CHAPTER 11-13a
AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER NEMATOCERA

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Figure 1. ***Triogma trisulcata*** among mosses. This species makes its home among wet mosses of bogs and swamps and is effectively a moss mimic. Photo by J. C. Schou, with permission.

DIPTERA – FLIES

Gerson (1969) suggested that the ancestral fly groups originated among mosses where it is always damp. Because the systematics of the fly groups are still poorly understood, I have divided the treatments into the two suborders, **Nematocera** and **Brachycera**. From there they are alphabetical within superfamilies, but the superfamilies are not delineated by name.

Diptera adults are distinguished by having only two wings, as reflected in the name of **Diptera** (*di* = 2; *pteron* = wing). In place of the second pair of wings the flies have a pair of **halteres** (Figure 2), thoracic projections that resemble lollipops, one on each side of the thorax. In the larval stage, they are distinguished by having only fleshy **prolegs** (Figure 9) or no legs. They lack the chitinized, jointed thoracic legs found in most larval insects (Johannsen 1969).

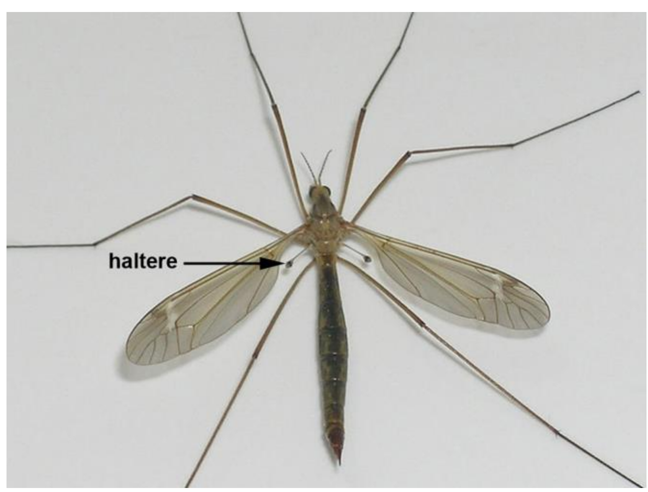

Figure 2. **Tipulidae** showing two wings and halteres. Photo by Pinza, through Creative Commons.

Gerson (1982) reported a number of bryophyte-dwelling **Diptera** of medical and veterinary importance because they bite. Among these are the sand flies [**Psychodidae** (see Chapter 13b; Quate 1955)], mosquitoes [**Culicidae** (see Chapter 13b; Fantham & Porter 1945)], black flies [**Simuliidae** (Figure 3); Snow *et al*. 1958)], biting midges [**Ceratopogonidae** (Figure 84-Figure 88; Séguy 1950)], and horse flies [**Tabanidae** (Figure 4; Teskey 1969)]. All of these are discussed in this chapter except **Tabanidae**. I found it only occasionally among bryophytes in Appalachian Mountain, USA, streams; the other studies I reviewed did not mention it.

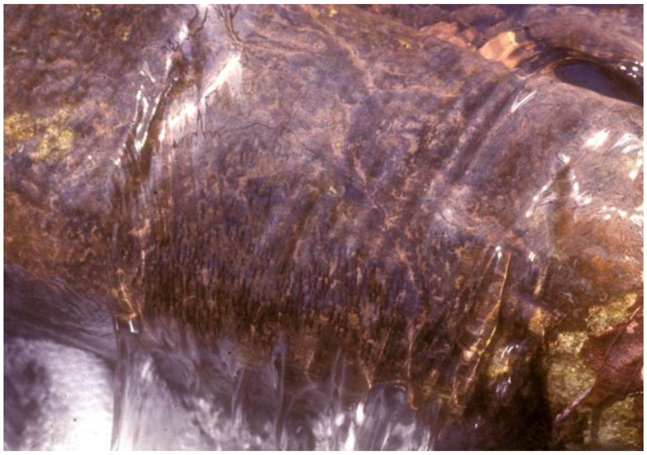

Figure 3. **Simuliidae** larvae in the rapid flow of a stream. Photo by Janice Glime.

Figure 4. ***Chrysops divaricatus*** (**Tabanidae**) adult, an adult pest (horse fly) whose larvae sometimes live among the bryophytes. Photo by Kallema, through Creative Commons.

In streams, bryophytes are often important contributors to biodiversity. Flow rates are important in determining the type of **Diptera** able to live there. The abundance of **Chironomidae** (see Chapter 13b) is negatively correlated with flow rate as it approaches clumps of mosses (***Fontinalis antipyretica***; Figure 5), whereas the abundance of the smallest **Simuliidae** (Figure 3) is positively correlated (Linhart *et al*. 2002a). In the Plitvice Lakes National Park in the Dinaric karst region of Croatia, Čmrlec (2013) found that the Diptera families were least abundant in silt and that mosses were the preferred substrate. These correlations with speed and silt do not prevent both groups of species from living in the same bryophyte clump – the slow-water silt lovers live near the bottom while the fast-water silt avoiders live near the surface of the bryophyte clump.

