CHAPTER 12-20
TERRESTRIAL INSECTS: HOLOMETABOLA – DIPTERA BRACHYCERA

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Figure 1. Beefly (**Syrphidae**) on ***Cratoneuron filicinum***. Many flies use bryophytes for resting sites where the bryophytes reduce the danger of dehydration or the flies take a drink of water. Photo by Serhat Ursavas, with permission.

BRACHYCERA

Rhagionidae *sensu stricto* – Snipe Flies

The **Rhagionidae** is a worldwide family that has some members among the most primitive of the **Brachycera**. One of its diagnostic characters is that its head points downward when at rest (Figure 2), earning it the name of "downlooker flies."

In the Czech Republic, ***Rhagio latipennis*** (Figure 2) is a predaceous fly that prefers moist soil rich in organic matter (Farkač *et al*. 2005). Some prefer decaying wood, mosses, or liverworts along the sides of water courses.

Figure 2. ***Rhagio latipennis*** adult, a species that sometimes is associated with streamside mosses or liverworts. Note the downward-pointing head. Photo by João Coelho, through Creative Commons.

Spaniidae

Members of the **Spaniidae** family are often included in the **Rhagionidae**. The **Spaniidae** feeding habits may be assumed to be similar, in most cases, to those of the **Rhagionidae**.

Both adults and larvae typically eat small insects. The adults live in forests, especially near moist places. Larvae occur in moist meadow soil, among mosses, in decaying wood, under bark, and a few in water.

Imada and Kato (2016a) investigated **Diptera** in the **Rhagionidae/Spaniidae** to determine apparent adaptations to bryophyte consumption. The **Spaniidae** has larval members with multiple bryophyte-feeding habits. ***Spania*** (Figure 30-Figure 34) and ***Litoleptis*** (thallus-miners of thallose liverworts; Figure 3, Figure 17) both have a toothed form of apical mandibular sclerite with an orifice on its dorsal surface, contrasting with those of the members of **Rhagionidae** that possess a blade-like mandibular hook with an adoral groove. On the other hand, the moss stem borer ***Ptiolina*** (Figure 25) has a weak groove on the adoral surface of the mandible and has a highly sclerotized maxilla with toothed projections. Imada and Kato hypothesized that the toothed mandibles with the dorsal orifice would facilitate the leaf miners in scraping plant tissue and imbibing it along with a large quantity of cell sap. Their phylogenetic analysis indicated that the loss or reduction of the adoral mandibular groove and mandibular brush coincides with the evolution of bryophyte feeding.

Litoleptis (Figure 3)

Imada and Kato (2016b) reported the feeding strategy for ***Litoleptis*** (Figure 3, Figure 17) in Japan. The larvae of this genus mine the thalli of thallose liverworts in the families **Aytoniaceae** and **Conocephalaceae**. These include species of ***Conocephalum*** (Figure 4), ***Reboulia*** (Figure 5), and ***Asterella*** (Figure 6). It is clear that bryophyte miners are an overlooked group of species. While I was working on ththe original preparation of this chapter, Imada and Kato (2016b) provided me with six new species they described in the genus ***Litoleptis***, all from thallose liverworts, in Japan.

Figure 3. ***Litoleptis japonica*** adult on ***Conocephalum*** sp. Photo courtesy of Yume Imada.

Figure 4. ***Conocephalum conicum*** on wet rock; the dipteran ***Litoleptis japonica*** deposits eggs on its thallus and the larvae mine the interior. Photo by Fotis Samaritakis, through Creative Commons.

Figure 5. ***Reboulia hemisphaerica*** with archegoniophores, a potential host plant for species of ***Litoleptis***. Photo by Michael Lüth, with permission.

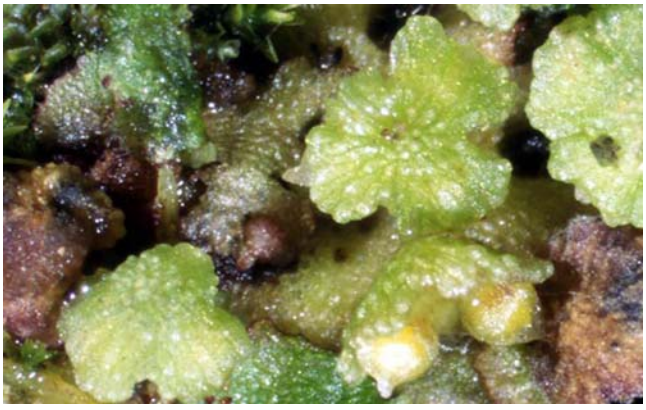

Figure 6. ***Asterella cruciata***, an endangered species in Japan and home of ***Litoleptis asterellaphile***. Photo by Misao Ito, with permission from Digital Museum of Hiroshima.

Litoleptis japonica (Figure 3) larvae occur in thalli of ***Conocephalum conicum*** (Figure 4) in shaded habitats in Japan (Figure 7-Figure 8). The adult female deposits eggs on the thallus of ***Conocephalum conicum*** (Figure 9-Figure 11), and its larvae (Figure 12-Figure 14) subsequently mine the thallus of this liverwort.

Figure 7. ***Litoleptis japonica*** habitat at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.

Figure 8. ***Litoleptis japonica*** habitat in Nanataki in Wakayama Pref., Japan. Photo by Yume Imada, with permission.

Figure 9. ***Litoleptis japonica*** adult on ***Conocephalum conicum***. Photo by Yume Imada, with permission.

Figure 10. ***Litoleptis japonica*** ovipositing on ***Conocephalum conicum*** at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.

Figure 11. ***Litoleptis japonica*** eggs (**arrows**), deposited on liverwort thallus. Photo by Yume Imada, with permission.

Figure 12. ***Litoleptis japonica*** first instar larva (**arrow**) mining in a thallus of ***Conocephalum conicum***. Photo by Yume Imada, with permission.

Figure 13. ***Litoleptis japonica*** larva. Photo by Yume Imada, with permission.

Figure 14. ***Litoleptis japonica*** larva mining ***Conocephalum conicum***. Photo by Yume Imada, with permission.

Figure 15. ***Litoleptis japonica*** pupa (**arrow**) on ***Conocephalum conicum***. Photo by Yume Imada, with permission.

Litoleptis kiiensis (Figure 16-Figure 17) occurs in ***Reboulia hemispherica*** (Figure 5) on rocky or clayey slopes in both evergreen and deciduous forests (Imada & Kato 2016b). ***Litoleptis kiiensis*** is a thallus miner on ***Reboulia hemisphaerica*** (Figure 5). The larvae mine the middle layer of the thalli, making mines nearly invisible from outside the thallus. The final instar of the larvae individually mine along the mid-vein and pupate near the adaxial layer of thalli in that mine in early spring. In their observations, this pupa was visible from the outside of the thallus. Adults emerge from the thallus later in the spring.

