CHAPTER 12-12 TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA BIOLOGY AND ECOLOGY

TABLE OF CONTENTS

CHAPTER 12-12 TERRESTRIAL INSECTS: HOLOMETABOLA – LEPIDOPTERA BIOLOGY AND ECOLOGY

Figure 1. These **Lepidoptera** seem to be on these epiphytic bryophytes for a reason, but often we don't know why. Photo by Janice Glime.

Lepidoptera

I was surprised to find that in one study in Romania Dincă (2005) found that 1.8% of the approximately 1000 Macrolepidoptera taxa were "moss" consumers. Pierce (1995) stated that larvae that live in mosses have an environment that is close to aquatic. But few **Lepidoptera** live in the water, so we can expect that these terrestrial insects may have other reasons for visiting or living in bryophytes. On the other hand, the **Trichoptera** and **Lepidoptera** are closely related (Crampton 1920; Shields 1988; Britannica 2008), and most **Trichoptera** larvae are aquatic. Shields contends that the **Lepidoptera** evolved from aquatic **Trichoptera**, so it is therefore predictable that some have strong needs for moisture. This divergence most likely occurred in the late Triassic at a time when many streams were dry and water was scarce, eliminating many insects that were dependent on water.

Klok and Chown (1997) report that water balance is important for the sub-Antarctic caterpillar, ***Pringleophaga marioni*** (**Tineidae**; Figure 2). But these moths seem to have no mechanisms for preserving or regulating their water, hence requiring moist habitats. One of these habitats for the larvae is in the mire moss ***Sanionia uncinata*** (Figure 3) (Burger 1978). These moths are wingless as adults and thus have a limited distribution on Marion Island.

Figure 2. ***Pringleophaga marioni*** adult, a sub-Antarctic moth with no known mechanism to regulate water. Photo by S. L. Chown, B. J. Sinclair, H. P. Leinaas, and K. J. Gaston, with permission.

Figure 3. ***Sanionia uncinata*** with capsules. This species is home for ***Pringleophaga marioni*** on Marion Island in the sub-Antarctic. Photo by Andrew Hodgson, with permission.

Like all creatures, adult **Lepidoptera** need water. Bryophytes collect water and it often stays at leaf bases and other capillary spaces where cohesion keeps it from rolling away. These water droplets are suitable for the tube-feeding adult **Lepidoptera** to get a drink of water (Figure 4). Martin (2015) has observed butterflies and moths pausing for a drink of water from the moss leaves in her moss garden.

Figure 4. Butterfly on ***Palustriella commutata***, a place where one can often find water droplets. Photo by Serhat Ursavas, with permission.

Life Cycle

All stages of **Lepidoptera** (egg-larva-pupa-adult) are known from bryophytes. The adult females of bryophyte-feeding larvae often lay eggs there. Several families include members whose larvae live in and feed on bryophytes, a number of which specialize on liverworts. These bryophyte-feeding larvae are often in primitive families that originated before flowering plants.

Eggs

For those **Lepidoptera** that use the bryophytes for egg-laying, the bryophytes provide a safe haven for emerging larvae. This is the case for the hemlock looper (***Lambdina fiscellaria***; Figure 5) (an inchworm; **Geometridae** – see Chapter 12-13), which is a serious conifer pest (Shepherd & Gray 1972).

Figure 5. The hemlock looper (***Lambdina fiscellaria***) larva hiding in moss in autumn. Photo from USFS, through public domain.

Some females create cocoons in which they lay eggs (Figure 6-Figure 7). Timea Deakova sent me images of a cocoon of eggs from the moss ***Climacium dendroides*** in Oregon, USA. The larvae eat moss and grass.

Figure 6. Moth cocoon on ***Climacium dendroides***. Photo courtesy of Timea Deakova.

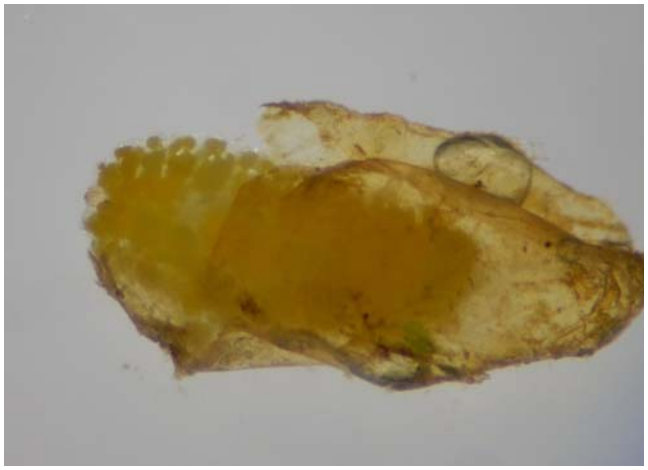

Figure 7. Cocoon from ***Climacium dendroides***, with eggs emerging. Photo courtesy of Timea Deakova.

Figure 8. Moth caterpillar on moss in ***Polytrichum juniperinum*** in Oregon, USA. This larva developed and hatched into the adult in Figure 9. Photo courtesy of Timea Deakova.

Figure 9. Adult that hatched from the above larva on mosses. The ragged wings are due to hungry larvae feeding on them in captivity. Photo courtesy of Timea Deakova.

Figure 10. Moth hatched from larva on moss. Photo courtesy of Timea Deakova.

Larvae

Larvae of **Lepidoptera** can be recognized by the presence of **crochets** (hooks; Figure 11) on their **prolegs** (fleshy short legs on the abdomen) Some **Lepidoptera** spin their cocoons in mosses or use bits of mosses or liverworts as part of the cocoon (Figure 12-Figure 13). Buchanan (1971) reported this behavior for ***Pyrausta cingulata*** (**Crambidae**; Figure 13-Figure 14), ***Phycis subornatella*** (**Pyralidae**), and ***Eana penziana*** (**Tortricidae**; Figure 15) near Perth, Australia. Buckler (1871) reported silken cocoons of larvae of ***Acronicta myricae*** (**Noctuidae**; see Figure 16**-**Figure 17) covered with moss.

Figure 11. ***Cossus cossus*** larval prolegs showing crochets. Photo by Anki Engström <www.krypinaturen.se>, with permission.

Figure 12. **Lepidoptera** larval cocoon of the liverwort ***Riccardia filicina***. Although the larva has left its cocoon, the liverwort fragments are still alive. Photo courtesy of David Glenny.

Figure 13. ***Pyrausta cingulata*** larva with bits of its cocoon. Photo by Bob Heckford, with permission.

Figure 14. ***Pyrausta cingulata*** adult, a species that spins its cocoon on mosses. Photo by Olaf Leillinger, through Creative Commons.

Figure 15. ***Eana penziana*** adult. Larvae of this species build cocoons on mosses. Photo by Kurt Kulac, through Creative Commons.

