# CHAPTER 12-19

TERRESTRIAL INSECTS: HOLOMETABOLA – DIPTERA NEMATOCERA 2

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Figure 1. Fungus gnat herbivory on Buxbaumia aphylla capsules. Note the topless setae. Photo by Jörg Müller, with permission.

Cecidomyiidae – Gall Midges

Some members of this family that are typical of trees can be found in moss tussocks or among the mosses on tree trunks. These include members of the genus Peromyia (Figure 2) (Perkovsky & Fedotova 2004). Mosses are so important to some species as to be the source of the name – including Bryocrypta dubia, Cryptoneurus muscicola, Bryomyia bergrothi, and Peromyia muscorum, as well as Peromyia palustris (Mamaev & Krivosheina 1993).

Stabaev (in Mamaev & Krivosheina 1993) found that larvae of gall midges comprised an important part of the fauna in primary soils under mosses. But Mamaev and Krivosheina comment that there has been little study of the moss-inhabiting gall midges, promising surprises for those who explore them.

Figure 2. Peromyia adult, a genus that sometimes lives among bryophytes on the ground and on tree trunks. Photo by Charley Eiseman, through Creative Commons.
Mycetophilidae – Fungus Gnats

This family primarily feeds on fungi, but a few species eat algae, mosses, and liverworts, while others are saprophagous (feeding on or obtaining nourishment from dead or decaying animal matter) in bird nests (Hackman et al. 1988; Økland 1994). *Cordyla fusca* (see Figure 3) is significantly correlated with mosses (Økland 1994). On the other hand, *Boletina gripha* (Figure 4) and *Acnernia nitidicollis* have high negative correlations with mosses. The correlation of some members of this family with mosses may relate to a concentration of host fungi in the soil that likewise correlates with the mosses or their habitat.

Figure 3. *Cordyla fissa* adult; the presence of *C. fusca* correlates with mosses in European forests. Photo by Hanna Koivula, through Creative Commons.

Pettet (1967) reported that larvae in the *Mycetophilidae* parasitize the thallose liverwort *Riccia frostii* (Figure 5). The infestation occurred when the Nile floodwaters receded in Sudan. The infestation spread and increased until virtually all thalli were infected and remained so until flooding returned. The infestation then completely disappeared and although Pettet watched for it closely for the next five years, it never returned. The larvae eat the internal tissues of the thalli, causing the thallus to become non-turgid and flabby. In the last stages of the infestation, the liverwort surface disintegrates. Each rosette revealed 5-25 small, yellow-orange larvae. Pupation likewise occurred inside the thallus. Such interactions can easily go unnoticed and close observation may reveal other interesting bryological habitats for insects.

Figure 4. *Boletina gripha* adult, a species that is negatively correlated with mosses. Photo by Hanna Koivula, through Creative Commons.

Figure 5. *Riccia frostii*, a species that is parasitized by *Mycetophilidae*. Photo by Rosemary Taylor, with permission.

Müller (2012) found several adult fungus gnats (Figure 1, Figure 6) feeding on spores in capsules of *Buxbaumia aphylla* (Figure 7) in Germany. It is likely that at least some of the spores escape being eaten and are transported by the fungus gnats, later being deposited elsewhere.
Ponge (1991) found that some of the Sciaridae larvae on the Scots pine (Pinus sylvestris) forest floor consumed mosses, but they also consumed fungi. But not all interactions of this family with bryophytes are so casual. Sawangproh (2014) notified me of finding the larvae of a black-winged fungus gnat, Scatopssciara cunicularius (Figure 8-Figure 14), feeding and tunnelling on a liverwort thallus, Marchantia polymorpha (Figure 8-Figure 10), in the greenhouse. The feeding causes serious damage to both growth and survival of the liverwort. The gnat population expands when the ambient temperature increases in early spring. When it is cool (12°C), the larvae take longer to develop and consequently do more damage to the thalli than when reared at 22°C (Sawangproh & Cronberg 2016; Sawangproh et al. 2016). Following the larval damage, the thalli are more susceptible to secondary attacks by other pests and fungal infections.