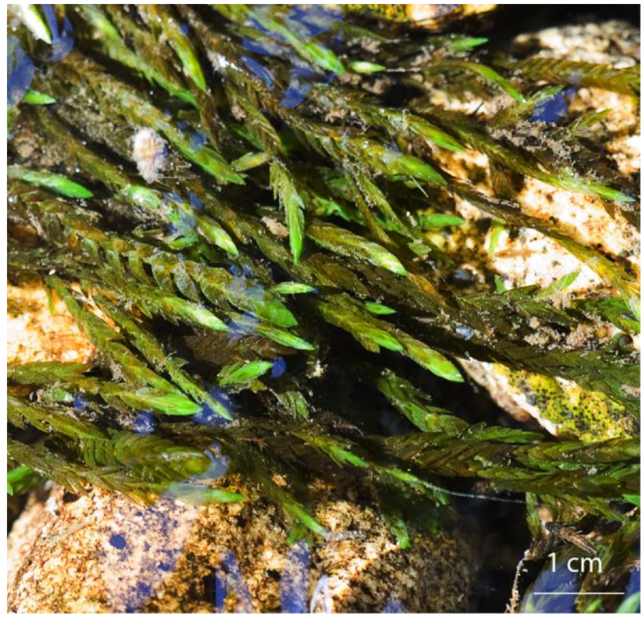

Figure 5. ***Fontinalis antipyretica***, home for numerous aquatic insects and suitable for larger ones. Photo from Projecto Musgo, through Creative Commons.

Bryophytes accumulate coarse (CPOM), fine (FPOM), and ultrafine (UPOM) particulate organic matter that serves as a food source for their inhabitants (Habdija *et al*. 2004). These conditions favor small forms of oligochaetes, **Diptera**, and **Coleoptera** that comprise 64-99% of the **macrophyte** (plant – especially aquatic – large enough to be seen without a lens) individuals. Collector gatherers dominate in spring and summer, collector-filterers in autumn, and scrapers in winter.

In a cool mountain stream in central Japan, five of the six taxa of Diptera identified (mostly at the level of family or subfamily) were significantly more abundant in clumps of the moss ***Platyhypnidium riparioides*** (Figure 6) than in areas of bare stones (Kato 1992). These included **Limoniidae** (***Antocha*** spp.; Figure 7), **Simuliidae** (Figure 3), and **Chironomidae** [Figure 8; **Tanypodinae, Diamesinae**, ***Orthocladius*** spp.].

Figure 6. Emergent but wet ***Platyhypnidium riparioides*** in Europe, a common home for **Diptera**. Photo by Michael Lüth, with permission.

Figure 7. ***Antocha***, a larva that inhabits the moss ***Platyhypnidium riparioides*** (Figure 6) in cool mountain streams in Japan. Photo by Bob Henricks, with permission.

In Alaska, **Diptera** dominate by an even larger proportion than in streams of temperate North America (Oswood 1989). The **Chironomidae** (Figure 8) exhibit a significant increase from south to north, whereas most other taxa (excluding **Nemouridae**) decrease.

Figure 8. **Chironomidae** larva, a common bryophyte-dwelling family whose numbers increase from south to north. Photo by Jason Neuswanger, with permission.

The **Diptera** have a variety of adaptations to their aquatic domicile of choice. For example, Bass and Cooling (1983) reported that **Muscidae** (**Brachycera**), **Ichneumonidae** (**Hymenoptera**), and **Simuliidae** (Figure 3) were associated with mosses below a reservoir in southern England. Both the larvae and pupae had posterior projections to anchor them to the mosses. Amos (1999) describes the role of the brook moss ***Fontinalis*** (Figure 5) in providing a safe habitat in the torrent, and this moss likes cold water (Glime 1987) where few tracheophytes persist. Here one can find many small invertebrates, but it seems still to be a challenge to stay put. The mountain midge larva (**Deuterophlebiidae,** Figure 9) survives the torrent by the use of strong suction to hold the rock. The suction cups of ***Deuterophlebia*** (Figure 9) are of little use among bryophytes, but are fantastic for adhering to "bare" rocks. Respiratory adaptations are numerous and will be discussed for the various families.

The floating community includes only a few species of bryophytes, notably ***Ricciocarpos natans*** (Figure 10) and ***Riccia fluitans*** (Figure 11). In some cases, the **Diptera** associated with the thallose floating liverwort ***Ricciocarpos natans*** are the same ones found among floating tracheophytes such as *Spirodela*, *Lemna minor* (Figure 10), and *Wolffia* (Scotland 1934).

Figure 9. ***Deuterophlebia*** ventral side showing suction cups. Photo from Aquatic Bioassessment Laboratory <www.dfg.ca.gov>, with permission.

Figure 10. ***Ricciocarpos natans*** and *Lemna minor*, floating plants that can harbor surface-dwellers. Photo by Jan-Peter Frahm, with permission.

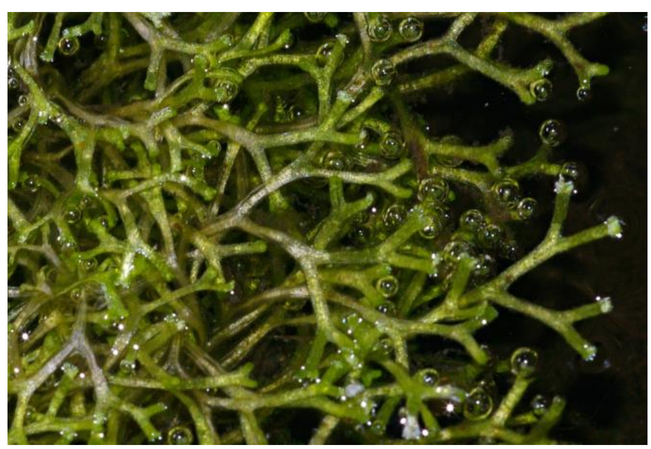

Figure 11. ***Riccia fluitans*** with pearling (oxygen bubbles produced by the plants), a floating community that provides cover and oxygen for aquatic insects. Photo by Christian Fischer, through Creative Commons.