Figure 16. ***Acronicta euphorbiae*** larva, a species related to the moss user ***Acronicta myricae***. Photo by Harald Süpfle, through Creative Commons.

Figure 17. ***Acronicta*** sp. adult. ***Acronicta myricae*** builds cocoons on mosses. Photo by Olaf Leillinger, through Creative Commons.

Pupation

Bryophytes offer a safe site for pupation of **Lepidoptera** (Figure 18-Figure 20). It is likely that a number of **Lepidoptera** pupate among the bryophytes, but this stage is difficult to identify and is easily overlooked. Hence the records of this stage may not be truly representative of the usage of mosses for overwintering and escape from desiccation. Nevertheless, I have been pleasantly surprised not only by the number of records, but by the identification of the bryophytes involved for both larvae and pupae.

Figure 18. **Lepidoptera** pupal shell in moss. Photo courtesy of Sarah Lloyd.

Figure 19. **Lepidoptera** pupal shell in moss. Photo courtesy of Sarah Lloyd.

Figure 20. **Lepidoptera** pupa on moss. Photo by Vinicius Santana Orsini Brazil.

Some **Lepidoptera** pupae, for example the privet hawk moth ***Sphinx ligustri*** (**Sphingidae**; Figure 21-Figure 24), survive winter in rotting logs covered with mosses, but the necessity for the moss has not been assessed (Brackenbury 1994).

Figure 21. ***Sphinx ligustri*** adult, a species that survives winter as pupae in logs covered with mosses. Photo by Olaf Leillinger, through Creative Commons.

Figure 22. ***Sphinx ligustri*** larva. Photo by Georg Slickers, through Creative Commons.

Figure 23. ***Sphinx ligustri*** pupating, an activity it commonly does in moss-covered logs. Photo ©entomart, through Creative Commons

Figure 24. ***Sphinx ligustri*** mature pupa, the overwintering stage in logs covered with mosses. Photo from ©entomart, through Creative Commons.

Food Sources

Gerson (1982) reviewed what could be found regarding bryophytes as food sources for **Lepidoptera**. He reported that the larvae of **Meessiinae** feed on both lichens and mosses, but they also incorporate the fragments of these two groups of organisms in their cases. ***Nudaria mundana*** eats both saxicolous lichens and liverworts (Forster & Wohlfahrt 1960). Some larvae have a safe haven while they feed on the bryophytes. The ***Sabatinca*** larva is a liverwort mimic with its greenish color and large setae (Tillyard 1922; Yasuda 1962; Gerson 1982; Holloway 1993).

Feeding on Leafy Gametophytes

As I worked on this chapter, I became amazed at the number of **Lepidoptera** that feed on bryophytes. Most feed on the leafy plants (Figure 25). Some of them feed on mosses and others feed exclusively on liverworts.

Figure 25. Caterpillar feeding on the moss ***Fabronia leikipiae***. The caterpillar has an ideal color and pattern to blend in with the bryophyte branches. Photo by Min Petiot.

As early as 1894, Chapman noted that some **Lepidoptera** larvae feed on mosses, especially in the primitive families. We now know that some are bryophyte specialists. Robin Stevenson shared his image with me to demonstrate feeding on mosses (***Tortula truncata***) by **Lepidoptera** larvae (Figure 26).

Figure 26. ***Tortula truncata*** showing feeding damage by larval **Lepidoptera**. Photo courtesy of C. Robin Stevenson

A number of **Lepidoptera** larvae feed on the leafy gametophytes of bryophytes. Members of the primitive lepidopteran suborder **Zeugloptera** are moss feeders (Chapman 1894; Tillyard 1926), suggesting that the advent of flowering plants opened new food sources for them. Among these bryophyte feeders is ***Micropterix calthella*** (**Micropterigidae**; Figure 27-Figure 28) (Chapman 1894).

Figure 27. ***Micropterix calthella*** adult, a bryophyte feeder in its larval stage**.** Photo by Wouter Bosgra, through Creative Commons.

Figure 28. ***Micropterix calthella*** adult of a larval bryophyte feeder. Photo by Tom Deroover, through Creative Commons.

Feeding on Capsules

Fang and Zhu (2012) reviewed accounts of **Lepidoptera** feeding on bryophyte capsules. They found that the known feeding habits of lepidopteran larvae included capsules in only four families: **Micropterygidae** (Gerson 1969), **Mnesarchaeidae** (Grehan 1984), **Arctiidae** (as **Lithosiidae**) (Liu 1989), and **Geometridae** (Maciel-Silva & dos Santos 2011). Thus, theirs is the first record of **Noctuidae** larvae that feed on mosses. ***Agrotis*** sp. (**Noctuidae**; Figure 29) larvae commonly feed on capsules of ***Haplocladium microphyllum*** (Figure 30) in Shanghai in the spring (Fang & Zhu 2012).

Figure 29. ***Agrotis*** feeding on capsules of ***Physcomitrium sphaericum***. Photo by Rui-Liang Zhu, with permission.

Figure 30. ***Haplocladium microphyllum*** capsules and setae where capsules have been completely eaten by a species of ***Agrotis***. Photo by Rui-Liang Zhu, with permission.

Butterflies

"Among those groups of butterflies that feed on plants, none is known to feed on bryophytes or on Psilopsida, Lycopsida, or Sphenopsida, nor is any known from ferns" (Ehrlich & Raven 1964). This statement surprised me because I had already found a number of **Lepidoptera** that feed on bryophytes. But I soon realized these are almost entirely moths. However, there are exceptions (see PAPILIONOIDEA in Chapter 12-14) in the **Lycaenidae** (Callaghan 1992), **Nymphalidae** (Singer & Mallet 1986; Hamm 2015), and **Rionidae** (DeVries 1988). It is interesting that two of these exceptions are butterfly larvae that feed on the epiphylls that live on tracheophyte leaves.

It is not unusual for **Lepidoptera** to eat plants, but it is unusual among the butterflies. While bryophytes are not a main fare, some satyrid butterflies do consume bryophytes (Singer & Mallet 1986). In Japan, the primitive ***Sabatinca*** (Figure 31) and ***Neomicropteryx nipponensis*** (both in **Micropterigidae**; Figure 32) feed on liverworts (Figure 33) (Yasuda 1962).

Figure 31. ***Sabatinca congruella*** larva on a leafy liverwort, demonstrating its cryptic form and color. Photo by George Gibbs, with permission.

Figure 32. ***Neomicropteryx nipponensis*** larva feeding on ***Conocephalum conicum***. Photo by Yume Imada, with permission.

Figure 33. ***Conocephalum conicum***, food for ***Sabatinca*** and ***Neomicropteryx nipponensis*** in Japan. Photo by Hermann Schachner, through Creative Commons.

Epiphylls as Food

Bodner *et al*. (2015) found that in southern Ecuador the caterpillar assemblages often did not feed on their expected hosts. Rather, they chose foliose lichens, dead leaves, and the epiphylls, including bryophytes.