**Sciaridae – Dark-winged Fungus Gnats**

Fungus gnats (Sciaridae) deposit eggs in organic matter, including mosses (Hurley 2006). When such habitats are present in greenhouses, the fungus gnats become pests. Shin et al. (2012) reported that these gnats inhabit peat bogs, thus making this a source of the gnats in nurseries and greenhouses. Peck and Moldenke (2010) are concerned with invertebrate invasions through commercial uses of mosses. Among those invertebrates, they found a few adult sciarid flies.
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It does not appear that these bryophagous fungus gnats need fungi. *Scatopsiara cunicularius* (Figure 8-Figure 14) can complete its entire life cycle with only liverworts as food (Sawangproh & Cronberg 2016; Sawangproh et al. 2016). This is an unusual relationship because few insects are known to eat liverworts. Sawangproh and coworkers (2016) suggested that the liverwort oil bodies with their essential oils may serve as a deterrent to herbivory. We still have little understanding of the mechanisms that permit some insects to eat the bryophytes, especially those with antiherbivore compounds, whereas most insects seem unable to. Just imagine what the world might be like with no insects. Bryophytes would most likely be far more speciose, whereas the insects may have eliminated those that did not develop antiherbivore compounds early in their evolution.

Figure 10. *Scatopsiara cunicularius* larva on one of the wounded patches of *Marchantia polymorpha*. Photo courtesy of Nils Cronberg.

Figure 11. *Scatopsiara cunicularius* larva from *Marchantia polymorpha*. Photo courtesy of Weerachon Sawangproh.

Figure 12. *Scatopsiara cunicularius* mature pupal stage on a liverwort thallus. Photo by Weerachon Sawangproh.

Figure 13. *Scatopsiara cunicularius* pupa from *Marchantia polymorpha*. Photo courtesy of Weerachon Sawangproh.

Figure 14. *Scatopsiara cunicularius* female adult. Photo courtesy of Weerachon Sawangproh.
Bradysia sp. (Figure 15-Figure 16) larvae (Figure 15) can be found under several species of Bryum [B. argenteum (Figure 17), B. dichotomum (Figure 18), and B. pachytheca (Figure 19)], at least in flower pots (Downing & Selkirk 1996). Downing and Selkirk observed that the mosses had a rough, patchy appearance, "like they had been ploughed." These larvae eat the moss rhizoids. My surprise was that after drenching the pots with a solution of 2 g Alsystrin in 10 L water the bryophytes grew back in two weeks!

Bradysia sp. (Figure 15-Figure 16) larvae, Bryum inhabitants. Photo by David Cappaert, through Creative Commons.

Figure 16. Bradysia praecox; some members of this genus live among the moss Bryum as larvae. Photo by James K. Lindsey, with permission.

Figure 17. Bryum argenteum, a species where Bradysia sp. larvae hide under the clump. Photo by Janice Glime.

Figure 18. Bryum dichotomum with gemmae, home for some species of Bradysia. Photo by David T. Holyoak, with permission.

Figure 19. Bryum pachytheca with capsules, cover for some Bradysia species. Photo by David Tng, with permission.

Ceratopogonidae – Biting Midges

One might not expect chocolate to be involved in this chapter, but certain members of the Ceratopogonidae (Figure 20) are associated with cacao (chocolate) flowers as important pollinators (Winder 1977). On the same trees, among the epiphytic mosses, one can find Atrichopogon (Figure 21-Figure 22), Stilobezzia (Figure 23), and Dasyhelea (Figure 24-Figure 26), all members of Ceratopogonidae.
Figure 20. *Jungermannia exertifolia* ssp *cordifolia* with *Diptera* larva (*Ceratopogonidae*). Photo by Michael Lüth, with permission.

Figure 21. *Atripogon* larva, a dweller among epiphytic mosses. Photo from Waterbugkey, through EPA public domain.

Figure 22. *Atripogon* female adult, a species associated with epiphytic bryophytes. Photo by Tom Murray, through Creative Commons.

Figure 23. *Stilobezzia* female adult, a genus known from epiphytic mosses. Photo by Tom Murray, through Creative Commons.

Figure 24. *Dasyhelea flavifrons* larva weaving its way under the bark. Photo by Walter Pfliegler, with permission.