Despite the number of families of **Diptera** among the bryophytes, and the presence of such mixed terrestrial/aquatic families as the **Tipulidae** (Figure 46-

Figure 73, Figure 75, Figure 77-Figure 76), it is interesting that this order is poorly represented among the wet emergent mosses in the River Rajcianka in Slovakia (Krno 1990). Only the **Psychodidae** (see Chapter 13b) were able to take advantage of the safety of the emergent bryophytes there. On the other hand, fauna of the submerged mosses were represented by not only the **Psychodidae**, but also the **Ceratopogonidae** (Figure 84-Figure 88) and **Simuliidae** (Figure 3). Conspicuously absent in these **eutrophic** (referring to lake or other body of water rich in nutrients and thus supporting dense plant/algal populations) waters were the **Tipulidae** and **Chironomidae** (Figure 8).

Occasionally, or perhaps frequently, the insects do something beneficial for the bryophytes they visit. In a study to determine the role of adult **Diptera** in dispersing algae and **Protozoa**, Revill *et al*. (1967) found that in addition to 21 species of viable algae and 5 of **Protozoa**, the washings from the four species of **Diptera** produced viable moss spores/protonemata as well. These transporting insects included ***Tipula triplex*** (**Tipulidae**; Figure 12), ***Bittacomorpha clavipes*** (**Ptychopteridae,** Figure 13), ***Chaoborus punctipennis*** (**Chaoboridae**, Figure 14-Figure 15), and ***Chironomus*** (**Chironomidae**; Figure 16).

Figure 12. ***Tipula triplex*** adult, a cranefly known to disperse bryophyte spores or protonemata. Photo by Paul Rhine <www.discoverlife.org>, through Creative Commons.

Figure 13. ***Bittacomorpha clavipes*** adult, a phantom cranefly that carries bryophyte spores or protonemata. Photo by Matt Muir, through Creative Commons.

Figure 14. ***Chaoborus punctipennis*** adult, a species known to carry bryophyte spores/protonemata. Photo by Tom Murray, through Creative Commons.

Figure 15. ***Chaoborus*** sp., larva of one of the **Diptera** known to carry bryophyte spores/protonemata. Photo by Viridiflavus, through Creative Commons.

Figure 16. ***Chironomus dorsalis*** adult, an insect known to transport bryophyte spores or protonemata. Photo by James K. Lindsey, with permission.

Suborder Nematocera

The name **Nematocera** means "thread horns" and refers to the long, threadlike antennae. These are elongated flies with thin, segmented antennae. The larvae are mostly aquatic and the family includes craneflies, gnats, midges, mosquitoes, and blackflies.

Nymphomyiidae

This is a family of tiny (2 mm) flies in the northern parts of the Northern Hemisphere, especially eastern North America and eastern and central Asia (Nymphomyiidae 2013). The adults are **neotenic** (retaining larval or immature characters in adulthood), with straplike wings having **poor venation** (few wing veins). They live in running waters, where they often are found on moss-covered rocks, and **pupation** (development process between larva and adult) usually occurs in the same place (Courtney 1994). Adults have aborted mouth parts and live only a short time, some dying while still in the copulatory (mating) position.

Nymphomyia is the only genus currently listed in this family (Myers *et al*. 2014). It lives among aquatic mosses in small, rapid streams (Courtney 1994; Courtney *et al*. 1996). Not only larvae, but also often pupae and adults of ***Nymphomyia***, live on rocky substrates covered with aquatic mosses such as ***Platyhypnidium riparioides*** (Figure 6), ***Fontinalis*** (Figure 5), and ***Hygroamblystegium*** (Figure 91) (Cutten & Kevan 1970; Adler *et al.* 1985).

Cylindrotomidae – Long-bodied Craneflies

The family **Cylindrotomidae** is often separated from the **Tipulidae** (Figure 46-Figure 73, Figure 75, Figure 77-Figure 76), which I have chosen to do to make it easy to discuss its unique characters relative to bryophytes. These are of moderate size (11-16 mm) and yellowish to pale brownish as adults (Cylindrotominae 2014). Most larvae live among mosses – terrestrial, semiaquatic, and aquatic mosses (Cylindrotominae 2014), and feed on mosses and **tracheophytes** (plants with lignified vascular tissue) (Gelhous *et al*. 2007). The family occurs mostly in the Holarctic and Oriental Regions, but there are scattered records in southern South America, New Guinea, and Australia.

The aquatic insects don't seem to have the elaborate camouflage known in some terrestrial insects, but some still do an excellent job at blending. The **Cylindrotomidae** in particular are bryophyte dwellers and are world-class mimics of that habitat – bryocamouflage!

The larvae of ***Triogma trisulcata*** (Figure 1, Figure 17) are known for their mimicry in a ***Sphagnum*** (Figure 69) habitat, but they also occur in streams where the larvae attach to ***Fontinalis antipyretica*** (Figure 5) (Gerson 1969). The leaflike appendages most likely are equally useful in that habitat as camouflage.

Figure 17. ***Triogma trisulcata*** larva posterior showing flanges that make it almost invisible among ***Sphagnum***. Photo by Walter Pfliegler, with permission.