Invertebrates on the Menu

One normally thinks of caterpillars, the larvae of the **Lepidoptera**, as plant eaters. But Murawski (2003) describes "killer" moths that are carnivores, usually on soft-bodied insects and spiders. They use camouflage, seductive odors, and armor shields to enable them to sneak up on their prey. Some (***Maculinea alcon*** – **Lycaenidae**; Figure 34) visit flowers to obtain a waxy cover of hydrocarbons that smell like ***Myrmica*** (Figure 35-Figure 36) ant larvae, enabling them to enter the ant nest. They then trick the ants into accepting them and feeding them while they attack the ant larvae! The ants whose nests are invaded include ***Myrmica scabrinodis*** (Figure 35), ***Myrmica ruginodis*** (Figure 36), and ***Myrmica rubra*** (Figure 37). All three of these ant species are associated with mosses, often nesting under them, hence the **Lepidoptera** live under mosses as well.

Figure 34. ***Maculinea alcon*** adult; larvae of this species trick ants into accepting them and feeding them. These ants typically associate with mosses, hence, so does the ***Maculinea alcon***. Photo by Joris Egger, through Creative Commons.

Figure 35. ***Myrmica scabrinodis***, an ant that is mimicked in smell by the larvae of ***Maculinea alcon***. Photo by Tim Faasen, with permission.

Figure 36. ***Myrmica ruginodis*** adult on moss, an ant species that is fooled by the odors of ***Maculinea alcon*** and takes care of their larvae. Photo by James K. Lindsey, with permission.

Figure 37. ***Myrmica rubra*** workers, a species whose nests are invaded by ***Maculinea alcon***. Photo by Gary Alpert, through Creative Commons.

Some **Lepidoptera** that are indeed carnivorous caterpillars take advantage of the mosses to gain their food in a quite different way. In Hawaii, these carnivores are camouflaged as leaf litter, lichens, twigs, or mosses (Figure 38), permitting them to stalk their invertebrate prey (Murawski 2003).

Figure 38. ***Adelpha serpa celerio***, a moss-mimicking caterpillar from Panama, but in this case, not a carnivore. Photo by Arthur Anker, with permission.

Antiherbivory

The limitation of **Lepidoptera** larvae primarily to leaves of seed plants may be due to antiherbivore compounds. Wada and Manakata (1971) demonstrated that some liverwort terpenoids inhibit feeding by **Lepidoptera** larvae. Ottosson and Anderson (1983) showed that fewer species were associated with ferns than with other tracheophytes and providd evidence that the wide range of chemical defenses in the ferns discouraged many insects from eating them. Nevertheless, the **Lepidoptera** seemed able to exhibit spatiotemporal adaptations that permitted them to avoid the unfavorable biochemistry of the ferns.

Krishnan and Murugan (2013) investigated feeding by **Lepidoptera** on bryophytes, using 20 species. They chose two species [corn earworm, *Helicoverpa zea* (Figure 39) – Noctuidae, and armyworm, *Spodoptera litura* (Figure 40) – Noctuidae)] that do not eat bryophytes. They compared the effects of protein extracts from bryophyte species with those from the normal food plant *Glycine max* (Figure 41) cultivar using bioassays. In these experiments, protein extracts from four species [***Octoblepharum albidum*** (Figure 42), ***Fissidens virens*** (see Figure 43), ***Bryum argenteum*** (Figure 44), and ***Marchantia linearis*** (Figure 45)] caused the greatest decrease in damage in leaf-disk assays and in insect larval growth. They also caused a reduction in efficiency of digestion and food conversion. Further discussion of antiherbivory in **Lepidoptera** is in the following subchapters.

Figure 39. ***Helicoverpa zea*** larva, a species that does not eat bryophytes and avoids extracts of them. Photo by R. L. Croissant, through Creative Commons.

Figure 40. ***Spodoptera litura*** adult, a species whose larvae do not eat bryophytes and avoid extracts of them. Photo by Merle Shepard, Gerald R. Carner, and P. A. C. Ooi, through Creative Commons.

Figure 41. ***Glycine max***, a normal food plant of larvae of ***Helicoverpa zea*** and ***Spodoptera litura***. When bryophyte extracts were applied to these leaves, the larvae of these two species reduced feeding on it. Photo by Pancrat, through Creative Commons.

Figure 42. ***Octoblepharum albidum***, a species that deters at least some **Lepidoptera** larvae from eating it. Photo by Niels Klazenga, with permission.

Figure 43. ***Fissidens dubius***; ***F. virens*** deters at least some **Lepidoptera** larvae from eating it. Photo by Kurt Stüber, through Creative Commons.

Figure 44. ***Bryum argenteum***, a species that deters at least some **Lepidoptera** larvae from eating it. Photo by Martin Hutten, with permission.

Figure 45. ***Marchantia linearis***, a species that deters at least some **Lepidoptera** larvae from eating it. Photo by Manju C. Nair, through Creative Commons.

Adaptations

Bryophytes can provide a number of characteristics that are favorable for small invertebrates. They absorb water rapidly, reduce evaporation, and provide insulation against extremes of temperature and wind (Gerson 1982).

Most adult **Lepidoptera** associated with bryophytes do not have morphological adaptations for the bryophytic habitat, but rather blend with the flowers they visit. Others, however, are dull grays and browns that permit them to blend with the bark where they rest.

Larvae, on the other hand, are usually colored with browns, grays, and greens, and have tubercles or spines. Some have behaviors that cause them to include bryophytes in the construction of cocoons or cases. Their biggest adaptation, however, seems to be the ability to eat and digest the bryophytes. On the other hand, for at least some families, this is a primitive trait (Powell *et al*. 1999; Hashimoto 2006).

Some of the larvae, but few of the adults, have color patterns that would camouflage them among the bryophytes (Figure 46-Figure 47). Intermixed greens, browns, and black would make it easy for the larvae to hide among bryophytes, but these colors do not always coincide with known uses. Is this just our lack of sufficient observations, or are they adapted to walking among the mosses on their way from one location to another?

Figure 46. Caterpillar on moss, showing greens, black, and a brown head capsule. But does it live there? Photo by Carrie Andrew, with permission.

Figure 47. Moth adult on bryophytes, showing cryptic coloration. Photo courtesy of Sarah Lloyd.

One type of mimicry that seems not to be reported elsewhere is that reported by Györffy (1952). He relays his adventures in checking out twin capsules, only to discover that one was not a capsule at all. On the setae of ***Atrichum undulatum*** (Figure 48) he found not only a capsule, but also a cocoon. He reared the cocoon successfully to its maturity, from which emerged a moth. He did not describe it in this case, so it is not clear if it truly resembled a capsule of the moss, but especially noticeable as the animal it was.

Figure 48. ***Atrichum undulatum*** with capsules, home for some **Lepidoptera** pupae on the setae. It is easy to see how a pupa might be inconspicuous among these capsules. Photo by Michael Lüth, with permission.