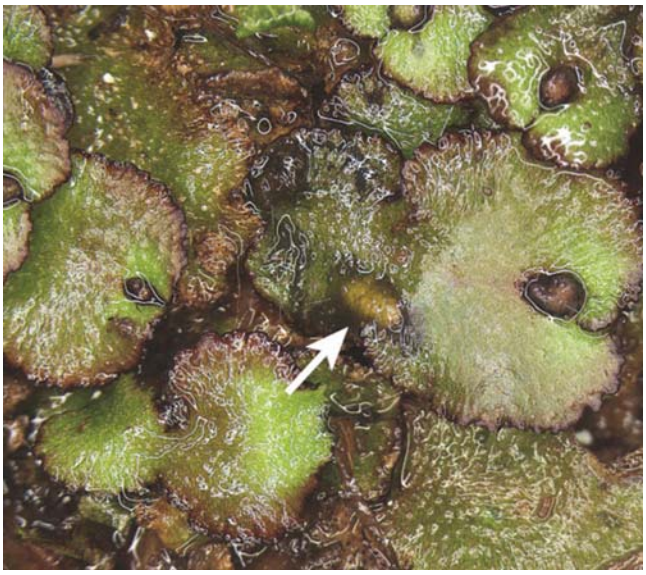

Figure 16. ***Litoleptis kiiensis*** larva (**arrow**) on thallose liverwort. Photo by Yume Imada, with permission.

Figure 17. ***Litoleptis kiiensis*** larva, a bryophyte inhabitant. Photo courtesy of Yume Imada.

Litoleptis niyodoensis occurs in ***Reboulia hemisphaerica*** (Figure 5) (Imada & Kato 2016b). ***Litoleptis himukaensis*** occurs along streams in ***Reboulia hemisphaerica***. ***Litoleptis izuensis*** occurs in ***Reboulia hemisphaerica*** on shaded clayey slopes along streams and roads in evergreen ***Castanopsis*** forests. ***Litoleptis asterellaphile*** (Figure 18) occurs in ***Asterella cruciata*** (an endangered species in Japan; Figure 6) on rocky cliffs along streams and roads in deciduous forests.

Figure 18. ***Litoleptis asterellaphile*** pupa (**arrow**) among liverworts. Photo by Yume Imada, with permission.

Ptiolina (Figure 19)

Lane and Anderson (1982) found immature adults of ***Ptiolina*** *cf.* ***zonata*** (Figure 19) by hand sorting moss-covered soil samples (Figure 20). Apparently mosses also provide oviposition sites for the genus (Figure 21-Figure 23), hence also providing homes for the larvae (Figure 24-Figure 26).

Figure 19. ***Ptiolina*** sp. on moss. Photo by Pristurus, through Creative Commons.

Figure 20. ***Ptiolina*** habitat at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.

Figure 21. ***Ptiolina*** sp. ovipositing on ***Brachythecium buchananii*** at Kibune, Kyoto Pref., Japan. Photo by Yume Imada, with permission.

Figure 22. ***Ptiolina*** sp. ovipositing on moss; the two yellow areas at the tip of the abdomen are egg masses. Photo by Pristurus, through Creative Commons.

Figure 23. ***Ptiolina*** sp. eggs (**arrow**), deposited on ***Brachythecium buchananii***. Photo by Yume Imada, with permission.

Figure 24. ***Ptiolina*** sp. larva. Photo by Yume Imada, with permission.

Figure 25. ***Ptiolina*** sp. larva, a bryophyte inhabitant. Photo courtesy of Yume Imada.

Figure 26. ***Ptiolina*** sp. second-instar larva (**arrow**), boring a shoot of the moss ***Plagiomnium vesicatum***. Photo by Yume Imada, with permission.

Since that publication, we have learned that a number of species in this family are adapted to mining bryophytes, and they seem to be very specific about their choice of bryophyte. Furthermore, they deposit their eggs on the same bryophyte that the larvae will later eat. ***Ptiolina*** sp. (Figure 19-Figure 22) deposits eggs (Figure 21, Figure 23) on the moss ***Brachythecium buchananii*** (Figure 27), and the larvae (Figure 25) are stem borers on this same species (Imada & Kato 2016a).

Figure 27. ***Brachythecium buchananii***; ***Ptiolina*** deposits eggs on this species and larvae are stem borers in it. Photo by Michael Lüth, with permission.

Spania

The original record I found of a member of **Spaniidae** among bryophytes is that of ***Spania nigra*** (Figure 29-Figure 34). Larvae of this species live on mosses and liverworts in damp shade such as the ghyll woodlands of Sussex (Roper 2001). Boyce (2002) reported it from the

thallose liverwort ***Pellia*** (Figure 35) in England. Yume Imada (pers. comm.) has also found ***Spania*** sp. tunnelling in ***Conocephalum*** (Figure 34).

Figure 28. ***Spania*** sp. habitat. Photo by Yume Imada, with permission.

Figure 29. ***Spania nigra*** adult, a species whose larvae live among forest mosses and liverworts in the UK. Photo by Marko Mutanen, through Creative Commons.

Imada and Kato (2016a) observed that ***Spania*** sp. (Figure 29) deposited eggs exclusively on the thallus of the liverwort ***Pellia endiviifolia*** (Figure 35), a species it also mines.

Figure 30. ***Spania*** sp. adult on ***Brachythecium buchananii***, Japan. Photo courtesy of Yume Imada.

Figure 31. ***Spania*** sp. ovipositing on ***Pellia endiviifolia***, at Higashiyoshinomura, Nara Pref., Japan. Photo by Yume Imada, with permission.

Figure 32. ***Spania*** sp. eggs (**arrows**) on ***Pellia endiviifolia***. Photo by Yume Imada, with permission.

Figure 33. ***Spania*** sp. larva. Photo by Yume Imada, with permission.

Figure 34. ***Spania*** sp. larva tunnelling in ***Conocephalum***. Photo courtesy of Yume Imada.

Figure 35. ***Pellia endiviifolia*** males and females; thalli are home for some ***Spania*** larvae that mine the interior. Photo by David T. Holyoak, with permission.

Dolichopodidae – Long-legged Flies

The **Dolichopodidae** is likewise a family of water-loving species. I mention here a few that are somewhat amphibious. ***Dolichopus maculipennis*** (Figure 36) lives in calcareous wet habitats near small permanent pools, in bryophyte flushes (Figure 37), flushed grasslands, and wet mires (Horsfield & MacGowan 1997), but it also occurs in bogs (Ringdahl 1928). ***Hydrophorus rufibarbis*** (see Figure 39-Figure 38) seems to prefer small, peaty pools, but it also lives in grassy flushes and bryophyte springs (Horsfield & MacGowan 1997).

Figure 36. ***Dolichopus maculipennis*** adult, a species whose larvae live in bryophyte flushes. Photo by I. Grichanov, with online permission.

Figure 37. Bryophyte flush in Wales, potential home for some **Dolichopodidae**. Photo by Janice Glime.

Empididae – Dance Flies

The **Empididae** are somewhat common on aquatic bryophytes (Gootaert 2004), so it is no surprise that some terrestrial species likewise find bryophytes to be suitable homes. Plant (1993) found adult females of ***Monodromia fragilis*** (Figure 40) by sweeping the damp mosses on a cloud forest floor at 550 m asl in New Zealand. In Malaysia the adults are only 3-5 mm long and are mostly yellow or black Gootaert 2004). These seem to prefer boulders covered with mosses or a splash zone where there is constant high humidity.