Triogma trisulcata (Figure 17) larvae are inhabitants of semiaquatic mosses, especially in stagnant water in bogs (Brinkmann 1997). In contrast to the tracheal gill respiration of ***Phalacrocera replicata*** (Figure 18), another bryophyte dweller in this family, the larvae lie on the leaves of the moss in a position that places the **spiracular disk** (apparatus that contains the breathing openings called spiracles) at the level of the water surface. Like ***P. replicata***, these larvae have appendages that match the color and mimic the morphology of the surrounding mosses. These have been variously interpreted as mimetic camouflage to protect them against enemies and as respiratory organs. It seems reasonable that both interpretations may be correct. The pupae remain in these same positions until a short time before the adults emerge (**ecdysis**). Just before ecdysis, they search for drier mosses. Eggs are laid singly on mosses just below the surface by females dipping the tip of the abdomen into the water to touch the leaves. The eggs are attached by an adhesive.

Figure 18. ***Phalacrocera replicata*** larva, an effective moss mimic that develops among mosses. Photo through Wikimedia Commons.

Phalacrocera replicata (Figure 18) lives among ***Sphagnum*** (Figure 69), ***Fontinalis antipyretica*** (Figure 5), and ***Warnstorfia fluitans*** (Figure 19) (Brinkmann 1997). Larvae in this species find tufts of mosses, then attach themselves to the leaves and stalks by affixing the anterior part of the body using the **mandibles** (crushing organs in an arthropod's mouthparts) to grab onto the edge of a leaf. They then crawl by crooking the body and securing the dorsal hooks. They have backward-pointing appendages that presumably help prevent them from being swept away by the current. At this stage they have functional spiracles that they do not use. Instead, the long, filiform appendages along the body function as tracheal gills, supplemented by **cutaneous** (referring to outer cuticle of insect body) gas exchange. But when it is time for pupation, the larvae move to the water surface to expose their **spiracles** (external openings through which insects breathe) to the atmospheric air. To maintain this contact with surface air, the pupae hang beneath the surface film, using their

respiratory horns, and cling to the stems of mosses or other plants with the appendages on the last of the abdominal segments, positioning their bodies horizontally.

Figure 19. ***Warnstorfia fluitans***, one of the homes of larvae of ***Phalacrocera replicata***. Photo by Michael Lüth, with permission.

Clymo and Hayward (1982) reported that ***Phalacrocera replicata*** feeds on ***Sphagnum*** (Figure 69). Miall and Shelford (1897) found that ***P. replicata*** (Figure 18) larvae eat ***Warnstorfia exannulata*** (Figure 20). They described pupae that attach to the moss leaves by dorsal appendages on posterior segments. The females lay about 60 eggs in **axils** (upper angle between leaf stalk or branch and stem from which it grows) of the moss leaves.

Figure 20. ***Warnstorfia exannulata***, food for ***Phalacrocera replicata*** (Figure 18). Photo by Michael Lüth, with permission.

Byers (1961) reported that the larvae of ***Liogma*** (Figure 21) use bryophytes for their larval habitats. Larvae of the genera ***Liogma*** and ***Triogma*** (Figure 17) have a green color with markings that make them look like leafy mosses (Gerson 1969). These two genera live among and eat the mosses ***Rhytidiadelphus squarrosus*** (Figure 22) and ***Hypnum cupressiforme*** (Figure 23). Larvae of ***Triogma trisulcata*** (Figure 17) inhabit the brook moss ***Fontinalis antipyretica*** (Figure 5) in mountain streams (Alexander 1920). These larvae have appendages that resemble leaves on a branch, and the color is typically green and black.

Figure 21. ***Liogma nodicornis*** adult, a species whose green larvae have markings that make them look like the leafy mosses where they live. Photo by Ilona L., through Creative Commons.

Figure 22. ***Rhytidiadelphus squarrosus***, home and food for ***Liogma*** (Figure 21) and ***Triogma*** (Figure 17) larvae. Photo by Michael Lüth, with permission.

Figure 23. ***Hypnum cupressiforme***, home and food for ***Liogma*** (Figure 21) and ***Triogma*** (Figure 17) larvae. Photo by Li Zhang, with permission.

Limoniidae – Limoniid Craneflies

The **Limoniidae** (Figure 24) family is an offshoot of the **Tipulidae** and thus many of the taxa discussed here were originally reported as members of **Tipulidae**. They are a worldwide family, mostly aquatic, and of moderate size (Limoniidae 2015). Their feeding groups vary considerably, including **phytophagous** (eating plants), **saprophagous** (eating dead organisms), **mycetophagous** (eating fungi), and **carnivorous** (eating animals) species.

Figure 24. **Limoniidae** adults mating, a family with larvae that often live among mosses, some consuming them. Photo by Anki Engström at <www.krypinaturen.se>, with permission.

From Cape Town, South Africa, we have a report of the **Limoniidae** occupying mosses in the stream of an isolated mountain (Harrison & Barnard 1972). The genus ***Geranomyia rostrata*** (see Figure 25) lives among algae, wet mosses, and thallose liverworts in the eastern part of North and South America (Rogers 1927; Johannsen 1969). These larvae are greenish and **translucent** (allowing light but not clear images to pass through), slow movers, and herbivores on algae and moss (Johannsen 1969). ***Geranomyia sexocellata*** (see Figure 25) larvae live in a gelatinous tube made with minute sand grains and attached to mosses in waterways that are only trickles.