Habitats

In their altitudinal study in Australia and New Zealand, Andrew *et al*. (2003) collected bryophytes and extracted invertebrates using the kerosene phase separation method. They identified these to family and found only one family of **Lepidoptera**. Nevertheless, bryophyte-dwelling **Lepidoptera** are more common than most of us might suspect in the forests and peatlands.

Forests

Diversity of **Lepidoptera** in forests is related to, but not limited to, the layers of the forest, disturbance, and management (Thorn *et al*. 2015). These researchers found that abundance of moth larvae of the **saproxylic** (pertaining to decaying wood) and detritus-feeding guilds was higher under a regime of natural disturbance and in multi-layered stands. Larvae of moss-feeding moths, on the other hand, was lower in multi-layered stands.

Some of the relationships may be indirect, but nevertheless, important. ***Liphyra brassolis*** (**Lycaenidae**; Figure 49-Figure 51) is a rarely found species, protected as larvae from ant bites by a leathery "hide." Larvae of this species enter green tree ant (***Oecophylla smaragdina*** – **Formicidae**; Figure 52) nests (Figure 53) to feast on larvae. These don't involve bryophytes, but similar behavior in aerial moss nests of ants is possible (See Chapter 12-10). It is certainly worth looking for them.

Figure 49. Ventral view of ***Liphyra brassolis*** larva, an insect that invades ant nests and is protected from attack by its leathery covering. Photo by Martin Lagerwey, with permission.

Figure 50. ***Liphyra brassolis*** larva showing head view, an insect that invades ant nests and is protected from attack by its leathery covering. Photo by Martin Lagerwey, with permission.

Figure 51. Dorsal view of ***Liphyra brassolis*** larva, showing its thick, leathery covering that protects it from ant attacks. Photo by Martin Lagerwey, with permission.

Figure 52. Tree-dwelling ***Oecophylla smaragdina*** carrying a grub. Photo by Zloulemark, through Creative Commons.

Figure 53. Aerial nest of ***Oecophylla smaragdina*** where caterpillars of ***Liphyra brassolis*** go to feed. Photo by J. M. Garg, through GNU Free License.

Epiphytes

In the tropical tree canopy, bryophyte and other epiphyte assemblages can be important food sources. Yanoviak *et al*. (2004). observed that larvae of the **Lepidoptera** on bryophytes occurred exclusively in the green fraction. The distribution of small epiphytes is influenced by the gross epiphyte morphology and location (Martin 1938; Gerson 1982).

Events such as hurricanes can have a severe impact on the epiphytic flora, including bryophytes, and the fauna living among them (Loope *et al*. 1994). Loss of bryophytes may not only be a loss of food and cover, but the **Lepidoptera** that live among them may be dispersed during the hurricane, but not necessarily to a suitable habitat.

But not all leaf dwellers feed on the leaves they inhabit. Some species of **Lepidoptera** occur regularly in the canopy leaf habitat and feed on the epiphylls, including bryophytes, algae, lichens, and fungi (Lucking 2000). Some are broad spectrum feeders, but the larvae of **Lepidoptera** seem to specialize on either the lichens or bryophytes.

Pettersson *et al*. (1995) found that larger invertebrates (>2.5 mm) served as food for foraging perching birds. These food invertebrates are higher in number in natural forests and include **Lepidoptera** among the dominant species. Their number and biomass relate to the abundance of lichens. This suggests that it would be worthwhile to look for similar relationships with bryophytes.

Bogs and Wetlands

Peatlands can be ideal habitats for many butterflies and moths. Spitzer and Jaroš (1993) found 569 **Lepidoptera** species in a single peat bog in Central Europe! Jaroš *et al*. (2014) found 1040 species of moths and butterflies in just five peat bogs in the Třeboň Basin up to the montane/subalpine zone of the Bohemian Forest. These included 33 relict species of cold-adapted **tyrphobionts** [species living only in peat bogs and mires (Peus 1928)] and 74 **tyrphophilous** species that prefer peatlands. Spitzer and Jaroš (2014) contend that the bogs are refugia for northern **Lepidoptera** species by creating a climate that is suitable. The ***Sphagnum*** (Figure 54) is responsible for temperature-buffered microclimates that are suitable for these northern relict species of **Lepidoptera**.

Väisänen (1992) used a belt transect to sample butterflies and day-active mothsin a raised bog in southeastern Finland. The species richness was higher in the adjacent mineral land, with the highest number of both species and individuals on the **lagg** [nutrient-enriched zone that grades to land (Paradis *et al*. 2015)] and marginal slope. The Lepidoptera communities were related primarily to the structural characteristics of the bog, including tree height and undergrowth floristic characteristics (Väisänen 1992).

Figure 54. ***Sphagnum magellanicum***, dominant ***Sphagnum*** in a raised bog that has 11 tyrphobiontic and 14 tyrphophilous **Lepidoptera**. Photo by James K. Lindsey, with permission.

A number of butterflies (**Lepidoptera**: especially **Lycaenidae**, **Nymphalidae**, and **Satyridae**) complete their entire life cycle within peatland habitats of the Lake Superior drainage basin in northwestern Wisconsin (Nekola 1998). Nekola surveyed 70 peatlands in the drainage basin. The highest number of taxa occur in the muskeg sites, including five species that do not occur in other peatlands. In both the muskegs and kettlehole peatlands, butterfly species richness correlates highly with habitat size. These sites provide the southernmost locations for these northern species.

Chapman (1894) noted that some moth caterpillars in bogs use ***Sphagnum*** (Figure 54) for nests. And some eat the ***Sphagnum***. But more commonly, the ***Sphagnum*** provides a suitable habitat for the host plant. For example, one species, ***Nola aerugula*** (**Nolidae**; Figure 55), seems to be present as a dominant in a number of bogs, at least in Lithuania (Dapkus 2004a, b). It occurs throughout most of Europe, east to Japan. The larvae feed on *Trifolium* (Figure 56) and *Lotus corniculatus* (Figure 57), but also on *Betula* (Figure 58), *Salix* (Figure 59), and *Populus* (Figure 60) species, indicating its wide habitat distribution, but not indicating any direct use of the bryophytes.

Figure 55. ***Nola aerugula*** adult, a species that is often dominant in Lithuanian bogs. Photo by André den Ouden, through Creative Commons.

Figure 56. ***Trifolium repens***, a genus that is food for ***Nola aerugula***. Photo by Forest and Kim Starr, through Creative Commons.

Figure 57. ***Lotus corniculatus***, food for ***Nola aerugula***. Photo by David G. Smith <www.delawarewildflowers.org>, with online permission.

Figure 58. ***Betula populifolia*** leaves, in a genus that is food for ***Nola aerugula***. Photo by Richtid, through Creative Commons.

Figure 59. ***Salix cinerea*** leaves, in a genus that is food for ***Nola aerugula***. Photo by Sten Porse, through Creative Commons.