Figure 38. ***Hydrophorus litoreus*** adult; ***H. rufibarbis*** lives in bryophyte springs and peaty pools. Photo by James K. Lindsey, with permission.

Figure 39. ***Hydrophorus oceanus*** larvae; ***H. rufibarbis*** lives in bryophyte springs and peaty pools. Photo by Hans Hillewaert, through Creative Commons.

The larvae of ***Hemerodromia*** (Figure 41) occur in fast-flowing streams and are predaceous. The adults are yellow or black and occur on moss-covered boulders or in the splash zone, both habitats that ensure moisture.

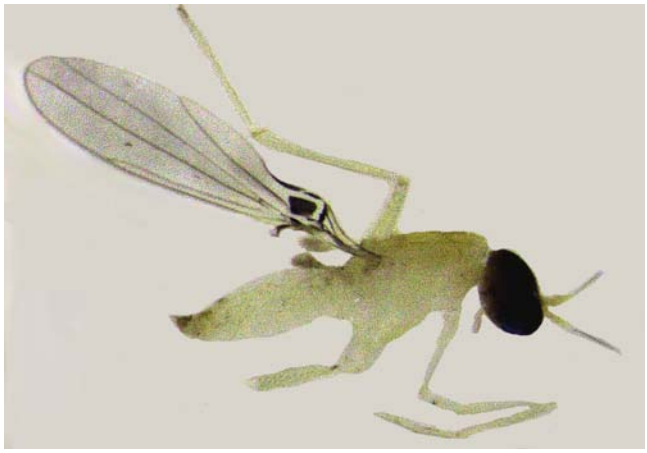

Figure 40. ***Monodromia fragilis*** adult, a species whose adults are associated with damp mosses on the floor of a New Zealand cloud forest. Photo modified from one by Stephen Thorpe, through Creative Commons.

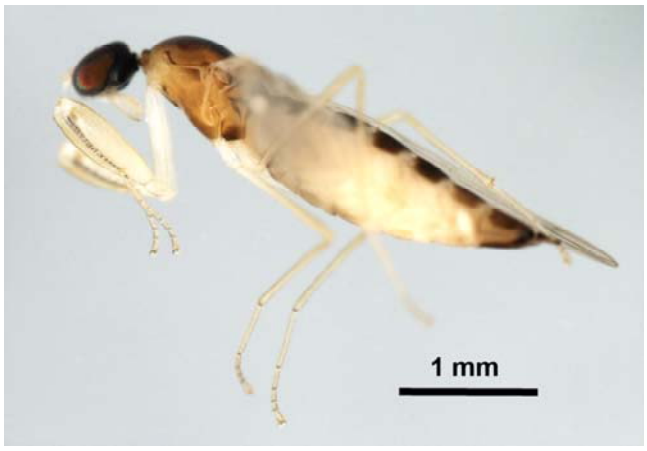

Figure 41. ***Hemerodromia*** adult, a genus whose adults are associated with moss-covered boulders or in the splash zone. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Some insects only use bryophytes as landing and resting places. That appears to be the case with the empidid fly in Sarah Lloyd's pictures below (Figure 42-Figure 44). This family is mostly predaceous on other small invertebrates (Tony Daley, pers. comm. 19 November 2011).

Figure 42. Empidoid fly, possibly **Hybotidae**, on a leafy liverwort. Note the greatly arched thorax and long legs. Photo courtesy of Sarah Lloyd.

Clinocera nivalis (*nivalis* refers to snow; Figure 44) in Scotland is primarily on wet stony and mossy slopes, especially below melting snow, and always above 850 m asl (Edwards 1933a, b; Horsfield & MacGowan 1997). It also is abundant on bryophyte springs and occurs in ***Racomitrium*** moss heaths (Figure 45) and moss-dominated snowbed communities. Horsfield and MacGowan consider that it might be restricted to areas with bryophyte springs and flushes, common in the highlands. J. M. Nelson found it in an ***Anthelia julacea*** (leafy liverwort; Figure 46-Figure 47) spring in Coire Raibert at around 1000 m.

Figure 43. Adult member of **Empididae** resting on a moss capsule. Photo courtesy of Sarah Lloyd.

Figure 44. ***Clinocera nivalis*** adult, a species of wet, stony, and mossy slopes and bryophyte springs. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 45. ***Racomitrium lanuginosum*** heath, home for ***Clinocera nivalis***. Photo by Mike Pennington, through Creative Commons.

Figure 46. ***Anthelia julacea***, home for ***Clinocera nivalis***. 1 Photo by Jean Faubert., with permission.

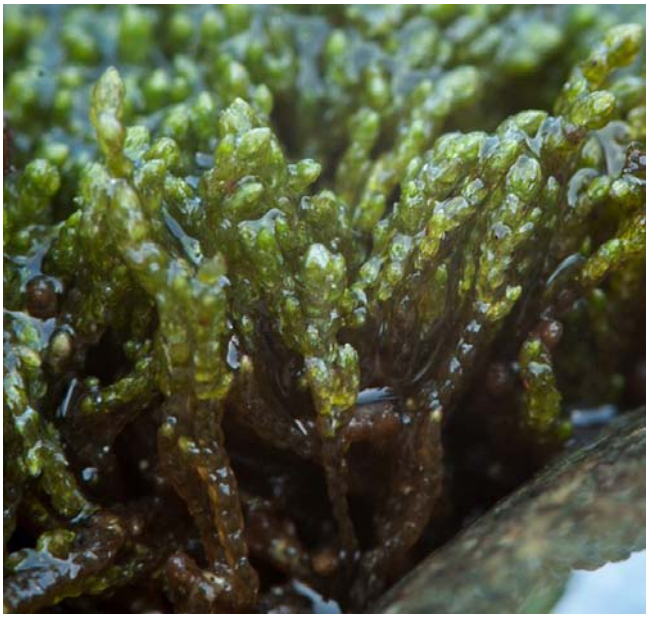

Figure 47. ***Anthelia julacea***, home for ***Clinocera nivalis***. Photo by Štěpán Koval, with permission.

Larvae of ***Wiedemannia impudica*** (see Figure 48) probably live in mosses on emergent boulders (Horsfield & MacGowan 1997), again where they will be constantly moist.

Figure 48. ***Wiedemannia*** *bistigma* adult; ***W. impudica*** is a likely moss inhabitant on emergent boulders. Photo by Marko Mutanen, through Creative Commons.

Hybotidae – Hybotid Dance Flies

Smith (1965) described a new species of ***Stilpon*** (Figure 49-Figure 50) from Portugal. The immature stages of this genus were still unknown, but the adults occur in grass tufts, heaps of cut sedge, and ***Sphagnum*** (Figure 51). The new species was similar to ***Stilpon nubilus***.

Figure 49. ***Stilpon*** sp. adult, a genus in which some adults occur in ***Sphagnum***. Photo by Tom Murray, through Creative Commons.