Figure 25. *Dasyhelea flavifrons* larvae; for some members of the genus this stage is spent in bryophytes on trees. Photo by Walter Pfliegler, with permission.
Many of the Ceratopogonidae have aquatic larvae, so it is natural that the adults hang out in moist conditions, near the water sources where they can lay eggs. Hence, some will naturally land on mosses to rest or obtain moisture (Figure 27).

Kolenohelea calcarata occurs among mosses in springs, and Serromyia femorata (Figure 28) occurs among damp mosses (Strenzke 1950). But Culicoides impunctatus (Figure 29) (biting midge) larvae at one site in western Scotland actually avoided most mosses (Blackwell et al. 1999). Their distribution and larval counts had a significantly negative correlation with all mosses other than species of Sphagnum. This species increases its number of eggs when provided with Sphagnum egg-laying sites (Carpenter et al. 2001). Members of the genus Forcipomyia (Figure 30), another biting midge, also builds nests in Sphagnum (Oldroyd 1964).
Chironomidae – Midges

Bettis (2008) compared the abundance of invertebrate fauna in two different *Grimmia* (Figure 31) morphotypes, one on exposed granitic outcropping and one at a protected seasonal riparian habitat. In both cases, *Chironomidae* larvae were among the major invertebrates present. Some of the *Chironomidae* can emerge from mosses in large numbers (Figure 32), especially in polar regions, and adults cover mosses as they emerge (Figure 33) (pers. obs.).

Although *Chironomidae* are abundant aquatic larvae, they also occur on land. The *Cricotopus* (Figure 34-Figure 35) larva occurs with epilithic (growing on rocks) and epiphytic (growing on plants, usually trees) liverworts in western Oregon and Washington, USA, and feeds on the leafy liverworts *Calypogeia* (Figure 36), *Gyrothyra underwoodiana* (Figure 37), *Jungermannia rubra* (Figure 38), *Porella navicularis* (Figure 39), and *Scapania bolanderi* (Figure 40) in the lab (Russell 1979). In the field they do considerable feeding damage to *Calypogeia fissa* (Figure 36) and *Jungermannia rubra*.

Figure 31. *Grimmia laevigata* on boulder, potential home for *Chironomidae*. Photo by Alan Cressler, with permission.

Figure 32. *Chironomidae* swarming in moss garden, a typical scene in summer. Photo by J. Paul Moore, with permission.

Figure 33. *Chironomidae* adults on moss at Helfdi, Myvatn, Iceland. Photo by Janice Glime.

Figure 34. *Cricotopus annulator* complex larva, member of a genus that occurs among liverworts on boulders and trees. Photo © Stroud Water Research Center, through Creative Commons.
Figure 35. *Cricotopus* adult, a genus whose larvae occur among liverworts on trees and boulders. Photo by G Drange, through Creative Commons.

Figure 36. *Calypogeia fissa*, home and food for larvae of *Cricotopus*. Photo by David T. Holyoak, with permission.

Figure 37. *Gyrothyra underwoodiana*, home and food for *Cricotopus* larvae. Photo by Li Zhang, with permission.

Figure 38. *Jungermannia rubra* with perianth. This species provides home and food for *Cricotopus* larvae among epiphytes. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 39. Branch with *Porella navicularis*, home and food for larvae of *Cricotopus*. Photo by Tanya Yoder, through Creative Commons.

Figure 40. *Scapania bolanderi* with capsules, a species that is home and food for *Cricotopus* larvae. Photo by Chris Wagner, with permission.
The *Chironomidae* may do an important service to some mosses. Harvey-Gibson and Miller-Brown (1927) reported that these midges, as adults, seem to be agents of fertilization for *Polytrichum commune* (Figure 41-Figure 42). In this species, the paraphyses (Figure 43) associated with both antheridia and archegonia exude mucilage (but no sugar). Small midges were among the continuous visitors to these gametangial areas. The insects lap the mucilage and get it on their body parts. If they visit at the right time, sperm may become attached as well and the midges that subsequently visit females may transfer live sperm to the appropriate location.

![Figure 41](image1.png)  
**Figure 41.** *Polytrichum commune* with capsules, indicating successful fertilization. Photo by Michael Lüth, with permission.

![Figure 42](image2.png)  
**Figure 42.** *Polytrichum commune* with male splash cups that attract adult *Chironomidae* that carry sperm to the female plants that are mixed with them. Photo by Li Zhang, with permission.

