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.

Figure 6. Fungus gnat herbivory on capsules of *Buxbaumia aphylla*. Photo courtesy of Jörg Müller.

Figure 7. *Buxbaumia aphylla* with fly. Photo courtesy of Sabovljevic.

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.

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, *Scatopsciara 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.
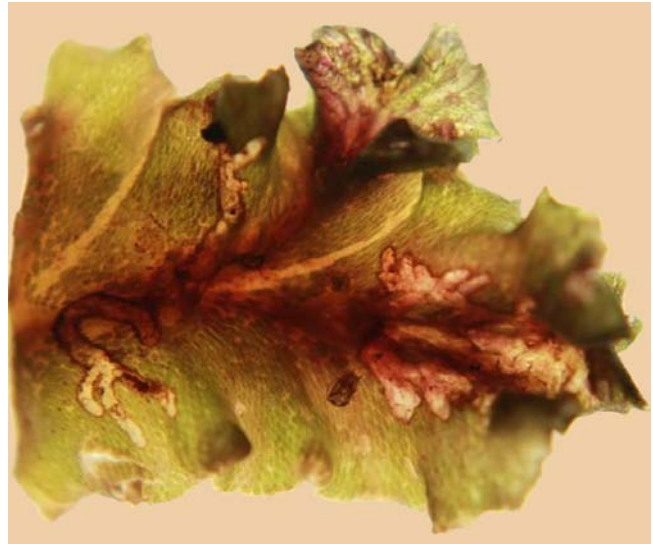

Figure 8. *Scatopsciara cunicularius* damage to *Marchantia polymorpha* by two third-instar larvae at 22°C in culture. Photo courtesy of Weerachon Sawangproh.

Figure 9. *Scatopsciara cunicularius* damage to *Marchantia polymorpha* by a group of larvae at day 2 after hatching. Photo courtesy of Weerachon Sawangproh.
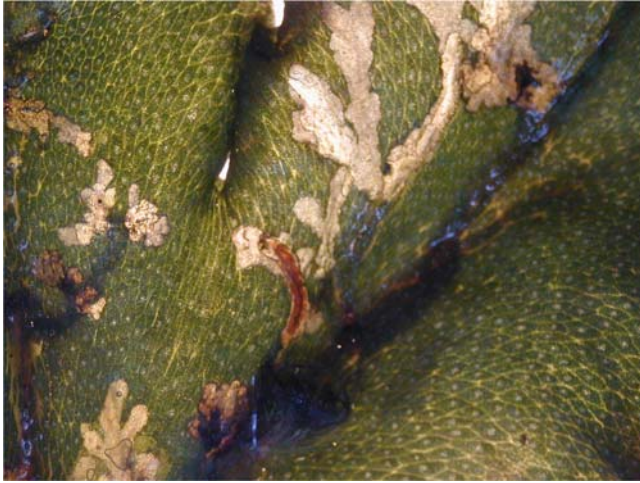
Figure 10. *Scatopsciara cunicularius* larva on one of the wounded patches of *Marchantia polymorpha*. Photo courtesy of Nils Cronberg.

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

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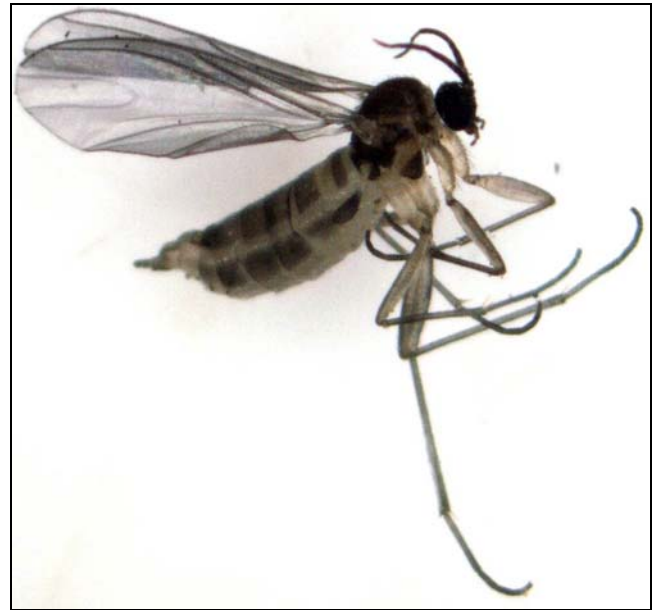

Figure 14. *Scatopsciara cunicularius* female adult. Photo courtesy of Weerachon Sawangproh.