Figure 50. ***Stilpon curvipes*** adult, member of a genus in which some adults occur in ***Sphagnum***. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 51. ***Sphagnum warnstorfii***; ***Sphagnum*** is a genus that is home to adult ***Stilpon*** (and possibly the unknown larvae). Photo by Michael Lüth, with permission

Syrphidae – Syrphid Flies

This is a family of flies that often resemble bees. If you find a "bee" with only two wings and a pair of halteres, you have found a beefly. ***Platycheirus melanopsis*** (Figure 52) is known from moss-dominated summit heaths (Figure 45) and grasslands in Scotland (Horsfield & MacGowan 1997). ***Cheilosia sahlbergi*** (Figure 53) occurs in habitats where bryophytes are abundant, including ericaceous dwarf shrub heaths, flushes, and bryophyte springs.

Figure 52. ***Platycheirus melanopsis*** adult, a species from moss-dominated summit heaths. Photo from America Pink, with online permission.

Figure 53. ***Cheilosia sahlbergi*** adult, a species that occurs in habitats with abundant bryophytes. Photo by Ladislav Tabi, with permission.

Phoridae – Scuttle Flies

Mosses often provide a safe overwintering shelter. Herbert and Braun (1958) reported moss polsters as the overwintering quarters for adult dipterans in the family **Phoridae** (Figure 54).

Figure 54. **Phoridae** mating in Rock Creek Park, MD. Photo by Katja Schulz, through Creative Commons.

Agromyzidae – Mine Flies

This family has bryophyte specialists, but not on mosses. Rather, these bryobionts are known only from hornworts and liverworts (Spencer 1990). D'Aguilar (1945) described a new species of ***Liriomyza*** (Figure 55) from the thallose liverwort ***Ricciocarpos natans*** (Figure 56). ***Phytoliriomyza mesnili*** (formerly ***Liriomyza***; see Figure 57-Figure 58) is known from ***Ricciocarpos natans*** in France as well as being present on the thallose liverwort ***Riccia beyrichiana*** (Figure 59). It feeds in the thallus and pupates there and also pupates in the thallus of ***Nothoceros vincentianus*** (Figure 60-Figure 62) in Peru. In Mexico, it is known on ***Dumortiera*** (Figure 63) and ***Monoclea*** (Figure 64).

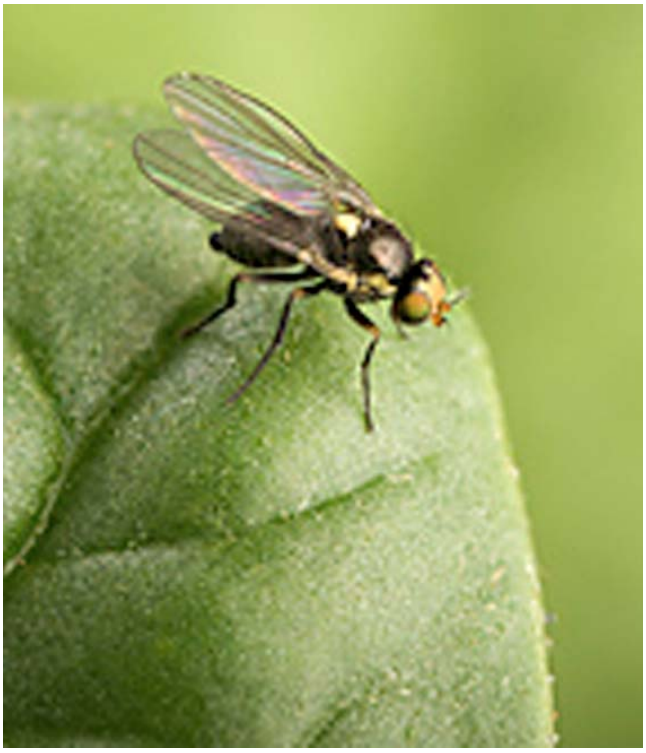

Figure 55. ***Liriomyza taraxaci*** adult, member of a genus known from the liverwort ***Ricciocarpos natans***. Photo by Peggy Greb, USDA, through public domain.

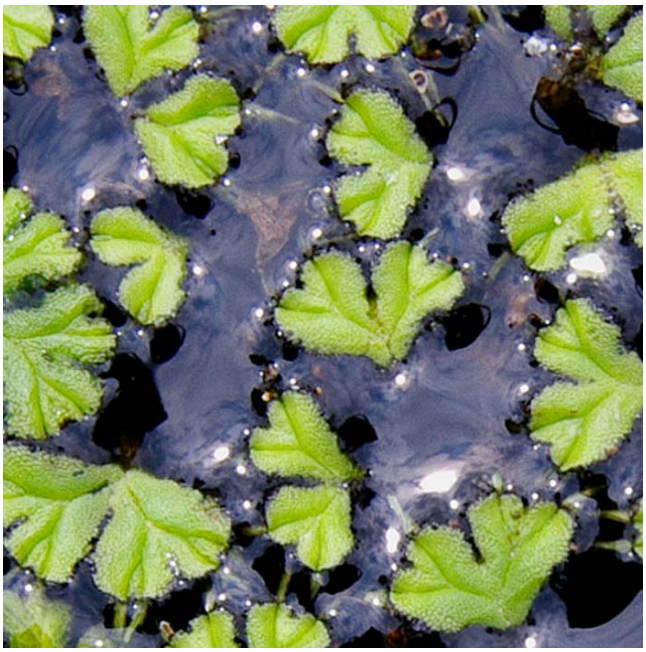

Figure 56. ***Ricciocarpos natans***, home for some species of ***Liriomyza***/***Phytoliriomyza***. Photo by Christian Fischer, through Creative Commons.

Figure 57. ***Phytoliriomyza arctica*** adult. Some members of this genus live in liverwort thalli. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 58. ***Phytoliriomyza melampyga*** larval tunnels in a leaf. Photo from Biodiversity Centre, through Creative Commons.

Figure 59. ***Riccia beyrichiana***, home and food for ***Phytoliriomyza mesnili***. Photo by Jan-Peter Frahm, with permission.

Figure 60. ***Nothoceros***, a genus where ***Phytoliriomyza mesnili*** is known to live in Peru. Photo by Juan Larrain, with permission.

Figure 61. ***Nothoceros*** with **Agromyzidae** leaf miners. Photo courtesy of Juan Carlos Villarreal.

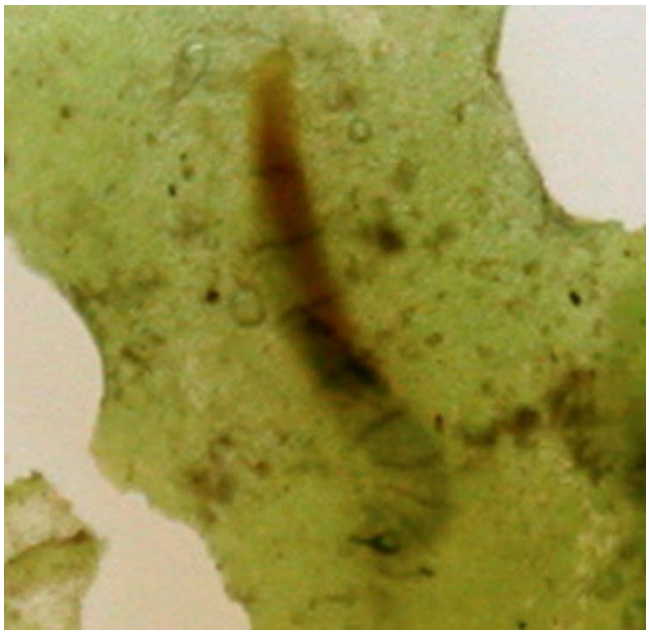

Figure 62. ***Nothoceros*** leaf miner seen through the thallus. Photo courtesy of Juan Carlos Villarreal.