![Figure 43](image3.png)  
**Figure 43.** *Polytrichum* showing two antheridia with adjacent paraphyses. Photo by George J. Shepherd, through Creative Commons.

Moss-dwelling *Chironomidae* are abundant in and around springs. Lencioni *et al.* (2011) studied *Chironomidae* distribution in 81 springs in the Italian PreAlps and Alps. In 173 samples they found 26,871 *Chironomidae* representing all life stages except eggs. To illustrate the abundance of moss-dwelling *Chironomidae*, Nolte (1991) sampled and compared mosses that were intermittently out of the water on semi-submersed mosses near a spring with those in permanently submersed locations 700 m downstream. All of these larvae were small, and 98% were less than 5 mm in length. The total sampling revealed 65 species of chironomids in 26 genera, with greater species richness near the source in the semi-submersed mosses. But the mean abundance was 5X higher in the permanently submersed mosses compared to those that were semi-submersed at the spring. On the other hand, the maximum abundance anywhere was 830 larvae per 10 cm² in one semi-submersed sample. The dominance of the various chironomid taxa was dependent primarily on the location of the moss along the stream.

Ponge (1991) examined gut contents of forest floor animals in a 5x5 cm Scots pine litter. The subsequent feces were followed to determine the ultimate fate of the ingested material. Some of the fecal material included bryophytes and was the primary material in feces of both enchytraeid and lumbricid worms. In turn, the chironomid larvae consumed and digested the fecal material.

*Chironomidae* may play an important role in initial stages of both primary and secondary succession. These species specialize on open patches created by these
successional conditions and live in the early stage that is fallow, having mosses and lichens as pioneers (Frouz & Kindlmann 2001). The habitat generally has good quality food, but it is prone to severe desiccation in the summer that can decimate the larval population. In the Czech Republic and elsewhere, winter conditions permit the populations to replenish. The larvae are poor dispersers, but winged adults have the opportunity to move about. To explore the ability of these species to survive in this hostile environment, Frouz and Kindlmann studied *Smittia aterrima* (Figure 44), an abundant species in old fields. They found that eggs laid by the females from adjoining more developed vegetation were sufficient to replenish the lost populations.

*Smittia aterrima* (Figure 44) is common in disturbed areas, with up to 12,000 individuals per m² (Delettre & Lagerlöf 1992). These larvae live in the surface soil horizon and feed on plant litter, fungi, soil algae, and mosses (Frouz & Lukešová 1995). In České Budějovice, Frouz and Kindlmann (2001) tested the source-sink hypothesis [idea that organisms move from a favorable habitat (source), often as a result of overcrowding, to a sink that is less favorable, where they remain and accumulate] with this species and demonstrated that as their preferred open habitat became unsuitable, the larval population disappeared there. Ducrotoy (1980) and Delettre (1986) had observed the same phenomenon for terrestrial chironomids living among mosses on rocks, again as a result of drought. The larvae continue to exist in sub-optimal habitats during the drought and re-colonize the preferred habitats (including mosses) when favorable conditions return (Frouz & Kindlmann 2001). This migration maintains the source-sink survival strategy.

Other *Chironomidae* species have similar abundance patterns in these pioneer habitats. *Bryophoenocladius* cf. *illimbatu* (Figure 45) is a parthenogenic (having unfertilized eggs that develop into new individuals) moss dweller that lives in habitats with open and low vegetation (Frouz 1997). Both *Bryophoenocladius* cf. *illimbatu* and *Smittia aterrima* (Figure 44) decreased from the first to third year of the study as the field became less open and forbs taller than 20 cm became more prominent. Soil algae and mosses form an important component of food for both species (Frouz & Lukešová 1995).