It does not appear that these bryophagous fungus gnats need fungi. *Scatopsciara 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 12. *Scatopsciara cunicularius* mature pupal stage on a liverwort thallus. Photo by 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!

Figure 15. *Bradysia* sp. 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.

Figure 26. *Dasyhelea* male adult, a genus that can be found among bryophytes on trees. Photo by Christophe Quintin, through Creative Commons.

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).

Figure 27. **Ceratopogonidae** male on moss. Photo by Christophe Quintin, through Creative Commons.

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).

Figure 28. *Serromyia femorata* female, a species associated with damp mosses. Photo by James K. Lindsey, with permission.

Figure 29. *Culicoides impunctatus* adult, a species that avoids mosses, except *Sphagnum*. Photo by Orikrin, through Creative Commons.

Figure 30. *Forcipomyia bipunctata* adult, member of a genus that builds nests in *Sphagnum*. Photo by James K. Lindsey, with permission.

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.).

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

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

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

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

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

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

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. Field of *Polytrichum commune* with capsules, indicating successful fertilization. Photo by Michael Lüth, with permission.

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.
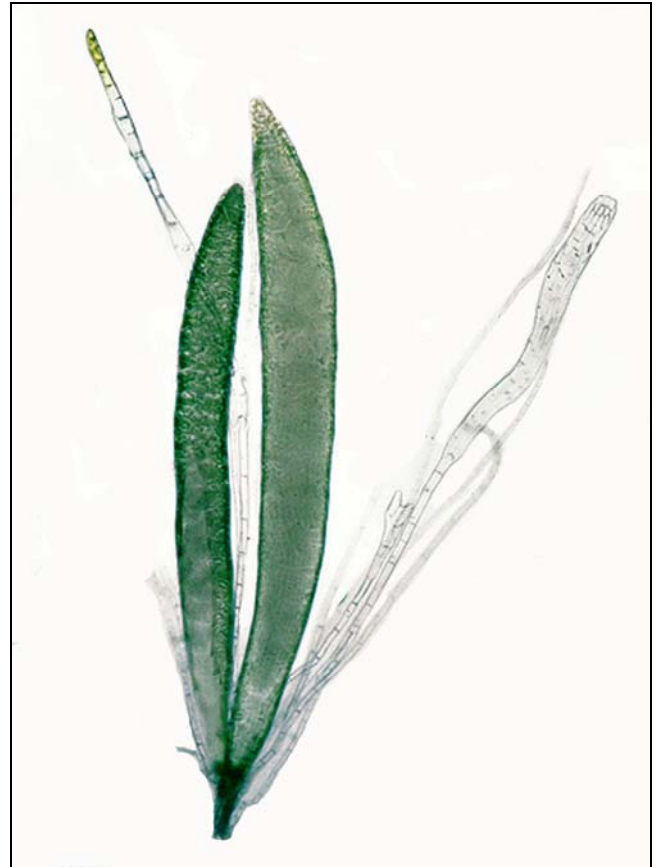

Figure 43. *Polytrichum* showing two antheridia with adjacent paraphyses. Photo by George J. Shepherd, through Creative Commons.

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 cm^2 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.

Figure 44. *Smittia aterrima* adult, a species that includes mosses in its diet. Photo by James K. Lindsey, with permission.

Smittia aterrima (Figure 44) is common in disturbed areas, with up to 12,000 individuals per m^2 (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. *Bryophaenocladius* cf. *illimbatus* (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 *Bryophaenocladius cf. illimbatus* 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).