Figure 60. ***Populus tremula*** leaf, in a genus that is food for ***Nola aerugula***. Photo by Treetime, through Creative Commons.

Dapkus (2000) compared **Lepidoptera** in two peatlands and a raised bog in Lithuania. The raised bog was dominated by ***Sphagnum magellanicum*** (Figure 54) and exhibited true tyrphophilic and tyrphobiontic species, but none was present in the two peatlands that had been affected by disturbance due to peat extraction. In all, the raised bog had 11 tyrphobiontic and 14 tyrphophilous **Lepidoptera**, whereas the Baloða peatland had 4 tyrphobiontic and 9 tyrphophilous **Lepidoptera** species. The Palios peatland fared even worse with only 3 tyrphophilous and no tyrphobiontic **Lepidoptera** species.

Spitzer and Jaroš (1993) conducted an extensive survey of the **Lepidoptera** of a bog in southern Bohemia. They noted that all the tyrphobionts feed on peat bog plants. But for some of the tyrphophilous species, mosses are on the dinner table. These include ***Bryotropha boreella*** (**Gelechiidae**; Figure 61-Figure 63), ***Phiaris micana*** (**Tortricidae**; Figure 64-Figure 65), and ***Phiaris palustrana*** (**Tortricidae**; Figure 66-Figure 67). In addition, ***Thumatha senex*** (**Erebidae**; Figure 68) feeds on both mosses and lichens.

Figure 61. ***Bryotropha boreella*** adult on ***Sphagnum***, a food source for its larvae. Photo by Stephen Palmer, with permission.

Figure 62. ***Bryotropha boreella*** larva on its food source, a moss. Note the net surrounding the larva. Photo © Bob Heckford, with permission.

Figure 63. ***Bryotropha boreella*** pupa on moss. Photo © Bob Heckford, with permission.

Figure 64. ***Phiaris micana*** larva, a moss eater in bogs. Photo by James K. Lindsey, with permission.

Figure 65. ***Phiaris micana*** adult, a bog species with larvae that eat mosses. Photo by James K. Lindsey, with permission.

Figure 66. ***Phiaris palustrana*** adult, a bog species with larvae that eat mosses. Photo by Donald Hobern, through Creative Commons.

Figure 67. ***Phiaris palustrana*** larva, a moss eater in bogs. Photo by Bob Heckford, with permission.

Figure 68. ***Thumatha senex*** adult, a species whose larvae feed on mosses and lichens. Photo by James K. Lindsey, with permission.

The question remains, why are bogs important to these tyrphobiontic and tyrphophilous species? What is the role of the bryophytes? Do they simply provide the habitat needed by tracheophyte food plants, or are they necessary to survive in some stage of the life cycle?

So far, it appears that few studies indicate that any bog species feed on the bryophytes. In New Zealand Grehan and Patrick (1984) found that the larvae of ***Cladoxycanus minos*** (**Hepialidae**; Figure 69) build feeding tunnels in the moss, extending to 300 mm deep and under the water. This species eats ***Sphagnum cristatum*** (Figure 70). Two other unidentified species of **Hepialidae** likewise make tunnels into the moss mat. In the same bog ***Wiseana umbraculata*** (**Hepialidae**; Figure 71) occurs on saturated mosses that are in close contact with the soil surface.

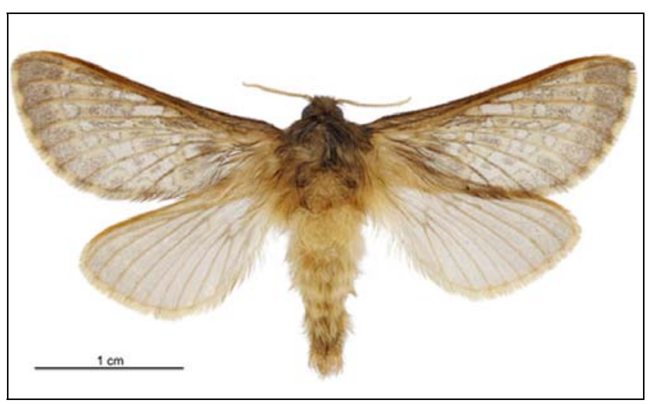

Figure 69. ***Cladoxycanus minos*** male adult; this species builds larval feeding tunnels in mosses. Photo from Landcare Research, Manaaki Whenua, with online permission.

Figure 70. ***Sphagnum cristatum***, food for ***Cladoxycanus minos*** in New Zealand. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

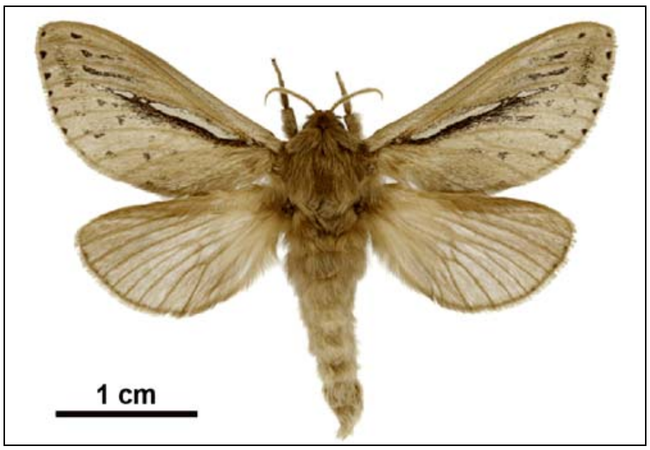

Figure 71. ***Wiseana umbraculata*** male adult, a species that occurs on saturated mosses. Photo from Landcare Research, Manaaki Whenua, with permission.

Sunny peatlands seem to be suitable for the mustard white butterfly, ***Pieris oleracea*** (**Pieridae**; Figure 72). But where ***Sphagnum*** (Figure 54) grows, danger often lurks. Chew (1978) observed one of these butterflies stuck to the sticky hairs of sundew leaves (Figure 73) in Vermont, USA, quite dead. And this species is not alone in being snared by bog-dwelling sundews (Figure 73). As these butterflies and moths struggle to get free, they only get further entangled in the sticky hairs.

Figure 72. ***Pieris oleracea*** adult, a bog resident that gets trapped by sundews. Photo by D. Gordon E. Robertson, through Creative Commons.

Figure 73. ***Drosera rotundifolia*** that has caught a bog butterfly. Photo by Noah Elhardt, through Creative Commons.

Disappearing Species

Local species extinctions have been occurring at a high rate, and members of **Lepidoptera** are no exception (Franco *et al*. 2006). Both climate change and habitat loss account for these losses. Typically, the species retract northward. Franco and coworkers concluded that mountain and northern species may be in jeopardy due to climate warming.