Sometimes one can find exciting new species by knowing the general habits of the genus. The snow-dwelling adults of *Bryophoenocladius thaleri* were discovered in barren areas of Dolomite Alps in Italy above 3100 m altitude. This species probably mates in leks (assembly areas where males gather during mating season to exhibit competing mating displays and attract females) on the ground because their males cannot fly (Willassen 1996). But the immature (larval) stages are so far unknown. Willassen suggests that we look for them among terrestrial mosses because that is a preferred habitat of other members of the genus. *Bryophoenocladius virgo* lives among mosses as larvae and adults and solves the flight problem by being parthenogenetic (giving birth without fertilization) (Cranston 1987). *Bryophoenocladius vernalis* (Figure 46) has been caught in the act of damaging rare mosses growing in chalk quarries in southern England.
**Limnophyes minimus** (Figure 47-Figure 49) is likewise a pioneer that lives in the shallow soil that is formed by the mosses, lichens, and raw humus (Delettre 1986). On rocks, mosses trap dust and soon accumulate a thin soil on rock surfaces. This provides suitable habitat for *Limnophyes minimus* in Brittany, France. This species also occurs in the sub-Antarctic where the adult females are parthenogenetic (Hänel & Chown 1998). And these females do not feed. As larvae, this species joins *Pringleophaga marioni* (*Lepidoptera, Tineidae*; Figure 50) in their contribution to nutrient recycling on sub-Antarctic Marion Island.

![Figure 47. Limnophyes minimus, a pioneer species in mosses on newly colonized areas. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.](image)

![Figure 48. Limnophyes minimus, a pioneer among mosses. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.](image)

![Figure 49. Limnophyes minimus adult, a pioneer species among mosses in early succession stages. Photo by James K. Lindsey, with permission.](image)

![Figure 50. Pringleophaga marioni adult, a lepidopteran moss-dwelling contributor to nutrient cycling on Marion Island in the sub-Antarctic. Photo by Steven L. Chown, with permission.](image)

The females of *Eretmoptera murphyi* (Figure 51) from the Antarctic and sub-Antarctic are brachypterous (short-winged), making dispersal difficult. Not only is the female apparently parthenogenetic, but males are unknown (Cranston 1985). This species has terrestrial larvae that live among damp mosses and peat.

![Figure 51. Eretmoptera murphyi on a leafy liverwort, Prince Olav Harbour, South Georgia. Photo courtesy of Roger S. Key.](image)
As already seen in the aquatic midges, living among mosses could present a danger from parasitic mites (Stur et al. 2005). But when those mosses are semi-terrestrial, the Chironomidae become unavailable to those aquatic parasitic mites.

**Belgica**

One of the best known of the moss-dwelling Chironomidae is *Belgica antarctica* (Figure 52-Figure 54). These larvae are abundant in damp mosses, grass roots, detritus, and around penguin rookeries and seabird nests in the Antarctic (Wirth & Gressitt 1967; Cranston 1985). The species overwinters as larvae (Strong 1967); all four larval instars overwinter (Benoit et al. 2007). Some also occur in meltwater pools and small ponds with algae.

*Belgica antarctica* (Figure 52-Figure 54) is the largest arthropod in Antarctica and is wingless (Gressitt 1967). The females lay their eggs in a gelatinous mass in damp mosses and the larvae disperse among the mosses about 10 days later. The mosses most likely make survival of this larger animal possible by providing a warmer refuge than the ambient temperature. Gressitt showed that temperatures in *Polytrichum* (Figure 41-Figure 42) there exceed that of the air by as much as 13°C. The temperatures in *Drepanocladus* (probably *Sanionia uncinata* – Figure 55) were closer to those of the air.

**Temperature is not the only factor limiting the distribution of Belgica antarctica** (Figure 52-Figure 54). Hayward et al. (2007) considered moisture to be as important as cold resistance in these polar invertebrates. With temperatures most of the year below 0°C, water is hence inaccessible for a long period of time. Hayward and coworkers found that when the larvae were desiccated at a high relative humidity (98.2%) they were more tolerant of desiccation and also exhibited increased freezing tolerance to -10 and -15°C. Nevertheless, all larvae were frozen at -10°C. Slow drying was important for this acclimation. The researchers found that osmolality increased, reaching its highest levels after five days at 98.2% RH, but that these values returned to predesiccation values with just one hour of rehydration, well before water content returned to predesiccation levels. They found no evidence of heat-shock proteins contributing to desiccation tolerance. Membrane phospholipid adaptation and metabolite synthesis appeared to be the important physiological mechanisms that enhanced both cold tolerance and desiccation tolerance, a conclusion also supported by Lee et al. (2006). I would consider it likely that the mosses are important in ensuring a high initial humidity and a slow rate of desiccation, permitting the larvae to acclimate.