Figure 45. *Bryophaenocladius illimbatus* adult, a species of mosses in sites with low, open vegetation. Photo by Marko Mutanen, through Creative Commons.

Sometimes one can find exciting new species by knowing the general habits of the genus. The snow-dwelling adults of *Bryophaenocladius 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. *Bryophaenocladius virgo* lives among mosses as larvae and adults and solves the flight problem by being **parthenogenetic** (giving birth without fertilization) (Cranston 1987). *Bryophaenocladius vernalis* (Figure 46) has been caught in the act of damaging rare mosses growing in chalk quarries in southern England.

Figure 46. *Bryophaenocladius* cf. *vernalis* adult male, a species that damages rare mosses in chalk quarries in England. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

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 parthenogenic (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 49. *Limnophyes minimus* adult, a pioneer species among mosses in early succession stages. Photo by James K. Lindsey, with permission.
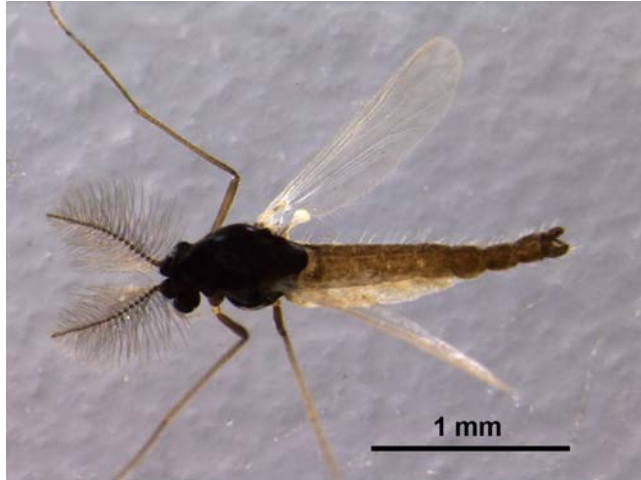

Figure 47. *Limnophyes minimus*, a pioneer species in mosses on newly colonized areas. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

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.

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 parthenogenic, but males are unknown (Cranston 1985). This species has terrestrial larvae that live among damp mosses and peat.

Figure 48. *Limnophyes minimus*, a pioneer among mosses. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Figure 51. *Eretmoptera murphyi* on a leafy liverwort, Prince Olav Harbour, South Georgia. Photo courtesy of Roger S. Key.

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.

Figure 52. *Belgica antarctica* eggs among mosses in Antarctica. Photo by Rick Lee, through Creative Commons.

Figure 53. *Belgica antarctica* larvae in Antarctica, a species that often lives among mosses. Photo by Rick Lee, through Creative Commons.

Figure 54. *Belgica antarctica* mating in Antarctica. Photo by Rick Lee, through Creative Commons.

Figure 55. *Sanionia uncinata*, potential home for *Belgica antarctica*, but temperatures in this moss differ little from that of the air. Photo by Franz Xaver, through Creative Commons.

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, detoxiWcations, 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!

Figure 56. Mosquito adult, member of a family (**Culicidae**) that struggles with low moisture in the Arctic. Photo by Brad Smith, through Creative Commons.

Figure 57.   The Common Gallinule (*Gallinula galeata*), a wading bird that is part of the food chain of moss inhabitants (Culicidae→spiders→wading birds).   Photo by Jim Rathert, USFWS, through public domain.

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 cm^2. 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.

Figure 59. *Prosimulium arvum* adult, member of a genus in which some members lay their eggs among streamside mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 60. *Prosimulium* female adult, member of a genus in which some members lay their eggs among streamside mosses. Photo by Tom Murray, through Creative Commons.

Figure 58. *Prosimulium hirtipes* larva, a species that begins life on land among mosses at streamside. Photo by Janice Glime.