By contrast, ***Dicranomyia capicola*** (syn. of ***Limonia capicola***?; see Figure 26) larvae live among mosses at the edge of a rapidly flowing streamlet (Harrison & Barnard 1972) and larvae of ***Limonia*** sp. and ***Ormosia*** sp. (Figure 28) live among bryophytes in Appalachian Mountain streams (Glime 1968). Harrison and Barnard (1972) also found ***Elephantomyia aurantiaca*** (see Figure 29) larvae among the damp mosses and liverworts.

Several researchers have reported ***Limonia*** species from bryophytes (Byers 1961; Hilsenhoff 1975; Suren 1991). Suren (1991) found that ***Limonia hudsoni*** (see Figure 27) apparently required more from the bryophytes than just a substrate. It failed to colonize the artificial bryophytes in his New Zealand stream studies. Instead, Suren and Winterbourn (1991) reported that it actually commonly consumes bryophytes. Apparently artificial ones couldn't fill the bill.

Figure 25. ***Geranomyia*** sp adult. ***Geranomyia rostrata*** larvae live among mosses and thallose liverworts in North and South America. Photo by Ted Kropiewnicki, through Creative Commons.

Figure 26. ***Dicranomyia modesta*** adult, member of a genus with some larvae that live among mosses at streambanks. Photo by James K. Lindsey, with permission.

Figure 27. ***Limonia wellingtonia***, member of a genus with some moss-dwelling members. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 28. ***Ormosia*** adult, a genus whose larvae sometimes live among mosses. Photo by Malcolm Storey, through Creative Commons.

Figure 29. ***Elephantomyia westwoodii*** adult female; larvae live among damp mosses and liverworts. Photo by Robert Lord Zimlich, through Creative Commons.

An important use of bryophytes can be that of providing a place for them to emerge. ***Rhipidia maculata*** emerges from the stream bed and also from thin moss layers on exposed rocks (Needham 1908; Johannsen 1969).

In my studies of Appalachian Mountain stream moss communities, both ***Hexatoma*** cf. ***longicornis*** and ***H.*** cf. ***spinosa*** occurred among the leafy liverworts ***Scapania undulata*** (Figure 30) (Glime 1968). ***Hexatoma*** (Figure 31-Figure 32) is known to ingest mosses (Percival & Whitehead 1929), so perhaps it is looking for food.

Figure 30. ***Scapania undulata***, home for several species of ***Hexatoma***. Photo by Michael Lüth, with permission.

Figure 31. ***Hexatoma*** larva; some members of this genus eat mosses. Photo by Jason Neuswanger, with permission.

Figure 32. ***Hexatoma*** (***Eriocera***) ***gravelyi*** male adult. Photo by Muhabbet Kemal, with permission.

Limnophila occurs among bryophytes in several locations (Alexander 1919; Hilsenhoff 1975). In the Appalachian Mountain streams several species occur among the bryophytes, including ***L.*** cf. ***macrocera*** (Glime 1968). ***Limnophila alleni*** (see Figure 33) lays its eggs

among mosses (Alexander 1919). Lauga and Thomas (1978) found that **Limoniidae** in France were more likely to be found among bryophytes when it was time for pupation and molting. The same relationship was seen for members of **Athericidae** and **Rhagionidae** (**Brachycera**).

Figure 33. ***Limnophila*** larva, member of a genus known to lay eggs in mosses. Photo by Tom Murray, through Creative Commons.

Erioptera (Figure 34), ***Pseudolimnophila*** (Figure 35), and ***Pilaria*** (Figure 36) in Wisconsin, USA, use mosses among their larval substrata (Hilsenhoff 1975). Byers (1961) reported that the larvae of ***Erioptera*** and ***Gonomyia*** (Figure 37) use bryophytes as larval habitats. In the Appalachian Mountain streams (USA), one can find the genus ***Antocha*** (Figure 7) (Glime 1968), a genus found in similar habitats in Japan.

Figure 34. ***Erioptera*** sp. larva, a moss inhabitant. Photo courtesy of the State Hygienic Laboratory at the University of Iowa, with permission.

Figure 35. ***Pseudolimnophila*** sp. larva breathing apparatus, a genus that lives among Wisconsin mosses. Photo by Urmas Kruus, with permission.

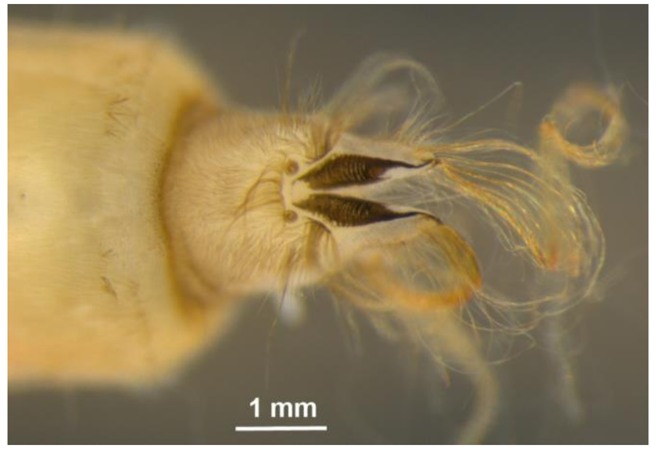

Figure 36. ***Pilaria*** sp. larva breathing apparatus, a genus that lives among Wisconsin mosses. Photo by Urmas Kruus, with permission.