Figure 63. ***Dumortiera hirsuta***, home to ***Phytoliriomyza mesnili*** in Mexico. Photo by Li Zhang, with permission.

Figure 64. ***Monoclea forsteri***, home to ***Phytoliriomyza mesnili*** in Mexico. Photo by Jan-Peter Frahm, with permission.

Reporting from Spain, Marta Infante and Patxi Heras (Bryonet 2 May 2019) described a larva living in ***Riccia cavernosa*** (Figure 65). They noted that it tried to defend itself from the dissecting needle. Later, they observed many pupae and larvae inside the thallus. The species proved to be ***Phytoliriomyza mesnili*** (Figure 66).

Ron Porley (Bryonet 3 May 2019) relayed a similar experience with ***Riccia cavernosa*** (Figure 65). Although he did not identify the insect, it was present as black pupae in the thalli of this species on the muddy margin of a reservoir in Algarve, Portugal, in November. Pettet (1967) reported a similar parasitism on ***Riccia frostii*** (Figure 67) by flies. Porley suggested that such habitation may only occur in section ***Ricciella*** because of its spongy thalli with large air chambers.

Figure 65. ***Riccia cavernosa***, home for pupae of ***Phytoliriomyza mesnili***. Photo from <www.aphotofauna.com>, with permission.

Figure 66. ***Phytoliriomyza melampyga*** adult; ***P. mesnili*** pupates within the thalli of ***Riccia cavernosa***. Photo through Wikimedia Commons.

Figure 67. ***Riccia frostii***, home for pupae of some **Agromyzidae**. Photo from Earth.com, with permission.

Manju Nair provided me with images of the pupae (Figure 68) of an **Agromyzidae** that appears to be

Phytoliriomyza (Figure 68). This pupa inhabits the thalli of ***Riccia beyrichiana*** (Figure 69) and ***Riccia hasskarliana*** (Figure 70).

Figure 68. ***Phytoliriomyza*** pupa from thallus of ***Riccia beyrichiana***. Photo by Manju Nair, with permission.

Figure 69. ***Phytoliriomyza*** pupa in thallus of ***Riccia beyrichiana***. Photo by Manju Nair, with permission.

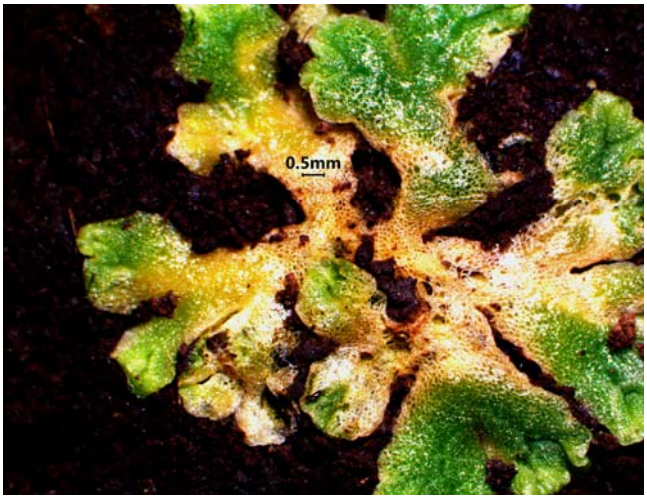

Figure 70. ***Riccia hasskarliana*** mined by ***Phytoliriomyza***. Photo by Manju Nair, with permission.

Some relationships of flies with their bryophyte hosts are obligatory. In Mexico, Juan Carlos Villarreal (pers. comm. 9 September 2014) found the larvae (Figure 71) of leaf-mining flies crawling within the hornwort ***Nothoceros aenigmaticus***, making traces. While in his custody, it became a pupa (Figure 72). Then one day a hatchling appeared. But it was not a young leaf miner. It was a parasitoid wasp that lived on the pupa! So far, no one has successfully reared the larvae or pupae of the agromyzid to adults, but using genetic bar-coding he determined it to be close to ***Phytomyza*** (Figure 73-Figure 78). He found similar **Diptera** from Panamanian ***Nothoceros vincentianus*** (Figure 75) and sequenced them. They most closely matched ***Phytomyza***. But with only an 87% match, perhaps this is a new species or even a new genus.

Figure 71. **Agromyzidae** larva from ***Nothoceros*** thallus. Photo courtesy of Juan Carlos Villarreal.

Figure 72. **Agromyzidae** pupa grown from larva that was living in ***Nothoceros***. Photo courtesy of Juan Carlos Villarreal.

Figure 73. ***Phytomyza*** egg from ***Nothoceros aenigmaticus*** Montage Mexico. Photo courtesy of Juan Carlos Villarreal.

Figure 74. ***Phytomyza ranunculi*** larval tunnels in a leaf, similar to those made by species in liverworts. Photo by James K. Lindsey, with permission.

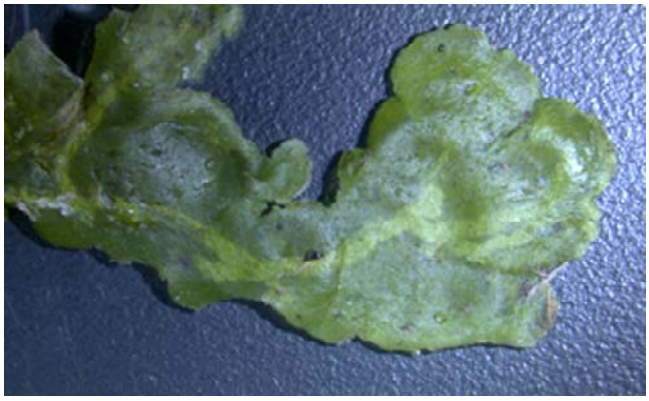

Figure 75. ***Nothoceros vincentianus*** with leaf miner, possibly ***Phytomyza*** sp., in Panama. Note the leaf miner trails on the thallus surface. Those are not midribs! Photo courtesy of Juan Carlos Villarreal.

Figure 76. ***Phytomyza vitalbae*** pupa, member of a genus with some members that live in liverwort thalli. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Figure 77. ***Phytomyza ranunculi*** adult, member of a genus that sometimes lays eggs in liverwort thalli. Photo by Dick Belgers, through Creative Commons.

Figure 78. ***Phytomyza ranunculi*** adult, member of a genus in which some species live in liverwort thalli. Photo by James K. Lindsey, with permission.

Villarreal was able to determine (via a letter belonging to John Engel) that Proskauer had seen leaf miners in ***Megaceros*** (Figure 79) and ***Nothoceros*** (Figure 75). Hering (1957) described ***Phytoliriomyza*** sp. (see Figure 57-Figure 58) larvae and pupae from ***Megaceros***.