Figure 61. *Brachythecium rivulare*, a site for egg-laying by *Prosimulium hirtipes*, *P. tomosvaryi*, and *P. subrufipes*. Photo by Norbert Stapper, with permission.

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.
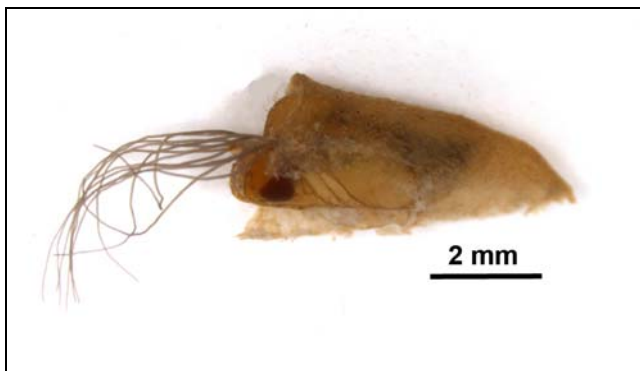

Figure 64. *Simulium* nr. *metallicum* pupa, a stage that is spent in fast water, often on bryophytes. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

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.

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).

Figure 70. **Pericoma** larva, a stage that often lives among bryophytes in damp places and along stream margins. Photo from <www.shl.uiowa.edu>, through public domain.

Figure 71. **Pericoma** larva, a stage that often lives among bryophytes in damp places and along stream margins. Photo from <www.dfg.ca.gov>, through public domain.

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.

For *Psychoda cinerea* (Figure 76) larvae, moisture is important, accounting for their habitat in mud and among mosses (Ježek 1990). *Paramormia ustulata* is more ubiquitous, living in a variety of habitats in both fresh and salt water, but it also includes mosses and moist soil (Vaillant 1971).

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

In some cases we don't know why the flies visit the mosses. Martin Cooper found a species of *Philosepedon* (Figure 77) 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.

Figure 77. *Philosepedon*, probably *P. humeralis* adult, on moss capsule. Photo by Martin Cooper, through Creative Commons.

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 the larva was unable to digest the moss leaves it consumed.

Figure 78. **Anisopodidae** larva; some larvae in this family eat wet mosses, apparently to obtain the detritus and associated organisms on the moss surface. Photo by Walter Pfliegler, with permission.

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**) live in moist places and are common on mosses. Few mosquitoes (**Culicidae**) or gall midges (**Cecidomyiidae**) are known to use mosses.

Literature Cited

Andersen, T. 1992. The moth fly *Sycorax silacea* Haliday in Curtis, 1839 (Dipt., Psychodidae: Sycoracinae) taken in west Norway. Fauna Norv. Ser. B 39: 93.

Baba, M. and Takaoka, H. 1989. Oviposition sites and the number of larval instars of two mountain blackfly species, *Simulium japonicum* and *S. rufibasis* (Diptera: Simuliidae). Jap. J. Sanit. Zool. 40: 307-313.

Baba, M. and Takaoka, H. 1991. Oviposition habits of a univoltine blackfly, *Prosimulium kiotoense* (Diptera: Simuliidae), in Kyushu, Japan. Med. Vet. Entomol. 5: 351-357.

Baust, J. G. and Edwards, J. S. 1979. Mechanisms of freezing tolerance in an Antarctic midge, *Belgica antarctica*. Physiol. Entomol. 4(1): 1-5.

Benoit, J. B., Lopez-Martinez, G., Michaud, M. R., Elnitsky, M. A., Lee, R. E., and Denlinger, D. L. 2007. Mechanisms to reduce dehydration stress in larvae of the Antarctic midge, *Belgica antarctica*. J. Ins. Physiol. 53: 656-667.

Bettis, C. J. 2008. Distribution and abundance of the fauna living in two *Grimmia* moss morphotypes at the McKenzie Table Mountain Preserve, Fresno County, California. M. S. Thesis, California State University, Fresno, 56 pp.

Blackwell, A., Lock, K. A., Marshall, B., Boag, B., and Gordon, S. C. 1999. The spatial distribution of larvae of *Culicoides impunctatus* biting midges. Med. Vet. Entomol. 13: 362-371.