Figure 37. ***Gonomyia*** adult, a genus whose larvae live among bryophytes. Photo by Joe Zito, through Creative Commons.

Blanket bogs have their own fauna, some of which is unique. Larvae that live in these habitats in Dartmoor, UK, include ***Molophilus occultus*** (Figure 38) whose larvae seem to require areas of bare, wet peat where they live in litter and among mosses (Boyce 2011). But this genus can also be found among bryophytes in Appalachian Mountain, USA, streams (Glime 1968). ***Phylidorea squalens*** (Figure 39) larvae in the Dartmoor blanket bogs live in the bog pools.

Figure 38. ***Molophilus*** sp. larva, a larva that seems to require bare, wet peat. Photo by Erin Hayes-Pontius, through Creative Commons.

Figure 39. ***Phylidorea squalens*** adult male, a species whose larvae live in bog pools. Photo by James K. Lindsey, with permission.

Pediciidae – Hairy-eyed Craneflies

The **Pediciidae** occur in the temperate zones of both hemispheres (Kits 2005b). These are medium to large (20-35 mm) flies (Pediciidae 2014) that resemble craneflies.

Pedicia (Figure 40) (now placed in **Pediciidae**) is one of the craneflies found among mosses as larvae (Figure 41) in some streams in the Appalachian Mountains, USA (Glime 1968). Hilsenhoff (1975) reported the genus in Wisconsin, USA, where it includes mosses among its substrata.

Figure 40. ***Pedicia rivosa*** adult on *Equisetum*. Larvae of some species live among mosses in Appalachian Mountain streams. Photo by Niels Sloth, with permission.

Figure 41. ***Pedicia albivitta*** larva, member of a genus of moss dwellers. Photo by Jason Neuswanger, with permission.

Tipulidae – Craneflies

This is a worldwide family that occupies a wide range of habitats as larvae, from water to mosses to dry logs (Hofsvang 1997). As adults they live only a few days and may not eat. That's right, they are not giant mosquitoes and won't bite you! But they do look like giant mosquitoes, with long legs and bodies 7-35 mm long (Tipulidae 2014), but narrow. Unlike the **Limoniidae**, the **Tipulidae** (Figure 42) are mostly terrestrial. Their larval food choices include algae, microflora, and both living and decomposing plant matter, including wood.

Figure 42. The cranefly ***Tipula*** occurs frequently among leaf litter that it helps to shred by eating it, but it can also occur among submerged and moist moss clones where its ecological role is unknown. Photo by Janice Glime.

The **Tipulidae** accomplish most of their respiration by using a posterior respiratory apparatus (Figure 43-Figure 44) (Pritchard 1983). They have a single pair of spiracles located there. The spiracles can't be closed, but there are tiny hairs on the walls of the spiracle opening that reduces water loss. There also seems to be cuticular respiration.

Figure 43. Larva of ***Tipula*** showing respiratory apparatus at right. Photo from Beentree, through Creative Commons.

Figure 44. Respiratory apparatus with spiracles of ***Tipula*** sp. Photo from Beentree, through Creative Commons.

Egg-laying (Figure 45) of tipulids on bryophytes has been known for a long time. For example, Alexander (1919) reported that ***Tipula nobilis*** laid her eggs in moss. Females already have mature eggs when they emerge from the pupa and after copulation they deposit them on wet soil or algae, or drop them (Tipulidae 2014). These eggs are usually black and may have a thin thread that could help to attach them in the water.

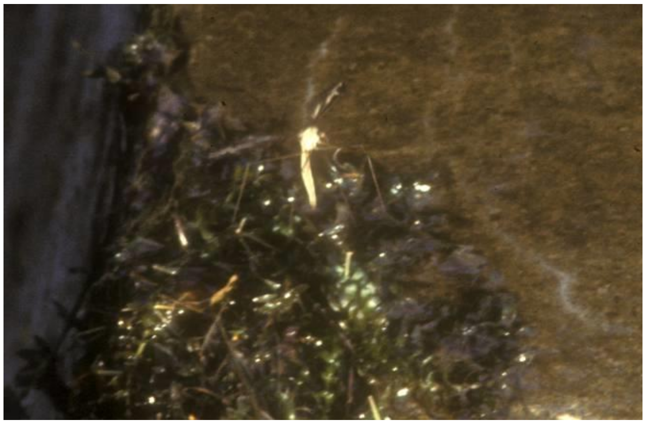

Figure 45. Cranefly laying eggs in submerged mosses. Photo by Janice Glime.

Tipulidae adults look like giant mosquitoes because of their long legs (Figure 46). In some regions they are known as daddy-long-legs for the same reason, but these are not to be confused with the 8-legged daddy-long-legs that are arachnids. Many **Tipulidae** live among aquatic leaf litter and mosses as larvae. Likewise, most of them pupate in soil near water, in mosses, or in litter (Byers 1978, 1996; Erman 1984).

Figure 46. ***Tipula*** adult. Photo by Micka 972, through Creative Commons in <Omnilexica.com>.

Larvae of craneflies are highly susceptible to desiccation (Pritchard 1983) and bryophytes seem to be an important habitat for maintaining moisture in bog species and terrestrial species. ***Tipula montana*** burrows into mosses when it is disturbed (Smith *et al*. 2001). ***Dolichopeza*** (Figure 77) species select their moss habitat for its suitability for making burrows (Byers 1961). The cranefly larvae seem to prefer compact mosses rather than loose ones in the same species (Todd 1993).

