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 they reduce the danger of dehydration or take a drink of water. Photo by Serhat Ursavas, with permission.

BRACHYCERA

Rhagionidae – Snipe Flies

This worldwide family has some members that are among the most primitive of the Brachycera. One of its diagnostic characters is that its head points downward when at rest (Figure 6), earning it the name of "downlooker flies."

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.

Lane and Anderson (1982) found immature adults of Ptiolina sp. near zonata (see Figure 2-Figure 4) by hand sorting moss-covered soil samples. Apparently mosses also provide oviposition sites for the genus (Figure 3-Figure 4), hence also providing homes for the larvae (Figure 5).

In the Czech Republic, Rhagio latipennis (Figure 6) 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.
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Figure 2. *Ptiolina* on moss; *P. zonata* apparently emerges on mosses. Photo by Pristurus, through Creative Commons.

Figure 3. *Ptiolina* sp. adult ovipositing on moss. Photo courtesy of Yume Imada.

Figure 4. *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 5. *Ptiolina* sp. larva, a bryophyte inhabitant. Photo courtesy of Yume Imada.

Figure 6. *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 – Snipe Flies**

Members of this family are often included in the *Rhagionidae* as the *Spaniinae*. Their feeding habits may be assumed to similar, in most cases, to those of the *Rhagionidae*. I found only one record for a bryophyte associate. But while I was working on this chapter, Imado and Kato (2016) provided me with six new species they described in the genus *Litoleptis*.

Imado and Kato (2016) reported a different feeding strategy for *Litoleptis* (Figure 7–Figure 8) in Japan. The larvae of this genus mine the thalli of thallose liverworts in the families *Aytoniaceae* and *Conocephalaceae*. These included species of *Conocephalum* (Figure 8), *Reboulia* (Figure 9), and *Asterella* (Figure 10). Imado and Kato described six new species from this unexplored group of substrates.

Figure 7. *Litoleptis kiiensis* larva, a bryophyte inhabitant. Photo courtesy of Yume Imada.
That original record I found of a member of Spaniidae among bryophytes is that of Spania nigra (Figure 11). Larvae of this species live on mosses and liverworts in the ghyll woodlands of Sussex (Roper 2001). Boyce (2002) reported it from the thallose liverwort Pellia in England. Yume Imada (pers. comm.) has also found Spania sp. (Figure 12-Figure 13) tunelling in Conocephalum.

Figure 8. Litoleptis japonica adult on Conocephalum sp. Photo courtesy of Yume Imada.

Figure 9. Reboulia hemisphaerica with archegoniophores, a potential host plant for species of Litoleptis. Photo by Michael Lüth, with permission.

Figure 10. Asterella tenella thallus, potential home for Litoleptis larvae. Note that something has eaten the thallus in the lower right. Photo by Michael Lüth, with permission.

Figure 11. Spania nigra adult, a species whose larvae live among forest mosses and liverworts in the UK. Photo by Marko Mutanen, through Creative Commons.

Figure 12. Spania sp. larva tunneling in Conocephalum. Photo courtesy of Yume Imada.
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 14) lives in calcareous wet habitats near small permanent pools, in bryophyte flushes (Figure 15), flushed grasslands, and wet mires (Horsfield & MacGowan 1997), but it also occurs in bogs (Ringdahl 1928). Hydrophorus rufibarbis (see Figure 16-Figure 17) seems to prefer small, peaty pools, but it also lives in grassy flushes and bryophyte springs (Horsfield & MacGowan 1997).

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 18) 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 18. *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.](image)

The larvae of *Hemerodromia* (Figure 19) 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 19. *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.](image)

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 20-Figure 22). This family is mostly predaceous on other small invertebrates (Tony Daley, pers. comm. 19 November 2011).

![Figure 20. Empidoid fly, possibly *Hybotidae*, on a leafy liverwort. Note the greatly arched thorax and long legs. Photo courtesy of Sarah Lloyd.](image)

![Figure 21. Adult member of *Empididae* resting on a moss capsule. Photo courtesy of Sarah Lloyd.](image)

*Clinocera nivalis* (*nivalis* refers to snow; Figure 22) 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 23) 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 24-Figure 25) spring in Coire Raibert at around 1000 m.
Figure 22. *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 23. *Racomitrium lanuginosum* heath, home for *Clinocera nivalis*. Photo by Mike Pennington, through Creative Commons.

Figure 24. *Anthelia julacea*, home for *Clinocera nivalis*. Photo by Jean Faubert., with permission.

