fang & Zhu 2012.

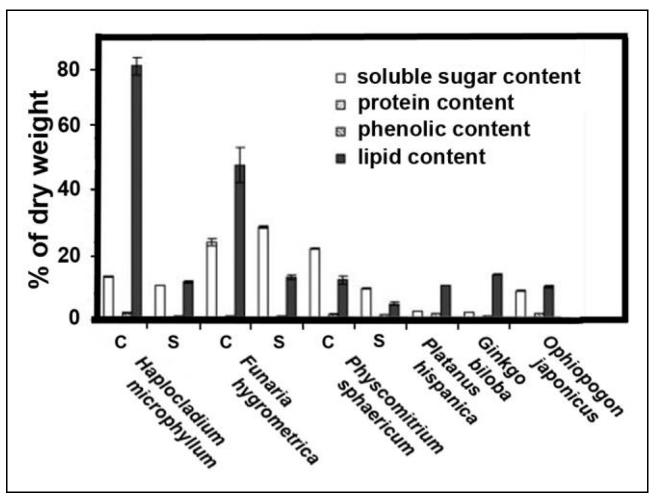

Figure 115. Percentage nutrient content of moss capsules (C) and setae (S) by weight, compared to that of three tracheophytes. Leaves of *Ophiopogon japonicus* (flowering plant) were fresh; the other two seed plant leaves were fallen. Redrawn from Fang & Zhu 2012.

In Europe under mosses on the spreading beech roots, one can find the brown pupae (Figure 116) of ***Herminia grisealis*** (**Noctuidae**; Figure 117-Figure 119) (Shield 1856).

Figure 116. ***Herminia grisealis*** pupa; these can be found under mosses on beech roots. Photo by Wolfgang Wagner, with permission.

Figure 117. ***Herminia grisealis*** larva, a species that pupates under mosses. Photo by Wolfgang Wagner, with permission.

Figure 118. ***Herminia grisealis*** adult, gray color variant, a species that pupates under mosses among beech roots. Photo by ©entomart, through Creative Commons.

Figure 119. ***Herminia grisealis*** brown color variant, a species that pupates under mosses among beech roots. Photo by Donald Hobern, through Creative Commons.

Larvae of the green mahoe moth (***Feredayia graminosa***; Figure 120-Figure 123) in New Zealand feeds on mahoe (*Melicytus ramiflorus*; Figure 124), a woody member of the violet family (Harris 2015). But when it becomes an adult, it rests on tree trunks, where its 18 mm length makes it very obvious on white bark. Fortunately for these moths, they are able to seek out epiphytic mosses on these trees, resting on them during the day undetected because their cryptic coloration hides them from the casual view of avian predators. They feed at night when their predators are sleeping. The males smell like vanilla and use their enlarged hind wings to fan this odor over females during mating.

Figure 120. ***Feredayia graminosa*** adult on moss, showing its ability to blend with mosses. Photo by Donald Hobern, through Creative Commons.

Figure 121. ***Feredayia graminosa*** adult looking like a patch of moss on bark. Photo by Jon Sullivan, with permission.

Figure 122. ***Feredayia graminosa*** blending with mosses and lichens on bark as it rests during the day. Photo by Pete McGregor, with permission.

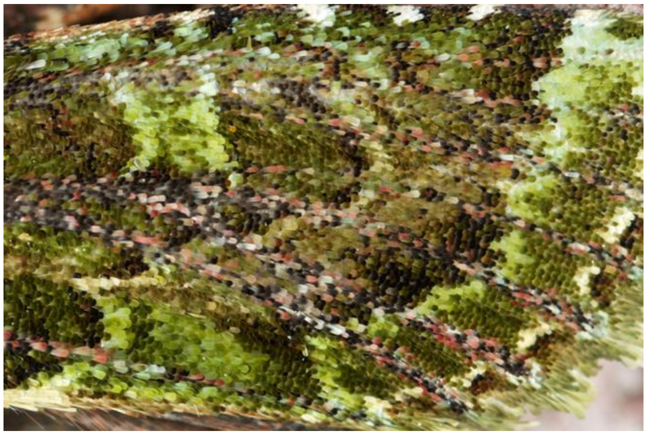

Figure 123. ***Feredayia graminosa*** wing scales showing cryptic coloration that blends with lichens and mosses on bark. Photo by Jon Sullivan, with permission.

Figure 124. ***Melicytus ramiflorus***, food plant of ***Feredayia graminosa***. Photo by Jon Sullivan, through Creative Commons.