By contrast, Nöske *et al*. (2008) compared moths in **Geometridae** and **Arctiidae** (**Erebidae**?) in mature and recovering forest and in open vegetation of the montane belt in Andes of Ecuador. There was no uniform pattern of change in species richness with increasing disturbance. Rather, species richness of geometrid moths was significantly higher in the recovering forest than in the mature forest or the open habitats. The **Arctiidae** were also most species-rich in the recovering forest, but also in the open vegetation compared to the mature forest.

Any recovery of species following logging depends on the availability of colonists (Niemelä 1997). Butterflies, in particular, suffer from logging of old-growth forests, as do bryophytes (Hydén & Sjökvist 1993), and sometimes the **Lepidoptera** may suffer because of loss of bryophytes.

Maelfait *et al*. (2007) reported the loss of the butterflies ***Aricia agestis*** (**Lycaenidae**; Figure 74-Figure 77) and ***Issoria lathonia*** (**Nymphalidae**; Figure 78-Figure 79) from Dutch coastal dunes. This loss was attributed to loss of the varied vegetation structure that included patches of mosses and bare sand, both of which disappear when tall grasses expand coverage (Brouwer *et al*. 2005).

Figure 74. ***Aricia agestis*** adult, a species that lives where there are bryophytes in the habitat. Photo by Hectonichus, through Creative Commons.

Figure 75. ***Aricia agestis*** adult, a species that lives where there are bryophytes in the habitat. Photo by Jérôme Albre, with permission.

Figure 76. ***Aricia agestis*** adult showing its antennae and eyes. Photo by Jérôme Albre, with permission.

Figure 77. ***Aricia agestis*** larva, a species that disappears when bryophytes disappear from its habitat. Photo by Jérôme Albre, with permission.

Figure 78. ***Issoria lathonia*** larva, a species that seems to depend on mosses in the dunes. Photo by Wolfgang Wagner, with permission.

Figure 79. ***Issoria lathonia*** adult, a species that disappears when dune mosses are replaced by grasses. Photo by Korall, through Creative Commons.

Schtickzelle and Baguette (2004) expressed the importance of demographic parameters in fragmented landscapes. For the bog fritillary butterfly (***Proclossiana eunomia*** – **Nymphalidae**; Figure 80), a specialist glacial relict, density dependence seemed to be related to parasitism of the larvae. Dispersal was dependent on the ability to move between patches of suitable bog habitat.

Hence, destruction of bogs can easily lead to the demise of this species, in part due to crowding and increased parasitism.

Figure 80. ***Proclossiana eunomia***, a bog dweller. Photo by Gilles San Martin, through Creative Commons.

Because of their vulnerability due to changes in drainage, bogs are disappearing habitats. Murdock (1994) claims that one-third of the threatened and endangered species in the USA live in wetlands. In the Southern Appalachian Mountains, USA, bogs and fens house many rare and unique species that occur in no other habitats. Among these is the rare Baltimore butterfly, ***Euphydryas phaeton*** (**Nymphalidae**; Figure 81-Figure 83).

Figure 81. ***Euphydryas phaeton*** (Baltimore butterfly) larva, a rare bog inhabitant in the Southern Appalachian Mountains, USA. Photo by Pennsylvania Department of Conservation and Natural Resources, through Creative Commons.

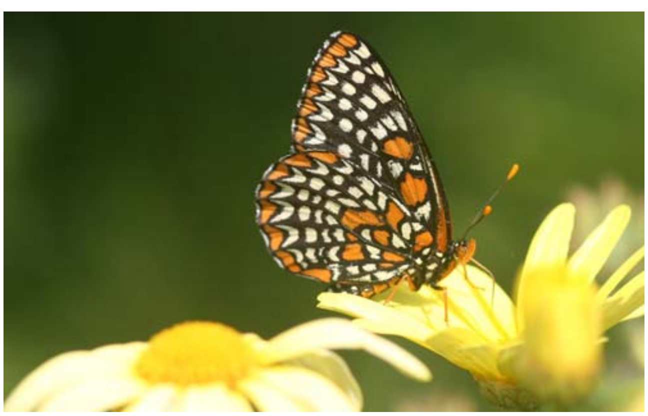

Figure 82. ***Euphydryas phaeton*** adult, a rare bog species in the Southern Appalachian Mountains, USA. Photo by Alison Hunter, through Creative Commons.

Figure 83. ***Euphydryas phaeton*** adult, a rare bog species. Photo by D. Gordon E. Robertson, through Creative Commons.

Many examples, such as those reported by Pescott *et al*. (2015), attest to the effect of changing air quality in causing the disappearance of bryophytes. They provided the first evidence for the indirect association between returning air quality and the increase of lichenivorous moths.

Changing climate can put life cycle stages out of sync. Food plants may mature at the wrong time for developing larvae. Males and females may respond to different stimuli, causing them to be ready for mating at different times. The Earth's mean global temperature has increased by about 0.6°C in the past century (Walther *et al*. 2002). Migrant butterflies are arriving at their spring destinations earlier and breeding earlier than times recorded before the 20th century. Bryophytes may play a role in retaining moisture as the climate dries.

Summary

The **Lepidoptera** are primarily plant eaters as larvae, and for some this includes bryophytes. This appears to be a relict trait from the early **Lepidoptera** that appeared at about the same time as bryophytes became abundant. Many of these bryophyte dwellers have similarities to their sister group, the **Trichoptera**, including case making, wings that rest like a pup tent, and hairs on the wings. Larvae often have appendages and coloration that help them to blend with the bryophytes. They are holometabolous, having eggs, larvae, pupae, and adults in their life cycle.

Pupae develop in bryophytes in some taxa. Adults use the bryophytes for resting sites, in some cases having coloration that camouflages them. Some lay their eggs among bryophytes. Butterflies are less represented than moths and few feed on them.

Although most of the lepidopteran bryophages eat the leaves, some are specialists on capsules. And some eat only liverworts, especially the thallose liverwort ***Conocephalum conicum***. Others specialize on epiphyllous bryophytes and some eat the periphyton on the bryophytes. But some bryophytes seem to be inedible, presenting terpenoids and other compounds that serve as chemical defense. A few larvae are carnivorous and ambush prey by resembling bryophytes and hiding there to attack.

Many of the bryophyte dwellers have poor or no flying ability and therefore have limited dispersal ability and distribution. This makes them susceptible to extinction as forests and bogs are destroyed. While peatlands can have a huge number of species, some of these are very rare and easily extirpated as these relict habitats disappear. Bog drainage, climate change, peat harvesting, pollution, and logging all contribute to the losses of these rare species.

Acknowledgments

Thank you to John Steel for his continued support and for sending me articles from the Otago Daily Times about Lepidoptera associated with mosses. David Glenny and Javier Martínez-Abaigar provided me with the paper on Micropterigidae that feed on *Conocephalum conicum*. David Glenny provided me with the *Riccardia* cocoon image. Yume Imada provided me with additional information on Japanese Micropterigidae and their diet. I appreciate help from Steve Palmer and John Grehan in getting permission for some of the images. Bob Heckford sent me many images of larvae and George Gibbs provided many images and several references. Hamish Patrick was helpful in providing additional information and images.