Carpenter, S., Mordue, A. J., and Mordue, W. 2001. Oviposition in Culicoides impunctatus under laboratory conditions. Entomol. Exper. Appl. 101(2): 123-129.

Convey, P. and Block, W. 1996. Antarctic Diptera: Ecology, physiology and distribution. Eur. J. Entomol. 93: 489-505.

Corbet, Gordon. 2006. Diptera - two-winged flies. Accessed 26 July 2016 at <http://publications.1fife.org.uk/uploadfiles/publications/c64_DIPTERANOFI20062.pdf>.

Cranston, P. S. 1985. *Eretmoptera murphyi* Schaeffer (Diptera: Chironomidae), an apparently parthenogenetic Antarctic midge. Bull. Brit. Antarct. Surv. 66: 35-45.

Cranston, P. S. 1987. A non-biting midge (Diptera: Chironomidae) of horticultural significance. Bull. Entomol. Res. 77: 661-667.

Delettre, Y. R. 1986. La colonisation des biotopes multiples: Une alternative a la résistance in situ aux conditions mesologiques défavorables. Cas de *Limnophyes minimus* (Mg.), Diptère Chironomidae des landes armoricaines. Rev. Ecol. Biol. Sol 23: 29-38.

Delettre, Y. R, and Lagerlöf, J. 1992. Abundance and life history of terrestrial Chironomidae (Diptera) in 4 Swedish agricultural cropping systems. Pedobiologia 36: 69-78.

Downing, A. and Selkirk, P. 1996. More bryophytes eating insects. Bryol. Times 88: 2.

Duckhouse, D. A. 1962. Some British Psychodidae (Diptera, Nematocera): Description of species and discussion on the problem of species pairs. Trans. Royal Entomol. Soc. London 114: 403-436.

Ducrotoy, J. P. 1980. Adaptations spatio-temporelles des chironomides (Insectes: Dipteres) dans un habitat semi-permanent du massif de Paimpont. Bull. Ecol. 11: 633-645.

Elnitsky, M. A., Hayward, S. A. L., Rinehart, J. P., Denlinger, D. L., and Lee, R. E. 2008. Cryoprotective dehydration and the resistance to inoculative freezing in the Antarctic midge, *Belgica antarctica*. J. Exper. Biol. 211: 524-530.

Frouz, J. 1997. The effect of vegetation patterns on oviposition habitat preference: A driving mechanism in terrestrial chironomid (Diptera: Chironomidae) succession? Res. Pop. Ecol. 39: 207-213.

Frouz, J. and Kindlmann, P. 2001. The role of sink to source re-colonisation in the population dynamics of insects living in unstable habitats: An example of terrestrial chironomids. Oikos 93: 50-58.

Frouz, J. and Lukešová, A. 1995. Food preference of two species of terrestrial chironomids (Diptera: Chironomidae). Dipterol. Bohemoslov. 7: 41-46.

Gressitt, J. L. 1967. Entomology of Antarctica. American Geophysical Union, Washington, D.C., 395 pp.

Hackman, W., Lastovka, P., Matile, L., and Väisäinen, R. 1988. Mycetophilidae. In: Soós, A. and Papp, L. (eds.). Catalogue of the Palearctic Diptera volume 3. Akadémiai Kiadó, Budapest, pp. 220-232.

Hänel, C. and Chown, S. L. 1998. The impact of a small, alien invertebrate on a sub-Antarctic terrestrial ecosystem: *Limnophyes minimus* (Diptera, Chironomidae) at Marion Island. Polar Biol. 20(2): 99-106.

Harvey-Gibson, R. J. and Miller-Brown, D. 1927. Fertilization of Bryophyta. *Polytrichum commune* (Preliminary note). Ann. Bot. (London) 41: 190-191.