Teets et al. (2011) examined the effects of repeated cold exposure on survival, energy content, and stress protein expression of the larvae of *Belgica antarctica* (Figure 53). Most of the larvae (>95%) survived a single 12-hour stint of -5°C when frozen in both the presence of...
water and in a dry environment. However, after five cycles of repeated cold exposure to -5°C, survival of frozen larvae dropped to below 70%. On the other hand, survival of controls and supercooled (dry) larvae remained unchanged. Freezing during these repeated cold exposures resulted in a drastic reduction in energy reserves. After five of these cold exposures, the larvae had 25% less lipid, 30% less glycogen, and nearly 40% less trehalose than supercooled larvae. There were further indications of protein damage in this frozen group. There seemed to be no difference in larvae frozen for 60 continuous hours and those that had a total of 60 hours accumulated from repeated cold exposure. Teets and coworkers concluded that both survival and energy conservation benefitted from a dry microhabitat that remained unfrozen during repeated cold exposures. Do bryophytes provide such an environment, or must the larvae migrate into the soil to survive?

The larvae of *Belgica antarctica* (Figure 53) spend most of the year (7-8 months) encased in ice with soil (Elnitsky et al. 2008; Lopez et al. 2009), creating desiccating conditions. Elnitsky et al. (2008) explored the possibility that they use cryoprotection to survive. They found that after 14 days of subzero exposure in the lab the larval survival remained above 95%. They interpreted this as an indication that the larvae underwent cryoprotective dehydration. But they also considered that in their natural environment cryoprotection (low-temperature protection) may be constrained by inoculative freezing (process in which organisms actually freeze) because of the close contact of the larvae with environmental ice. Their ability to undergo cryoprotective dehydration during slow cooling within frozen soil is dependent on the soil moisture. The percentage of larvae that were able to resist inoculative freezing increased as the soil moisture decreased. The researchers suggest that the larvae are likely to undergo cryoprotection under the right conditions.

Lee and coworkers (2006) demonstrated that rapid cold-hardening (physiological or anatomical preparation for cold) increases freezing tolerance in *Belgica antarctica* (Figure 53). Larvae that were summer acclimated had less cold tolerance at -10°C for 24 hours than those that were cold-acclimated. Cold-acclimated larvae had higher supercooling points than summer larvae. But when summer-acclimated larvae were maintained at 4°C, then transferred to -5°C for 1 hour prior to exposures to -10, -15 or -20°C, rapid cold hardening occurred; rapid cold hardening significantly increased larval freeze tolerance to both -15 and -20°C. Adults, which typically live for only a week, did not respond to rapid cold hardening. Living among mosses can protect the larvae from sudden changes in temperature, permitting them to acclimate.

But even during the summer the larvae are subject to summer storms, osmotic stress from salt spray, and desiccation due to wind and sunlight (Lopez-Martinez et al. 2009). In contrast to Hayward et al. (2007), Lopez-Martinez and coworkers found that the genes that were the most responsive to hydration changes were the ones encoding heat-shock proteins, as well as those for antioxidants, detoxifications, and those involved in altering cell membranes. Fast dehydration elicited both the highest expression and the greater number of genes expressed. As the larvae were rehydrated, most of the same genes were once again expressed. Fatty acid desaturase was the only gene upregulated during rehydration.

Strong (1967) considers the living mosses to serve only as shelter for *Belgica antarctica* (Figure 52-Figure 54), providing little nourishment. Instead, detritus, algae, lichens, and fungal hyphae are the primary food sources. Other researchers include mosses as part of the diet during the two-year life cycle (Sugg et al. 1983; Convey & Block 1996). But there is no comprehensive food study to indicate the diet throughout the life cycle and seasonal changes. The larvae demonstrate cryoprotectants, including erythritol, glucose, sucrose, and trehalose, but adults are freezing-susceptible and lack adequate quantities of these cryoprotectants (Baust & Edwards 1979). Maintenance on artificial diets indicate that cryoprotectant complexes are dependent on food source and temperature. We have seen how gene expression changes as freezing occurs. Could it be that these new compounds are supported by a change in diet to one that includes more bryophytes?