Rennie (1857) discovered interesting behavior of a species of the moth in the genus ***Bryophila*** (Figure 125-Figure 126). This caterpillar is small and feeds on minute mosses and lichens on old walls. It builds its cocoons from moss branchlets cut into suitable lengths, including a portion of earth with these detached pieces (Figure 126). In making its cocoon, it arranges the earth on the inside and moss on the outside to make a vault. If this species is deprived of soil in the lab, but provided with moss, it will build a hollow ball by interweaving the moss.

Shield (1856) reported that larvae of ***Bryophila domestica*** (=*Cryphia domestica*; Figure 125) include bits of mosses in their webbing (Figure 126). They bite their way out of these cocoons when the weather is warm, returning to them and resealing them when it is again too cold. The included mosses and other bits help to conceal them while they are in hiding. Shield observed them biting off bits of moss and weaving them between the threads of silk, completely hiding the larva inside.

Figure 125. ***Bryophila domestica*** adult, a species whose larvae include mosses in their webbing. Photo by Ian Kimber, with permission.

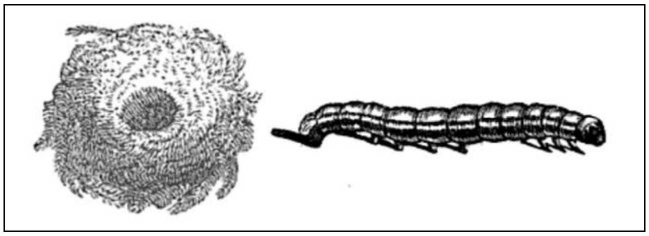

Figure 126. ***Bryophila domestica*** (maybe) nest with mosses and caterpillar. Image by James Rennie (book from 1800's), through public domain.

Acronicta myricae (see Figure 127) is also among the moths that spin silken cocoons, in this case covered with mosses (Buckler 1871).

Figure 127. ***Acronicta euphorbiae*** larva; ***Acronicta myricae*** builds its cocoons on mosses. Photo by Harald Süpfle, through Creative Commons.

We don't always know the role of the mosses, and they may only be indicators of a suitable environment. For example, in areas with boreal forest, ***Xestia rhaetica*** (Figure 128) is distributed in the old, moist spruce forests where mosses form a thick layer (Mönkkönen & Mutanen 2003). But what is the role of these mosses, if any?

Figure 128. ***Xestia rhaetica*** adult, an occupant of old, moist spruce forests with a thick layer of mosses. Photo by Dumi, through Creative Commons.

Now there appears to be a new noctuid added to the bryophages. Timea Deakova has sent me images that appear to be those of ***Noctua pronuba*** (Figure 129-Figure 130). A hoard of these hungry larvae devoured a large portion of her experiments on nitrogen. Could it be the nitrogen in the experiment or do these larvae just like mosses?

Figure 129. ***Noctua pronuba*** larva eating ***Bryum capillare*** and surrounded by frass. Photo courtesy of Timea Deakova.

Figure 130. ***Noctua pronuba*** larva on ***Polytrichum juniperinum***. Photo courtesy of Timea Deakova.

Summary

In the **Geometridae**, larvae are often colored to blend with their surroundings (including bryophytes), having patterns of brown, green, and gray. Some of these larvae can do considerable damage to the bryophytes, particularly mosses, through herbivory. Some overwinter among mosses as pupae. Others lay eggs on mosses, close to the tree leaves that are eaten by the larvae. And some use the water associated with the bryophytes. The hemlock looper often lays eggs among mosses, then becomes a nuisance when its larvae migrate to conifer leaves and consume the leaf tips, killing the leaves.

One member of the **Lasiocampidae** swarm on mosses in autumn – for whatever reason. Few of the **Arctiidae** are bryophyte associates, but some members of the subfamily **Lithosiinae** eat bryophyte capsules. Other members feed on liverwort leaves or moss leaves. The **Erebidae**, sometimes included in the **Arctiidae**, includes most of the bryophyte dwellers that were once **Arctiidae**. **Lymantridae** sometimes use mosses in place of making a web to hide themselves.

Some **Noctuidae** find bryophytes distasteful; in ***Climacium americanum***, digestibility, assimilation, and overall use efficiency did not differ from that of lettuce, but there was far more consumption of lettuce. However, some species do feed on mosses. And a species of ***Agrotis*** feeds on moss capsules, but avoids those of ***Pogonatum inflexum***. In fact, the other moss capsules contained more lipids than the local tracheophytes. Some species also use mosses for pupation sites. And some adults have coloration that permits them to rest on tree-trunk bryophytes without being seen easily. Some species incorporate bryophytes in their cocoons.

Acknowledgments

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