Figure 79. ***Megaceros*** sp. with capsules, home for some of the leaf-mining flies. Photo by David Tng <www.davidtng.com>, with permission.

In the larvae of ***Phytoliriomyza mesnili*** (see Figure 57-Figure 58), living in the hornwort ***Nothoceros vincentianus*** (Figure 75), the anterior spiracles of the larva penetrate the epidermis of the thallus to permit breathing (Herring 1966; Spencer 1990). Members of this family also mine ***Dumortiera hirsuta*** (Figure 63) and ***Monoclea*** (Figure 64) in Mexico (Spencer 1990). Although their substrate is generally thallose liverworts and hornworts (never mosses), some feed on ferns, but none is known to feed on flowering plants.

Mining flies seem to have a widespread distribution, albeit scattered. Herring (1957) found leaf-mining flies in ***Megaceros*** spp. (Figure 79) in the West Indies, Juan Fernandez Islands, and New Zealand. Several reports have revealed them in Europe. And Villarreal has found them in Mexico and Panama.

The combination of thallose liverworts or hornworts, mining fly, and parasitic wasp apparently also has far-reaching geographic presence, although the species involved may differ. Sara Altenfelder (pers. comm.) found ***Riccia glauca*** (Figure 80) and ***R. warnstorfii*** (Figure 81) with leaf-mining flies in arable fields in Germany, and these, like the ones found by Villarreal, were parasitized by wasps. She determined that the fly is ***Phytoliriomyza mesnili*** (see Figure 57-Figure 58), first described by Aguilar (1945) feeding on ***Ricciocarpos natans*** (Figure 56) and later reported by Sellier (1947) from ***Riccia beyrichiana*** (Figure 59). The larva eats the thallus, then pupates there (Spencer 1990). Fulnek (1962) mentioned a parasitic wasp – ***Dacnusa taras*** – that lives on some members of ***Phytoliriomyza***.

Figure 80. ***Riccia glauca***, home for ***Phytoliriomyza mesnili***. Photo by Bernd Haynold, through Creative Commons.

Figure 81. ***Riccia warnstorfii***, a species that is home to larvae of ***Phytoliriomyza mesnili***. Photo by Bernd Haynold, through Creative Commons.

In 2018, Ohgue *et al*. reported the first bryophyte galls (Figure 82) induced by insects. These were created by a species of **Agromyzidae**, probably related to ***Phytoliriomyza*** (Figure 57-Figure 58, Figure 66, Figure 68). These occur on the thallose liverwort ***Monoclea gottschei*** **subsp.** ***elongata*** (Figure 82) in a tropical mountain forest. The galls form swellings on the thallus surface, but they resemble the thallus, having no ornamentation or sclerotization. The larvae become pupae (Figure 83) within the gall and adult flies (Figure 84) emerge from the gall by making an exit hole in the upper epidermis of the galled thallus. The galls appear in the apical part of the thallus where archegonia or antheridia would normally occur. Although archegonia and antheridia were plentiful in the population, thalli with galls produced no sporophytes. The need to raise larvae to adults for identification has caused many of these thallus-inhabiting larvae to remain unnamed.

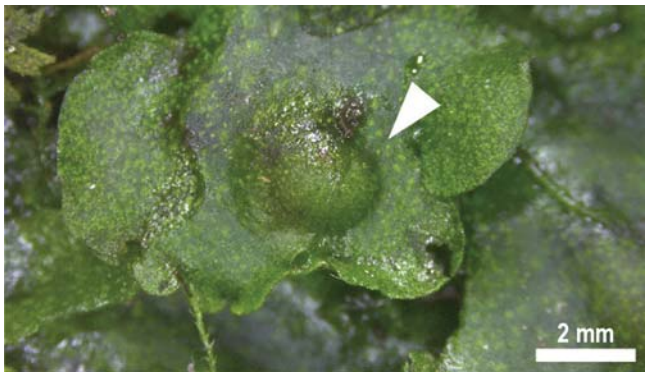

Figure 82. ***Monoclea gottschei*** thallus with a gall of **Agromyzidae**; triangle indicates gall. Photo by Takayuki Ohgue 2018, with permission from Yume Imada.

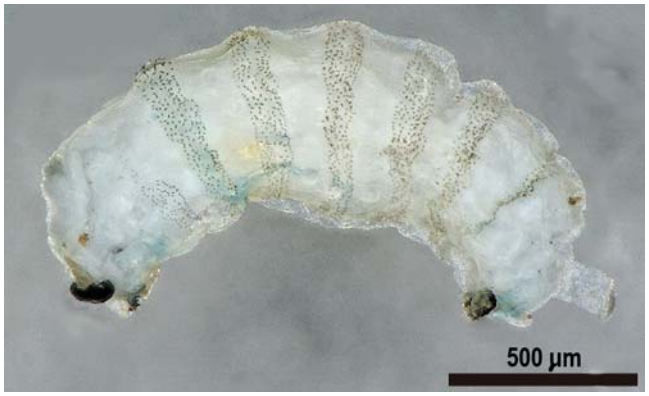

Figure 83. **Agromyzidae** thallus gall larva from ***Monoclea gottschei***. Photo by Takayuki Ohgue, with permission from Yume Imada.

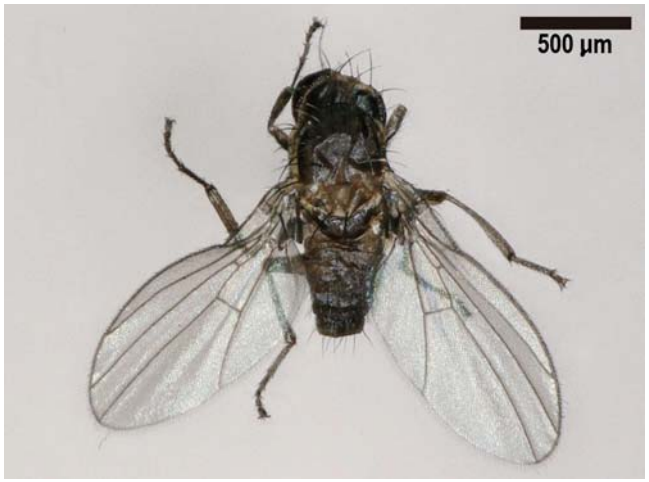

Figure 84. **Agromyzidae** thallus gall larva from ***Monoclea gottschei***. Photo by Takayuki Ohgue, with permission from Yume Imada.

Kato *et al*. (2022) found that liverwort-mining **Agromyzidae** were "overwhelmingly widespread and diverse" in the Japanese Archipelago. They found 39 species, 37 of which were new species! All of these were placed in ***Phytoliriomyza*** (*e.g.* Figure 57-Figure 58, Figure 66, Figure 68). Five of these were associated with ***Marchantia*** (Figure 85), two on ***Dumortiera*** (**Dumortieraceae**; Figure 63), three on ***Plagiochasma*** (Figure 86), one on ***Asterella*** (Figure 6), six on ***Reboulia*** (**Aytoniaceae**; Figure 5), one on ***Wiesnerella*** (**Wiesnerellaceae**; Figure 87), fifteen on ***Conocephalum*** (**Conocephalaceae**; Figure 4), and three on ***Riccia*** (**Ricciaceae**; Figure 59, Figure 65, Figure 67, Figure 70, Figure 80, Figure 81). Another 3 species were associated with hornworts: 1 on ***Folioceros*** (**Anthocerotaceae**; Figure 88), 1 on ***Megaceros*** (**Dendrocerotaceae**; Figure 79), and 1 on ***Notothylas*** (Figure 89), ***Phaeoceros*** (**Notothyladaceae**; Figure 90), and ***Anthoceros*** (**Anthocerotaceae**; Figure 91).