**Culicidae – Mosquitoes**

Gert Mogensen told an interesting mosquito story on Bryonet (13 March 2011). Arctic mosquitoes (Figure 56) struggle with low moisture on sunny days. They compensate for this dry atmosphere by spending much time on mosses, keeping in the shadows when possible. They are able to shelter on the undersides of leaves of shrubs (Figure 56), but there they are subject to spider predation. These spiders, in turn, are food for the group of birds called waders (Figure 57). The chicks of these waders benefit from the dwarfed nature of the shrubs. The females migrate south again once the eggs are laid and the males remain behind to care for the young!
Simuliidae – Blackflies

I have discussed this family in the chapter on aquatic insects. But when I began researching the terrestrial Diptera, I was quite surprised to find that not all Simuliidae begin life in the water. Prosimulium hirtipes (see Figure 58-Figure 60), *P. tomosvaryi*, and *P. subrufipes* all oviposit on moist terrestrial mosses, usually about 20 cm above streams (Zwick & Zwick 1990). This is no small contribution as they lay up to 20,000 eggs per cm². The eggs form a dense crust on mosses with small leaves, especially *Brachythecium rivulare* (Figure 61). These eggs are dependent on moisture and cannot survive complete desiccation.
Two Japanese blackfly species, *Simulium japonicum* and *S. rufibasis* (see Figure 62-Figure 65), lay their eggs in bryophytes (Baba & Takaoka 1989). These do not make large masses and lay their eggs singly on bryophytes on water-splashed rocks. Later, Baba and Takaoka (1991) discovered that *Prosimulium kiotoense* likewise oviposited on land, using mosses on riverbank rocks as their oviposition sites. They likewise laid eggs singly, but the females deposited many eggs in small areas, often forming large, irregular egg masses. These wet oviposition sites had dense bryophyte cover and were 0-15 cm above water level. If you want to watch, the event occurs mostly between 12:00 and 14:00 hours in the latter part of April on Kyushu Island, Japan.

Figure 62. *Simuliidae* larvae, a stage that is spent in fast water. Photo by Sarah Gregg, through Creative Commons.

Figure 63. *Simulium heiroglyphicum* pupa, an aquatic stage that is often on mosses. Photo by Luis Hernandez Triana, through Creative Commons.

Figure 64. *Simulium nr. metallicum* pupa, a stage that is spent in fast water, often on bryophytes. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 65. *Simulium equinum* adult, member of a genus in which some species oviposit on land among mosses. Photo by Ladislav Tábi, with permission.

**Psychodidae – Drain Flies, Sink Flies, Moth Flies, or Sewer Gnats**

This family includes species with aquatic larvae, so it is not surprising that terrestrial species are often associated with bryophytes in locations where they can maintain high moisture. Roper (2001) reports several of these species in the ghyll woodlands (linear valley features cut into the sandy beds of the Weald of south-eastern England where temperatures are buffered and moisture levels are high; they have a rich flora of bryophytes). In Sussex, England, the very ornate *Sycorax* species occur among mosses near springs and "trickles" (Roper 2001).

*Sycorax silacea* larvae are wormlike and live on wet stones or mosses near cascades, springs, trickles (Andersen 1992), on mosses in the neighborhood of streams (Omelkova & Ježek 2012), and on mosses on half-submerged tree branches (Kroča & Ježek 2015), making them semiaquatic. Their decorations are quite ornate, permitting them to blend well among the mosses (Roper 2001).

Like *Sycorax silacea*, many of the *Psychodidae* are semi-aquatic. *Peripsychoda fusca* lives in wet mosses and leaf litter piles in Europe (Kroča & Ježek 2015). Another European psychodid, *Feuerborniella obscura*, lives among wet moss cushions, springs, and small streams. *Parabazarella subneglecta* (Figure 66) similarly prefers wet moss cushions, springs, and streams. *Pneumia stammeri* (Figure 67) lives among mosses in wetlands. Larvae of *Bazarella neglecta* occur among mosses around mill races and waterfalls (Roper 2001). This species has been reared successfully on the moss *Platyhypnidium riparioides* (Figure 68-Figure 69), a moss that typically occurs around the water-air interface where it is almost constantly wet or submerged. *Parajungiella longicornis* is a widespread and common species in Europe and western Siberia (Omelkova & Jezek 2012; Kroča & Ježek 2015). This species lives in both shaded and unshaded habitats in moss cushions on banks of streams, as well as ponds and forest seepages.
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Figure 66. *Parabazarella subneglecta* adult, a species whose larvae prefer wet moss cushions and mosses of springs and streams. Photo from Bergen Museum, through Creative Commons.