Hayward, S. A. L., Rinehart, J. P., Sandro, L. H., Lee, R. E. Jr. and Denlinger, D. L. 2007. Slow dehydration promotes desiccation and freeze tolerance in the Antarctic midge *Belgica antarctica*. J. Exper. Biol. 210: 836-844.

Hurley, B. P. 2006. Fungus gnats in forestry nurseries and their possible role as vectors of *Fusarium circinatum*. Ph.D. dissertation, University of Pretoria, Pretoria, South Africa.

Ježek, J. 1990. Redescriptions of nine common Palaearctic and Holarctic species of Psychodini End. (Diptera: Psychodidae). Acta Entomol. Musei Natl. Pragae 43: 33-83.

Kroča, J. and Ježek, J. 2015. Moth flies (Psychodidae: Diptera) of the Moravskoslezské Beskydy Mts and Podbeskydská pahorkatina Upland (Czech Republic). Acta Mus. Siles. Sci. Nat. 64: 27-50.

Lee, R. E. Jr., Elnitsky, M. A., Rinehart, J. P., Hayward, S. A. L., Sandro, L. H., and Denlinger, D. L. 2006. Rapid cold-hardening increases the freezing tolerance of the Antarctic midge **Belgica antarctica**. J. Exper Biol. 209: 399-406.

Lencioni, V., Marziali, L., and Rossaro, B. 2011. Diversity and distribution of chironomids (Diptera, Chironomidae) in pristine alpine and pre-alpine springs (Northern Italy). J. Limnol. 70: 106-121.

Lopez-Martinez, G., Benoit, J. B., Rinehart, J. P., Elnitsky, M. A., Lee, R. E. Jr., and Denlinger, D. L. 2009. Dehydration, rehydration, and overhydration alter patterns of gene expression in the Antarctic midge, *Belgica antarctica*. J. Comp. Physiol. B 179: 481-491.

Mamaev, B. M. and Krivosheina, N. P. 1993. The Larvae of the Gall Midges (Diptera, Cecidomyiidae). A. A. Balkema Publishers, Rotterdam, Netherlands, 303 pp.

Müller, J. 2012. Beobachtung von Herbivorie an *Buxbaumia aphylla* Hedw. [Observation of herbivory on *Buxbaumia aphylla* Hedw. in Brandenburg.]. Arch. Bryol. 135: 1-5.

Nolte, U. 1991. Seasonal dynamics of moss-dwelling chironomid communities. Hydrobiologia 222: 197-211.

Økland, B. 1994. Mycetophilidae (Diptera), an insect group vulnerable to forestry practices? A comparison of clearcut, managed and semi-natural spruce forests in southern Norway. Biodiv. Conserv. 3: 68-85.

Oldroyd, H. 1964. The natural history of flies. Wiedenfeld & Nicholson, London.

Omelkova, M. and Ježek, J. 2012. A new species of the genus *Trichomyia* (Diptera: Psychodidae) and new faunistic data on non-phlebotomine moth flies from the Podyji NP and its surroundings (Czech Republic). Acta Entomol. Musei Natl. Pragae 52: 505-533.

Peck, J. L. and Moldenke, A. R. 2010. Identifying pathways of biological invasion: Can commercial moss harbor potential stowaways? Biol. Invas. 12: 2395-2398.

Perkovsky, E. E. and Fedotova, Z. A. 2004. New species of gall midges (Diptera, Cecidomyiidae) from Rovno amber: Subfamily Lestremiinae, tribes Micromyiini and Peromyiini. Paleontol. J. C/C Paleontol. Zhurn. 38: 396-406.

Pettet, A. 1967. Parasitism of *Riccia frostii* Aust. by flies. Bryological note. Trans. Brit. Bryol. Soc. 5: 348-350.

Ponge, J. F. 1991. Food resources and diets of soil animals in a small area of Scots pine litter. Geoderma 49: 33-62.

Roper, Patrick. 2001. A note on the two -winged flies (Diptera) associated with ghyll woodlands in Sussex. accessed on 21 July 2008 at <http://www.prassociates.co.uk/environmental/articles/ghyll.pdf>.