Figure 85. ***Marchantia polymorpha***; the genus ***Marchantia*** serves as home for species of ***Phytoliriomyza***. Photo by Denis Barthel, through Creative Commons.

Figure 86. ***Plagiochasma*** sp., home for species of ***Phytoliriomyza***. Photo by Zhang Li, with permission.

Figure 87. ***Wiesnerella denudata***, home for species of ***Phytoliriomyza***. Photo by Masaki Shimamura, with permission.

Figure 88. ***Folioceros cf glandulosus***, a hornwort in a genus that can serve as home for ***Phytoliriomyza***. Photo by Li Zhang, with permission.

Figure 89. ***Notothylas orbicularis***, a hornwort in a genus that can serve as home for ***Phytoliriomyza***. Photo by Blair Young, through Creative Commons.

Figure 90. ***Phaeoceros laevis***, a hornwort in a genus that can serve as home for ***Phytoliriomyza***. Photo by Oliver S. Beneutzer, through Creative Commons.

Figure 91. ***Anthoceros neesii*** with sporophytes dehiscing, a hornwort in a genus that can serve as home for ***Phytoliriomyza***. Photo from Earth.com, with permission.

Lauxaniidae

Sarah Lloyd described her experiences with some of the mine flies – ***Ceratolauxania atrimana*** (Figure 92-Figure 94). They like wet places (she never saw them in open, drier areas) and they tend to land on high points, but they sometimes also land on the mosses. That might be a location to rehydrate. They also oviposit on bryophytes, as shown on the ***Bazzania adnexa*** below (Figure 93).

Figure 92. ***Ceratolauxania atrimana*** laying eggs on ***Bazzania adnexa*** in Eucalypt forest in Tasmania. Photo courtesy of Sarah Lloyd.

Figure 93. ***Ceratolauxania atrimana*** laying eggs on ***Bazzania adnexa*** in Eucalypt forest in Tasmania. Photo courtesy of Sarah Lloyd.

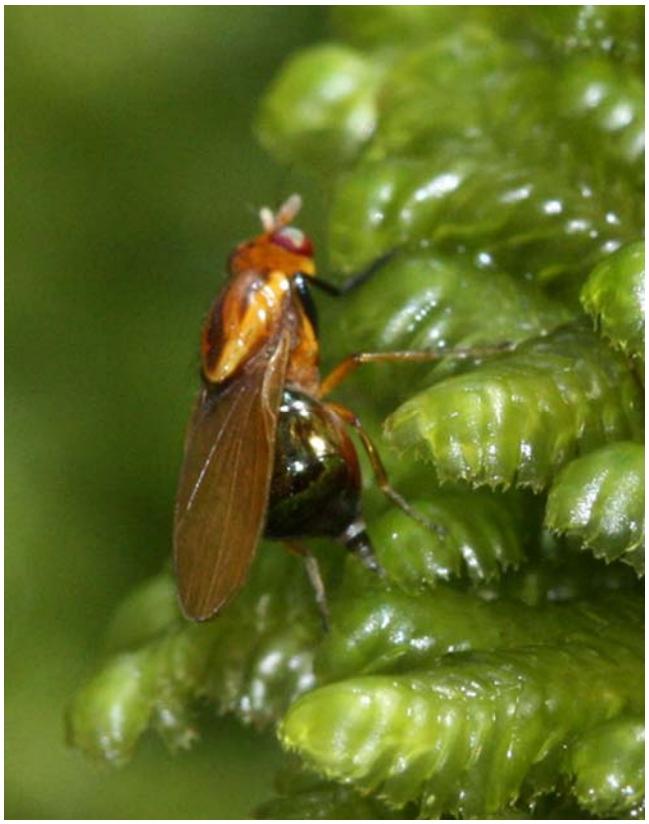

Figure 94. ***Ceratolauxania atrimana*** adult on ***Bazzania adnexa*** in a Tasmanian ***Eucalyptus*** forest. Photo courtesy of Sarah Lloyd.

Anthomyiidae – Root-maggot Flies

Thus far I can find only one paper that discusses the **Anthomyiidae** from bryophytes (Horsfield & MacGowan 1997). From very high altitudes in Britain, ***Alliopsis albipennis*** (see Figure 95) includes moss-dominated late snow-bed vegetation among its habitats, as well as flushes which are likely to be moss-dominated, but it is not restricted to these mossy habitats. ***Alliopsis atronitens*** (see Figure 95) exhibits one of its most frequent occurrences in ***Racomitrium lanuginosum*** moss heaths (Figure 45) on summit plateaus in Scotland.

Figure 95. ***Alliopsis billbergi*** adult; ***Alliopsis albipennis*** lives in moss-dominated late snowbeds. Photo by James K. Lindsey, with permission.

Delia caledonica (see Figure 96) occurs in blanket bogs and ***Racomitrium lanuginosum*** heath (Figure 45), among other montane habitats (Horsfield & MacGowan 1997). ***Delia piliventris*** (see Figure 96) occurs mostly in the ***Racomitrium lanuginosum***, grasslands, and tall herb communities in the montane area of Scotland.

Figure 96. ***Delia radicum*** adult. ***Delia caledonica*** is a species living in blanket bogs and ***Racomitrium lanuginosum*** heaths; ***D. piliventris*** lives mostly in ***Racomitrium lanuginosum*** heaths. Photo by Ladislav Tábi, with permission.

Botanophila moriens (see Figure 97-Figure 98) occurs in bryophyte springs and in ***Racomitrium lanuginosum*** (Figure 45) heaths at high elevations (760-1310 m alt) (Horsfield & MacGowan 1997). ***Zaphne spiniclunis*** (Figure 99) includes moss heaths (Figure 45) and bryophyte springs among its many habitats, mostly above 800 m near melting snow.

Figure 97. ***Botanophila*** larva, a species of bryophyte springs and ***Racomitrium lanuginosum*** heaths. Photo by Malcolm Storey, through Creative Commons.

Figure 98. ***Botanophila*** cf. ***fugax*** adult, a species of bryophyte springs and ***Racomitrium lanuginosum*** heaths. Photo by Martin Cooper, through Creative Commons.

Figure 99. ***Zaphne ambigua*** adult; ***Zaphne spiniculunis*** lives in moss heaths and bryophyte springs near melting snow. Photo by James K. Lindsey, with permission.

Heleomyzidae

Only ***Scoliocentra scutellaris*** (Figure 100) seems to utilize mosses for its habitat. This species in Scotland lives in moss heaths (Figure 45), as well as other montane habitats.