Figure 25. *Anthelia julacea*, home for *Clinocera nivalis*. Photo by Štěpán Koval, with permission.

Larvae of *Wiedemannia impudica* (see Figure 26) probably live in mosses on emergent boulders (Horsfield & MacGowan 1997), again where they will be constantly moist.

Figure 26. *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 27-Figure 28) 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 29). The new species was similar to *Stilpon nubilus*. 
Figure 27. *Stilpon* sp. adult, a genus in which some adults occur in *Sphagnum*. Photo by Tom Murray, through Creative Commons.

Figure 28. *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 29. *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 bee fly. *Platychaerus melanopsis* (Figure 30) is known from moss-dominated summit heaths (Figure 23) and grasslands in Scotland (Horsfield & MacGowan 1997). *Cheilosia sahlbergi* (Figure 31) occurs in habitats where bryophytes are abundant, including ericaceous dwarf shrub heaths, flushes, and bryophyte springs.

Figure 30. *Platychaerus melanopsis* adult, a species from moss-dominated summit heaths. Photo from America Pink, with online permission.

Figure 31. *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 32).

Figure 32. *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 33) from the thallose liverwort *Ricciocarpos natans* (Figure 34). *Phytoliriomyza mesnili* (formerly *Liriomyza*; see Figure 35–Figure 36) is known from *Ricciocarpos natans* in France as well as being present on the thallose liverwort *Riccia beyrichiana* (Figure 37). It feeds in the thallus and pupates there and also pupates in the thallus of *Nothoceros vincentianus* (Figure 38–Figure 40) in Peru. In Mexico, it is known on *Dumortiera* (Figure 41) and *Monoclea* (Figure 42).

Figure 33. *Liriomyza taraxaci* adult, member of a genus known from the liverwort *Ricciocarpos natans*. Photo by Peggy Greb, USDA, through public domain.

Figure 34. *Ricciocarpos natans*, home for some species of *Liriomyza*. Photo by Christian Fischer, through Creative Commons.

Figure 35. *Phytoliriomyza arctica* adult. Some members of this genus live in liverwort thalli. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 36. *Phytoliriomyza melampyga* larval tunnels in a leaf. Photo from Biodiversity Centre, through Creative Commons.

Figure 37. *Riccia beyrichiana*, home and food for *Phytoliriomyza mesnili*. Photo by Jan-Peter Frahm, with permission.
Figure 38. *Nothoceros*, a genus where *Phytoliriomyza mesnili* is known to live in Peru. Photo by Juan Larraín, with permission.

Figure 39. *Nothoceros* with *Agromyzidae* leaf miners. Photo courtesy of Juan Carlos Villarreal.

Figure 40. *Nothoceros* leaf miner seen through the thallus. Photo courtesy of Juan Carlos Villarreal.

Figure 41. *Dumortiera hirsuta*, home to *Phytoliriomyza mesnili* in Mexico. Photo by Li Zhang, with permission.

Figure 42. *Monoclea forsteri*, home to *Phytoliriomyza mesnili* in Mexico. Photo by Jan-Peter Frahm, 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 43) of leaf-mining flies crawling within the hornwort *Nothoceros aenigmaticus*, making traces. While in his custody, it became a pupa (Figure 44). 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 45-Figure 50). He found similar *Diptera* from Panamanian *Nothoceros vincentianus* (Figure 47) 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 43. Agromyzidae larva from Nothoceros thallus. Photo courtesy of Juan Carlos Villarreal.

Figure 44. Agromyzidae pupa grown from larvae that were living in Nothoceros. Photo courtesy of Juan Carlos Villarreal.

Figure 45. Phytomyza egg from Nothoceros aenigmaticus Montage Mexico. Photo courtesy of Juan Carlos Villarreal.

Figure 46. Phytomyza ranunculi larval tunnels in a leaf, similar to the made by species in liverworts. Photo by James K. Lindsey, with permission.

Figure 47. 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 48. 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 49. Phytomyza ranunculi adult, member of a genus that sometimes lays eggs in liverwort thalli. Photo by Dick Belgers, through Creative Commons.
Villarreal was able to determine (via a letter belonging to John Engel) that Proskauer had seen leaf miners in *Megaceros* and *Nothoceros*. Hering (1957) described *Phytoliriomyza* sp. (see Figure 35-Figure 36) larvae and pupae from *Megaceros*.