Rose, F. 1953. A survey of the ecology of the British lowland bogs. Proc. Linn. Soc. London 164: 186-211.

Rosenberg, D. M. and Danks, H. V. 1987. Aquatic insects of peatlands and marshes in Canada: Introduction. Mem. Entomol. Soc. Can. 119: 1-4.

Russell, L. K. 1979. A Biological and Systematic Study of the Armored Boreid, *Caurinus dectes*, with Comparative Notes on Related Mecoptera. Ph. D. Dissertation, Department of Entomology, Oregon State University, Corvallis, OR, 281 pp.

Satchell, G. H. 1949. The early stages of the British species of *Pericoma* Walker (Diptera: Psychodidae). Trans. Royal Entomol. Soc. London 100: 411-447.

Sawangproh, W. 2014. The herbivoral interaction between midge species, *Scatopsciara cunicularius* (Sciaridae: Diptera) and the thallose bryophyte, *Marchantia polymorpha* L. M. S. thesis, Department of Biology, Lund University.

Sawangproh, W. and Cronberg, N. 2016. Life history traits of the liverwort herbivore *Scatopsciara cunicularius* (Diptera: Sciaridae). Ann. Entomol. Soc. Amer. (in press).

Sawangproh, W., Ekroos, J., and Cronberg, N. 2016. The effect of ambient temperature on larvae of *Scatopsciara cunicularius* (Diptera: Sciaridae) feeding on the thallose

liverwort *Marchantia polymorpha*. Eur. J. Entomol. 113: 259-264.

Shin, S. G., Lee, H. S., and Lee, S. 2012. Dark winged fungus gnats (Diptera: Sciaridae) collected from shiitake mushroom in Korea. J. Asia-Pacific Entomol. 15: 174-181.

Strenzke, K. 1950. Systematik, Morphologie und Okologie der terrestrischen Chironomiden. Arch. Hydrobiol. Suppl. 18: 207-414.

Strong, J. 1967. Ecology of terrestrial arthropods at Palmer Station, Antarctic Peninsula. In: Gressitt, J. L. (ed.). Entomology of Antarctica. Antarctic Research Series, American Geophysical Union 10: 357-371.

Stur, E., Martin, P., and Ekrem, T. 2005. Non-biting midges as hosts for water mite larvae in spring habitats in Luxembourg. Ann. Limnol. 41: 225-236.

Sugg, P., Edwards, J. S., and Baust, J. 1983. Phenology and life history of *Belgica antarctica*, an Antarctic midge (Diptera: Chironomidae). Ecol. Entomol. 8: 105-113.

Teets, N. M., Kawarasaki, Y., Lee, R. E. Jr., and Denlinger, D. L. 2011. Survival and energetic costs of repeated cold exposure in the Antarctic midge, *Belgica antarctica*: A comparison between frozen and supercooled larvae. J. Exper. Biol. 214: 806-814.

Vaillant, F. 1971. Psychodidae-Psychodinae. In: Lindner, E. (ed.). Die Fliegen der palaearktischen Region. Vol. 287, Stuttgart, pp. 1-48.

Willassen, E. 1996. A nival *Bryophaenocladius* Thienemann, 1934, with reduced wings (Insecta: Diptera: Chironomidae). Ann. Naturhist. Mus. Wien. Ser. B Bot. Zool. 98: 507-512.

Winder, J. A. 1977. Field observations on Ceratopogonidae and other Diptera: Nematocera associated with cocoa flowers in Brazil. Bull. Entomol. Res. 67: 57-63.

Wirth, W. W. and Gressitt, J. L. 1967. Diptera: Chironomidae (midges). In: Gressitt, J. L. (ed.). Entomology of Antarctica. Antarctic Research Series 10: 197-203.

Zwick, H. and Zwick, P. 1990. Terrestrial mass-oviposition of *Prosimulium*-species (Diptera: Simuliidae). Aquat. Ins. 12: 33-46.