Figure 67. *Pneumia stammeri* adult, a species that lives among mosses in wetlands. Photo by Aina Maerk Aspaas, NTNU University Museum, through Creative Commons.

Figure 68. *Platyhypnidium riparioides*, showing its partly submersed and partly emergent location. Photo by Hermann Schachner, through Creative Commons.

Figure 69. *Platyhypnidium riparioides*, home and food for *Bazarella neglecta*. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

*Pericoma* larvae (Figure 70-Figure 71) and pupae both live in damp locations along streams in the UK, frequently among mosses (Satchell 1949). Suitable habitats can often support several species within a few meters. *Pericoma* species, including *P. nubila* (Figure 72-Figure 73), *P. fuliginosa* (Figure 74), and *Tonnoiriella pulchra* (syn. = *P. pulchra*) emerge in ghyll woodlands from rotting vegetation and mosses along streambanks (Roper 2001). *Pericoma blandula* (Figure 75) and *P. fallax* are both widespread species in Europe and parts of Asia, living among mosses in both shaded and unshaded locations (Omelkova & Jezek 2012; Kroča & Ježek 2015). The latter species is mostly aquatic, but also occurs in swampy meadows and bottomlands. *Pericoma blandula* is more common among mosses on riverbanks and the banks of springs (Duckhouse 1962).
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Figure 72. *Pericoma nubila* adult, a terrestrial stage often closely associated with aquatic habitats and mosses. Photo by Malcolm Storey, through Creative Commons.

Figure 73. *Pericoma nubila* adult, a stage often closely associated with aquatic habitats and mosses. Photo by Malcolm Storey, through Creative Commons.

Figure 74. *Pericoma fuliginosa* adult, a species that pupates in rotting vegetation and mosses on streambanks. Photo by James K. Lindsey, with permission.

Figure 75. *Pericoma blandula* adult, a species whose larvae live among mosses in both shaded and unshaded situations. Photo ©Nick Upton <www.diptera.info>, with permission.

Figure 76. *Psychoda cinerea* adult. Larvae of this species live in mud and among mosses. Photo by Luis Miguel Bugallo Sanchez, through Creative Commons.

Figure 77. *Philosepedon* resting on the capsules of a moss, but perhaps it was just a convenient resting place, serving no other purpose. Its larvae are known from dead snails (Corbet 2006)! It is clear that we need more behavioral studies on these flies and their interactions with bryophytes.
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Anisopodidae (=Rhyphidae) – Wood Gnats

I was introduced to the larvae (Figure 78) of this family when I found a larva feeding on mosses on a wet ledge. The larva was green and blended well with the bright green mosses. I watched for a time and found that mosses went in the mouth covered with detritus and came out the other end clean. It appeared the larva was unable to digest the moss leaves it consumed.

Summary

Some adult members of fungus gnats (Mycetophilidae) feed on spores in the capsules of Buxbaumia aphylla. Others, as larvae, develop within the thalli of liverworts, also completing pupation there. The dark-winged fungus gnats (Sciaridae) tunnel in liverwort thalli.

The midge (Chironomidae) adults include some members that are attracted to exudates from antheridia and archegonia of mosses, accomplishing the transfer of sperm to the eggs. And even the blackflies (Simuliidae) have some members that begin their lives among mosses on land. The moth flies (Psychodidae) live among bryophytes as larvae in both aquatic and terrestrial habitats. The biting midges (Ceratopogonidae) Few mosquitoes (Culicidae) or gall midges (Cecidomyiidae) are known to use mosses.

Acknowledgments

Thank you to Sara Altenfelder for alerting me to the mine flies that live on mosses and liverworts and supplying me with copies of old papers. My appreciation to Weerachon Sawangproh for providing me with images and information of the herbivory on liverworts by Scatopsicciara cunicularius. Irene Bisang answered my questions about the liverwort thallus parasite. As usual, many photographers provided kind permission for use of their images.

Literature Cited