In the larvae of *Phytoliriomyza mesnili* (see Figure 35-Figure 36), living in the hornwort *Nothoceros vincentianus* (Figure 47), 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 41) and *Monoclea* (Figure 42) 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 51) 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 has also has far-reaching geographic presence, although the species involved may differ. Sara Altenfelder (pers. comm.) found *Riccia glauca* (Figure 52) and *R. warnstorffii* (Figure 53) 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 35-Figure 36), first described by Aguilar (1945) feeding on *Ricciocarpos natans* (Figure 34) and later reported by Sellier (1947) from *Riccia beyrichiana* (Figure 37). 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*.

**Lauxaniidae**

Sarah Lloyd described her experiences with some of the mine flies – *Ceratolauxania atrimana* (Figure 54-Figure 56). 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 56).
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 57) 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 57) exhibits one of its most frequent occurrences in Racomitrium lanuginosum moss heaths (Figure 23) on summit plateaus in Scotland.

Delia caledonica (see Figure 58) occurs in blanket bogs and Racomitrium lanuginosum heath (Figure 23), among other montane habitats (Horsfield & MacGowan 1997). Delia piliventris (see Figure 58) occurs mostly in the Racomitrium lanuginosum, grasslands, and tall herb communities in the montane area of Scotland.

Botanophila moriens (see Figure 59-Figure 60) occurs in bryophyte springs and in Racomitrium lanuginosum (Figure 23) heaths at high elevations (760-1310 m alt) (Horsfield & MacGowan 1997). Zaphne spiniclunis (Figure 60-Figure 61) includes moss heaths (Figure 23) and bryophyte springs among its many habitats, mostly above 800 m near melting snow.
Heleomyzidae

Only *Scoliocentra scutellaris* (Figure 62) seems to utilize mosses for its habitat. This species in Scotland lives in moss heaths (Figure 23), as well as other montane habitats.

**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 63), *Eudasyphora cyanicolor* (Figure 64), *Palpibracus chilensis*, and *Palpibracus* spp.

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Figure 59. *Botanophila* larva, a species of bryophyte springs and *Racomitrium lanuginosum* heaths. Photo by Malcolm Storey, through Creative Commons.

Figure 60. *Botanophila* cf. *fugax* adult, a species of bryophyte springs and *Racomitrium lanuginosum* heaths. Photo by Martin Cooper, through Creative Commons.

Figure 61. *Zaphne ambigua* adult; *Zaphne spiniculunis* lives in moss heaths and bryophyte springs near melting snow. Photo by James K. Lindsey, with permission.

Figure 62. *Scoliocentra scutellaris* adult, a species of moss heaths. Photo by Gunnar M. Kvifte, through Creative Commons.

Figure 63. *Myospila meditabunda* female, one of the flies that facilitates transfer of spores in the *Splachnaceae*. Photo by James K. Lindsey, with permission.
In montane areas of Scotland, Horsfield and MacGowan (1997) both *Phaonia subfuscinervis* (Figure 65) and *Spilogona triangulifera* (see Figure 66) from *Racomitrium lanuginosum* heath (Figure 23), 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 67-Figure 69) live in soil and mosses of broad-leaved forests (Gregor *et al.* 2002; Lutovinovas & Rozkošný 2009).
**Figure 69.** *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 70-Figure 71) 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 70) 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 72) 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 70.** *Limnophora riparia* larva, a species whose larval mouthparts are adapted for eating vegetable matter. Photo by Niels Sloth, with permission.

**Figure 71.** *Limnophora riparia* adult, a species whose adults often hang out on mosses. Photo by Marko Mutanen, through Creative Commons.

**Figure 72.** *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 73) is a montane species in Scotland, and like many others there, one of its habitats is in *Racomitrium lanuginosum* heaths (Figure 23) (Horsfield & MacGowan 1997).

**Figure 73.** *Gonatherus planiceps* adult, a species of *Racomitrium* heaths. Photo by Marko Mutanen, through Creative Commons.
Bratton (2012) swept two females of *Gimnomera tarsea* (Figure 74) from mosses beside Loch a’ Roe in the Outer Hebrides.

![Gimnomera tarsea](image1.png)

Figure 74. *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 75) (Horsfield & MacGowan 1997). Like many other flies in the montane Scotland, these included *Racomitrium lanuginosum* among their habitats.

![Calliphora stelviana](image2.png)

Figure 75. *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**. The **Anthomyiidae** live among mosses in late snow-bed vegetation; others live in **Racomitrium** heaths. One **Helomyzidae** 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 (**Ceratoluxania 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.

**Literature Cited**