Literature Cited

Andrew, N. R., Rodgerson, L., and Dunlop, M. 2003. Variation in invertebrate-bryophyte community structure at different spatial scales along altitudinal gradients. J. Biogeogr. 30: 731-746.

Bodner, F., Brehm, G., and Fiedler, K. 2015. Many caterpillars in a montane rain forest in Ecuador are not classical herbivores. J. Trop. Ecol. 31: 473-476.

Brackenbury, J. 1994. Insects. Life Cycles and the Seasons. Blandford, London, p. 183

Britannica. 2008. Panorpid Complex. Accessed on 27 July 2008 at <http://www.britannica.com/EBchecked/topic/441463/panorpoid-complex#tab=active~checked%2Citems~checked&title=panorpoid%20complex%20--%20Britannica%20Online%20Encyclopedia>.

Brouwer, E., Duinen, G.-J. van, Nijssen, M., and Esselink, H. 2005. Development of a decision support system for LIFE-Nature and similar projects: From trial-and-error to knowledge based nature management. In: Herrier, J.-L., Mees, J., Salman, A., Seys, J., Nieuwenhuyse, H. Van, Dobbelaere, I. (eds.). Proceedings of Dunes and Estuaries 2005, International Conference on Nature Restoration Practices in European Coastal Habitats, Koksijde, Belgium. VLIZ Special Publications 19, pp. 229-238.

Buchanan White, F. 1971. Captures of Lepidoptera near Perth in 1870. Entomol. Month. Mag. 7: 140.

Buckler, W. 1871. Description of the larva of *Acronycta myricae*. Entomol. Month. Mag. 7: 83.

Burger, A. E. 1978. Terrestrial invertebrates: A food resource for birds at Marion Island. S. Afr. J. Antarct. Res. 8: 87-99.

Callaghan, C. J. 1992. Biology of epiphyll feeding butterflies in a Nigerian cola forest (Lycaenidae: Lipteninae). J. Lepidopt. Soc. 46: 203-214.

Chapman, T. A. 1894. Some notes on microlepidoptera whose larvae are external feeders and chiefly on the early stages of *Eriocephala Calthella* (Zygaenidae, Lymacodidae, Eriocephalidae). Trans. Roy. Entomol. Soc. Lond. 1894: 335-350.

Chew, F. S. 1978. *Pieris napi oleracea* (Pieridae) caught by insectivorous plant. J. Lepidop. Soc. 32: 129.

Crampton, G. C. 1920. A comparison of the external anatomy of the lower Lepidoptera and Trichoptera from the standpoint of phylogeny. Psyche 27: 23-33.

Dapkus, D. 2000. Comparison of Lepidoptera communities of Čepkeliai raised bog, Baloša and Palios peatlands. Acta Zool. Lituanica 10: 85-88.

Dapkus, D. 2004a. Lepidoptera associated with pine bogs of different successional stages. Acta Zool. Lituanica 14: 26-30.

Dapkus, D. 2004b. Lepidoptera of a raised bog and adjacent forest in Lithuania. Eur. J. Entomol. 101: 63-67.

DeVries, P. 1988. The use of epiphylls as larval hostplants by the tropical rionid butterfly, *Sarota gyas*. J. Nat. Hist. 22: 1447-1450.

Dincă, V. 2005. The Macrolepidoptera (Insecta: Lepidoptera) from Istriţa Hill (Buzău County, Romania). Entomol. Rom. 10: 5-24.

Ehrlich, P. R. and Raven, P. H. 1964. Butterflies and plants: A study in coevolution. Evolution 18: 586-608.

Fang, Y. and Zhu, R.-L. 2012. *Haplocladium microphyllum* (Hedw.) Broth. capsules as food for *Agrotis* sp. (Lepidoptera) larvae. J. Bryol. 34: 108-113.

Forster, W. and Wohlfahrt, T. A. 1960. Die Schmetterlinge Mitteleuropas. 3. Spinner und Schwärmer: (Bombyces und Sphinges). Franckh'sche Verlagshandlung, Stuttgart.

Franco, A. M. A., Hill, J. K., Kitschke, C., Collingham, Y. C., Roy, D. B., Fox, R., Huntley, B., and Thomas, C. D. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. Global Change Biol. 12: 1545-1553.

Gerson, U. 1969. Moss-arthropod associations. Bryologist 72: 495-500.

Gerson, U. 1982. Bryophytes and invertebrates, Chapt. 9. In: Smith, A. J. E. (ed.). Bryophyte Ecology. Chapman and Hall, New York, pp. 291-332.

Grehan, J. R. 1984. The host range of *Aenetus virescens* (Lepidoptera: Hepialidae) and its evolution. N. Z. Entomol. 8: 52-61.

Grehan, J. R. and Patrick, B. H. 1984. Notes on bog inhabiting Hepialidae (Lepidoptera) of New Zealand. N. Z. Entomol 8: 63-67.

Györffy, I. 1952. Moos-Seten als Asyle für Arthropoden. [Moss setae as an asylum for arthropods.]. Rev. Bryol. Lichenol. 21: 285-286.

Hamm, C. A. 2015. *Selaginella* and the satyr: *Euptychia westwoodi* larval performance on an ancient plant lineage. Available at <http://dx.doi.org/10.7287/peerj.preprints.775v1>.

Hashimoto, S. 2006. A taxonomic study of the family Micropterigidae (Lepidoptera, Micropterigoidea) of Japan, with the phylogenetic relationships among the Northern Hemisphere genera. Bull. Kitakyushu Mus. Nat. Hist. Hum. Hist. Ser. A 4: 39-109.

Holloway, J. D. 1993. Lepidoptera in New Caledonia: Diversity and endemism in a plant-feeding insect group. Biodiv. Lett. 1: 92-101.

Hydén, N. and Sjökvist, P. 1993. Barrskogsfjällflyet, *Xestia sincera* (Lepidoptera, Noctuidea), och det moderna storskaliga skogsbruket. (*Xestia sincera* [Lepidoptera, Noctuidea] and the modern large scale forestry). Entomol. Tidskr. 114: 1-11.

Jaroš, J., Spitzer, K., and Zikmundová, H. 2014. Variability of Lepidoptera communities (moths and butterflies) along an altitudinal gradient of peat bogs from the Třeboň Basin up to the Bohemian Forest (South Bohemia, Central Europe). Silva Gabreta 20: 55-95.

Klok, C. J. and Chown, S. L. 1997. Critical thermal limits, temperature tolerance and water balance of a sub-Antarctic caterpillar, *Pringleophaga marioni* (Lepidoptera: Tineidae). J. Ins. Physiol. 43: 685-694.