Tipula ignobilis occurs throughout the year among mosses on boulders in a Tennessee, USA, springbrook (Stern & Stern 1969). Slightly farther north in the Appalachian Mountains, I found what appeared to be seven different species of ***Tipula*** among bryophytes in the 28 streams I studied, including ***Tipula collaris*** (Figure 47) (Glime 1968). At Barrow, Alaska, USA, ***Tipula carinifrons*** (Figure 48) is common in the dry moss hummocks (MacLean 1980).

Figure 47. ***Tipula collaris*** adult, a species whose larvae live among bryophytes in Appalachian Mountain streams. Photo through Carnegie Museum of Natural History, through Creative Commons.

Figure 48. ***Tipula carnifrons*** adult male, a common species in dry moss hummocks of Alaska. Photo by Ashley Bradford, through Creative Commons.

Byers (1961) listed bryophytes as the larval habitat of many ***Tipula*** species. The genus ***Tipula*** is typically a consumer of leaf litter. But mosses can be a major part of the diet in some species. Dangles (2002) found that in the four study streams of Vosges Mountains in northeastern France bryophytes comprised 96% of the diet of ***Tipula*** (***Savtshenkia***) (Figure 49).

Figure 49. ***Tipula*** (***Savtshenkia***) adult, a genus in which the larvae can eat considerable amounts of bryophytes. Photo by James K. Lindsey, with permission.

Tipulidae larvae commonly feed on mosses (Coulson 1962; Freeman 1967; MacLean 1980; Richardson 1981; Todd 1993), and these mosses often form a significant portion of the diet (Coulson 1962). Larvae of ***Tipula signata*** (Figure 50) feed on aquatic mosses (Hemmingsen 1965).

Figure 50. ***Tipula signata*** adult male, a species whose larvae eat aquatic mosses. Photo by James K. Lindsey, with permission.

Tipula montana is a bog dweller and is surrounded by bryophytes as a larva. Smith *et al*. (2001) experimented with food preference in larvae of this species. The research team gave the larvae trials with five individual species of mosses, then with two-species pairs, to determine their growth responses and preferences. Larvae grew on diets of each of the five species of mosses [***Racomitrium lanuginosum*** (Figure 51), ***Dicranum fuscescens*** (Figure 52), ***Sphagnum girgensohnii*** (Figure 53), ***Pleurozium schreberi*** (Figure 54), and ***Polytrichum commune*** (Figure 55)], but there was a wide range in which mean weights differed by a factor of two. The highest development rate, by far, was for larvae fed ***Pleurozium schreberi***, with nearly 50% reaching the fourth instar, whereas fewer than 5% of those fed on the other moss species reached that stage (Figure 56). ***Pleurozium schreberi*** also was the best moss for promoting growth, with weight gain double that of larvae fed on ***Sphagnum girgensohnii*** (Figure 57). Nevertheless, there was little difference among the survivorships of the larvae fed on each on the five mosses (Figure 58). But the larvae preferred ***Racomitrium lanuginosum*** to the other mosses and often avoided ***Pleurozium schreberi*** when given a choice (***Sphagnum girgensohnii*** was the least preferred). This avoidance of ***Pleurozium schreberi*** is likely because of the high **phenolic** content (compounds that taste bad, including tannic acid) of ***P. schreberi*** (Liao 1993; Glime 2006; Hribljan 2009; see chapter 10-3 on Isopoda in this volume).

Figure 51. ***Racomitrium lanuginosum***, a preferred food for ***Tipula montana***. Photo by Michael Lüth, with permission.

Figure 52. ***Dicranum fuscescens***, a moss with a high relative percentage of observations of being eaten by ***Tipula montana***. Photo by Michael Lüth, with permission.

Figure 53. ***Sphagnum girgensohnii***, the least preferred moss among choices given to ***Tipula montana***. Photo by Michael Lüth, with permission.

Figure 54. ***Pleurozium schreberi*** a moss that gives ***Tipula montana*** good growth performance but that is not preferred. Photo by Janice Glime.

Figure 55. ***Polytrichum commune***, a potential food avoided by ***Tipula montana***. Photo by Michael Lüth, with permission.

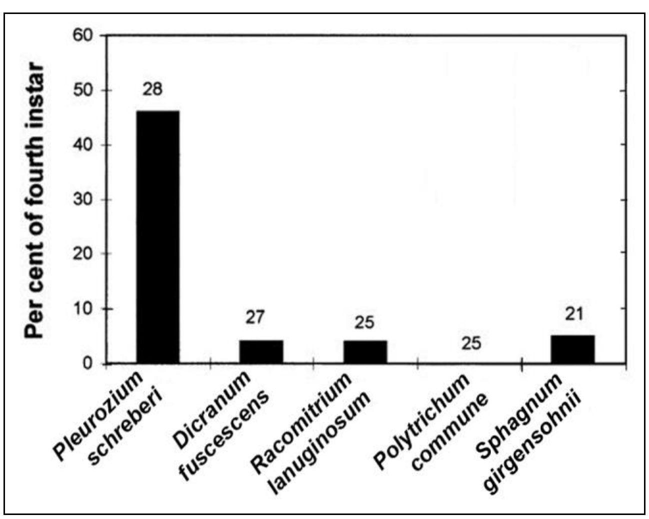

Figure 56. Survival percentages of ***Tipula montana*** larvae, starting with second-instar larvae, entering fourth instar after 52 days of feeding on diets of five moss species. Sample sizes appear above bars. Redrawn from Smith *et al*. 2001.