Figure 100. ***Scoliocentra scutellaris*** adult, a species of moss heaths. Photo by Gunnar M. Kvifte, through Creative Commons.

Muscidae – House Flies

This is one of the families you are undoubtedly familiar with because it includes the common housefly. The **Muscidae** have been discussed in part in the first of the **Diptera** subchapters because of their role in dispersing spores of the **Splachnaceae**. Hence we have already seen a relationship with ***Myospila meditabunda*** (Figure 101), ***Eudasyphora cyanicolor*** (Figure 102), ***Palpibracus chilensis***, and ***Palpibracus*** spp.

Figure 101. ***Myospila meditabunda*** female, one of the flies that facilitates transfer of spores in the **Splachnaceae**. Photo by James. K. Lindsey, with permission.

Figure 102. ***Eudasyphora cyanicolor*** adult male, one of the flies that facilitates transfer of spores in the **Splachnaceae**. Photo by Tristram Brelstaff, through Creative Commons.

In montane areas of Scotland, Horsfield and MacGowan (1997) both ***Phaonia subfuscinervis*** (Figure 103) and ***Spilogona triangulifera*** (see Figure 104) from ***Racomitrium lanuginosum*** heath (Figure 45), as well as other non-mossy habitats. These two flies have a habit of sunning themselves on rocks and typically associate with snowbeds. In Lithuania, the predaceous larvae of ***Phaonia fuscata*** (Figure 105-Figure 107) live in soil and mosses of broad-leaved forests (Gregor *et al*. 2002; Lutovinovas & Rozkošný 2009).

Figure 103. ***Phaonia subfuscinervis*** adult, a species of ***Racomitrium lanuginosum*** heaths. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 104. ***Spilogona*** *falleni* adult; ***Spilogona triangulifera*** lives in ***Racomitrium lanuginosum*** heaths. Photo by James K. Lindsey, through Creative Commons.

Figure 105. ***Phaonia subventa*** larva, pupa, adult male. Photo by Martin Cooper, through Creative Commons.

Figure 106. ***Phaonia fuscata*** adult female, a species whose larvae live among and under mosses in broad-leaved forests in Lithuania. Photo by James K. Lindsey, with permission.

Figure 107. ***Phaonia fuscata*** adult male, a species whose larvae live among and under mosses in broad-leaved forests in Lithuania. Photo by James K. Lindsey, with permission.

Limnophora is mostly aquatic in the larval stage (Roper 2001), but some are more limnoterrestrial. The carnivorous ***Limnophora exurda*** (current name not found) larvae and pupae live in tufts of wet mosses and liverworts that receive direct water or spray from waterfalls (Tate 1939). ***Limnophora riparia*** (Figure 108-Figure 109) adults occur singly on stones or mosses or algae in Armenia, but occasionally they may occur as small groups (Pont *et al*. 2011). Roberts (1971) suggested that the mouth parts and musculature of the carnivorous ***Limnophora riparia*** larvae (Figure 108) were adapted to the type of food they consumed. Larvae of this species are aquatic and prefer mosses as a substrate. They attach to their substrate to anchor themselves as they attack their prey, which includes other invertebrates, especially **Chironomidae** and **Simuliidae** larvae. ***Limnophora petallifera*** (Figure 110) females and others in the genus use mosses for oviposition, as well as algae (Werner & Pont 2006; Pont *et al*. 2011). They arrived for this purpose at about midday when the rock substrate was in direct sunlight with a temperature of 42°C (Werner & Pont 2006). The female was "running around the rock close to the water and stopped when she found a small indentation, then injected her eggs many times in the mosses and algae. Her forelegs were pointed upward and her abdomen pushed into the wet mosses. She laid the eggs singly, but each egg was placed next to the first one so that ultimately the eggs were in clusters.

Figure 108. ***Limnophora riparia*** larva, a species whose larval mouthparts are adapted for eating vegetable matter. Photo by Niels Sloth, with permission.

Figure 109. ***Limnophora riparia*** adult, a species whose adults often hang out on mosses. Photo by Marko Mutanen, through Creative Commons.

Figure 110. ***Limnophora petallifera*** adults eating larva of *Obuchovia popowae* (Simuliidae). ***Limnophora petallifera*** oviposits among mosses. Photo by Doreen Werner, permission pending.

Scathophagidae – Dung Flies

This is another poorly represented family in bryophytic habitats. ***Gonatherus planiceps*** (Figure 111) is a montane species in Scotland, and like many others there, one of its habitats is in ***Racomitrium lanuginosum*** heaths (Figure 45) (Horsfield & MacGowan 1997).

Figure 111. ***Gonatherus planiceps*** adult, a species of ***Racomitrium*** heaths. Photo by Marko Mutanen, through Creative Commons.

Bratton (2012) swept two females of ***Gimnomera tarsea*** (Figure 112) from mosses beside Loch a' Roe in the Outer Hebrides.

Figure 112. ***Gimnomera tarsea*** adult, a species whose adults hang out near mosses beside lakes. Photo by Marko Mutanen, through Creative Commons.

Calliphoridae – Blow Flies

And another! For the **Calliphoridae** I found only ***Calliphora stelviana*** (Figure 113) (Horsfield & MacGowan 1997). Like many other flies in the montane Scotland, these included ***Racomitrium lanuginosum*** among their habitats.

Figure 113. ***Calliphora stelviana*** adult, a species that lives in ***Racomitrium lanuginosum*** heaths. Photo by Marko Mutanen, through Creative Commons.

Summary

The **Rhagionidae** may live among bryophytes and lay their eggs there. The **Spaniidae** are leaf miners and ***Litoleptis*** species and some ***Spania*** species mine the thalli of thick thallose liverworts. The **Dolichopodidae** tend to be amphibious, living in wet bryophytes. The **Empididae** may be found on damp mosses as well as aquatic ones. Some **Hybotidae** live among ***Sphagnum*** as adults. The **Syrphidae** are likewise often aquatic, but some live among terrestrial mosses as larvae. The **Phoridae** are not normal bryophyte inhabitants, but they do overwinter in moss polsters. Several members of **Agromyzidae** are leaf miners in large thallose liverworts and hornworts. The **Lauxaniidae** like wet places and often land on protruding mosses; others oviposit on species of the leafy liverwort ***Bazzania***. **Anthomyiidae** live among mosses in late snow-bed vegetation; others live in ***Racomitrium*** heaths. One **Heleomyzidae** lives in moss heaths. The **Muscidae** are among the important spore dispersers for the moss family **Splachnaceae**. Others occur in ***Racomitrium*** heaths. The **Scathophagidae** and **Calliphoridae** also sometimes live in ***Racomitrium*** heaths.

Hence, ***Racomitrium***, with its often large hummocks, serves as a home for some members in many of the **Nematocera** families. This habitat is well insulated and capable of maintaining moisture for a longer time than most other terrestrial habitats.

Acknowledgments

Thank you to Yume Imada for sharing his research and images of the **Spaniidae**. Thank you to for alerting me to the mine flies (***Ceratolauxania atrimana***) that live on liverworts and sharing her research and images with me. Likewise, I appreciate Juan Carlos Villarreal for sharing his research on **Anthocerotophyta** and the flies that live in them, providing me with images for this chapter.

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