Krishnan, R. and Murugan, K. 2013. Evaluation of bryophyte protein-based defense against selected phytophagous insects. In: Prospects in Bioscience: Addressing the Issues, pp. 19-32. Springer India.

Liu, Y.-F. 1989. Insect fauna at Jianfengling in Hainan island. Lithosiidae. Sci. Silv. Sinicae 25: 17529. (In Chinese)

Loope, L., Duever, M., Herndon, A., Snyder, J., and Jansen, D. 1994. Hurricane impact on uplands and freshwater swamp forest: Large trees and epiphytes sustained the greatest damage during Hurricane Andrew. Bioscience 44: 238-246.

Lucking, Robert. 2000. Biological Interactions in the Phyllosphere. Accessed 12 August at <http://www.old.uni-bayreuth.de/departments/planta2/ass/robert/lichens/phyllosphere.html>.

Maciel-Silva, A. S. and Santos, N. D. dos. 2011. Detecting herbivory in two mosses from an Atlantic Forest, Brazil. J. Bryol. 33: 140-147.

Maelfait, J.-P., Desender, K., and Baert, L. 2007. Colonisation and source-sink dynamics in spiders and ground beetles after dry dune habitat restoration along the Belgian coast. Coastline Reports 7: 41-52.

Martin, A. 2015. The Magical World of Moss Gardening. Timber Press, Portland, OR, 238 pp.

Martin, N. M. 1938. Some observations on the epiphytic moss flora of trees in Argyll. J. Ecol. 26: 82-95.

Murawski, D. A. 2003. Killer caterpillars. Natl. Geogr. 203(6): 100-111.

Murdock, N. A. 1994. Rare and endangered plants and animals of southern Appalachian wetlands. Water Air Soil Pollut. 77: 385-405.

Nekola, J. C. 1998. Butterfly (Lepidoptera: Lycaenidae, Nymphalidae, and Satyridae) faunas of three peatland habitat types in the Lake Superior drainage basin of Wisconsin. Great Lakes Entomol. 31: 27-38.

Niemelä, J. 1997. Invertebrates and boreal forest management. Conserv. Biol. 11: 601-610.

Nöske, N. M., Hilt, N., Werner, F. A., Brehm, G., Fiedler, K., Sipman, H. J. M., and Gradstein, S. R. 2008. Disturbance effects on diversity of epiphytes and moths in a montane forest in Ecuador. Basic Appl. Ecol. 9: 4-12.

Ottosson, J. G. and Anderson, J. M. 1983. Number, seasonality and feeding habits of insects attacking ferns in Britain: An ecological consideration. J. Anim. Ecol. 52: 385-406.

Paradis, É, Rochefort, L., and Langlois, M. 2015. The lagg ecotone: An integrative part of bog ecosystems in North America. Plant Ecol. 216: 999-1018.

Pescott, O. L., Simkin, J. M., August, T. A., Randle, Z., Dore, A. J., and Botham, M. S. 2015. Air pollution and its effects on lichens, bryophytes, and lichen-feeding Lepidoptera: Review and evidence from biological records. Biol. J. Linn. Soc. 115: 611-635.

Pettersson, R. B., Ball, J. P., Renhorn, K. E., Esseen, P. A., and Sjöberg, K. 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. Biol. Conserv. 74: 57-63.

Peus, F. 1928. Beitrâge zur Kenntnis der Tierwelt nordwestdeutscher Hochmoore. Zeit. Morphol. Okol. Tiere 12: 533-683.

Pierce, N. E. 1995. Predatory and parasitic Lepidoptera: Carnivores living on plants. J. Lepidop. Soc. 49: 412-453.

Powell, J. A., Mitter, C., and Farrell, B. 1999. Evolution of larval food preferences in Lepidoptera. 20. Handbuch der Zoologie: Eine Naturgeschichte der Stämme des Tierreiches. Vol. 4, Arthropoda: Hälfte 2, Insecta: Teilbd. 35, Lepidoptera, Moths and Butterflies: Vol. 1. Evolution, Systematics, and Biogeography 4: 403 pp.

Schtickzelle, N. and Baguette, M. 2004. Metapopulation viability analysis of the bog fritillary butterfly using RAMAS/GIS. Oikos 104: 277-290.

Shepherd, R. F. and Gray, T. G. 1972. Solution separation and maximum likelihood density estimates of hemlock looper (Lepidoptera: Geometridae) eggs in moss. Can. Entomol. 104: 751-754.

Shields, O. 1988. Mesozoic history and neontology of Lepidoptera in relation to Trichoptera, Mecoptera, and angiosperms. J. Paleontol. 62: 251-258.

Singer, M. C. and Mallet, J. 1986. Moss-feeding by a satyrine butterfly. J. Res. Lepidoptera 24: 392.

Spitzer, K. and Jaroš, J. 1993. Lepidoptera associated with Červené Blato bog (Central Europe): Conservation implications. Eur. J. Entomol. 90: 323-336.

Spitzer, K. and Jaroš, J. 2014. A unique guild of Lepidoptera associated with the glacial relict populations of Labrador tea (*Ledum palustre* Linnaeus, 1753) in Central European peatlands (Insecta: Lepidoptera) SHILAP Rev. Lepidopterol. 42: 319-327.

Thorn, S., Hacker, H. H., Seibold, S., Jehl, H., Bässler, C., and Müller, J. 2015. Guild-specific responses of forest Lepidoptera highlight conservation-oriented forest management – Implications from conifer-dominated forests. Forest Ecol. Mgmt. 337: 41-47.

Tillyard, R. J. 1926. The Insects of Australia and New Zealand. Angus & Robertson, Sydney.

Väisänen, R. 1992. Distribution and abundance of diurnal Lepidoptera on a raised bog in southern Finland. Ann. Zool. Fenn. 29: 75-92.

Wada, K. and Munakata, K. 1971. Insect feeding inhibitors in plants. III. Feeding inhibitory activity of terpenoids in plants. Agr. Biol. Chem. 35: 115-118.

Walther, G.-R., Post, E., Convey, P., Menzel, A., and Parmesan, C., Beebee, T. J. C., and Fromentin, J.-M. 2002. Ecological responses to recent climate change. Nature 416: 389-395.

WDNR. 2009. Bog Fritillary (*Boloria eunomia*). Wisconsin Department of Natural Resources. Updated 9 July 2009. Accessed 15 June 2011 at <http://dnr.wi.gov/ORG/LAND/ER/biodiversity/index.asp?mode=info&Grp=9&SpecCode=IILEPJ7020>.

Yanoviak, S.P., Walker, H., and Nadkarni, N.M. 2004. Arthropod assemblages in vegetative vs. humic portions of epiphyte mats in a neotropical cloud forest. Pedobiologia 48: 51-58.

Yasuda, T. 1962. On the larva and pupa of *Neomicropteryx nipponensis* Issiki with its biological notes (Lepidoptera: Micropterygidae). Kontyu 30: 130-136.