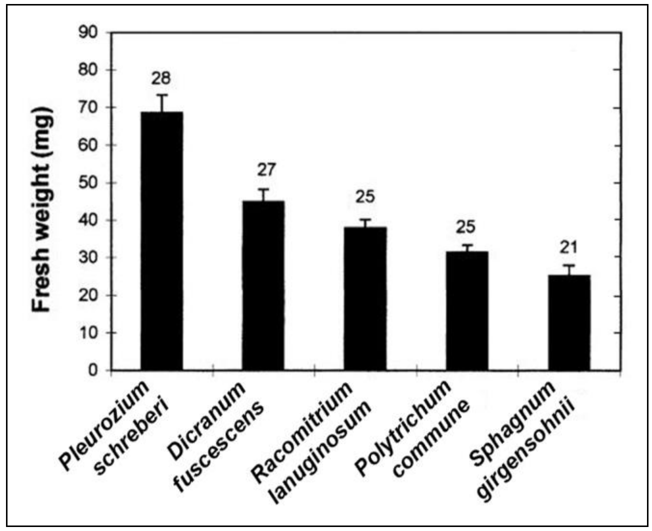

Figure 57. Mean fresh weight (+ standard error) of larvae of ***Tipula montana***, starting with second-instars, after 52 days on each of five moss species. Sample sizes appear above bars. Redrawn from Smith *et al*. 2001.

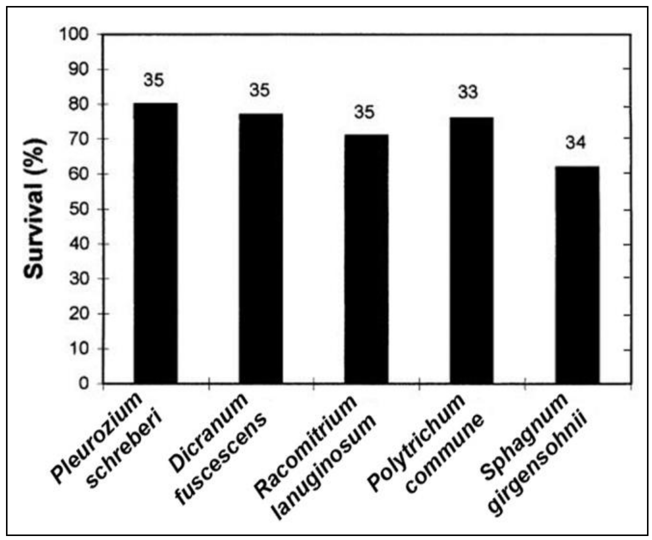

Figure 58. Percent survival of ***Tipula montana*** larvae fed on each of five moss species for 52 days. Sample sizes appear above bars. Redrawn from Smith *et al*. 2001.

Smith *et al*. (2001) issued a note of caution: The fecal indications of moss herbivory did not match the observational data. They suggested this may have been due to behavior differences between the larvae and the observers. The observers noted feeding behavior between 8:30 hours and 19:30 hours, but the larvae may have been feeding actively above ground at night, with daylight causing them to avoid the greater exposure on the sedge *Carex bigelowii*. This could explain the estimated lower percentage of *Carex bigelowii* in the observed diet in the field when using observations, and accounting for the higher percentage of ***Dicranum fuscescens*** (Figure 52) in the observations when compared to the ratio in the feces. Ratios of other mosses were similar using both methods. In the field, when *Carex bigelowii* was readily available, it was the clear choice compared to the mosses. The researchers also concluded that the bryophytes may be more important as a refuge than as a food source in nature. As pointed out by the researchers, experiments in which

development and growth on the sedge compared to those of the mosses would be instructive. It may be that the best growth is on a combination of these, with reduced growth or development resulting when no mosses are eaten. On the other hand, avoidance of predators may force the larvae to remain among the mosses and to eat them in the daytime. Several birds are primary predators on these larvae (Galbraith *et al*. 1993; Nethersole-Thompson 1966).

Tipula subnodicornis (Figure 59) feeds on liverworts in British moorland blanket bogs and consumes large quantities of ***Sphagnum*** (Figure 53, Figure 69) leaves (Coulson 1962; MacLean 1980). MacLean estimates that more than 25% of the energy consumption may be derived from the living plants of ***Sphagnum***.

Figure 59. ***Tipula subnodicornis*** adult, a cranefly whose larvae feed on liverworts in British blanket bogs but seem to have little preference in experiments with moss species. Photo by James K. Lindsey, with permission.

In the genus ***Tipula***, later instars ingest only slightly more vegetable matter as they grow to larger and larger instars. Rather, the early and late instars ingest similar-sized particles. In feeding experiments, Todd (1993) found that ***Tipula confusa*** (Figure 60) preferred woodland moss species, whereas ***T. subnodicornis*** (Figure 59) showed no preference between woodland and moorland mosses. ***Tipula confusa*** had a hierarchical preference among the 10 moss species offered, whereas ***T. subnodicornis*** showed much less hierarchy in food choices. Brindle (1960) noted that ***T. subnodicornis*** (Figure 59) typically associates with wet species such as those of ***Sphagnum*** (Figure 69) and ***Hypnum*** (Figure 23) in moorlands. Among 11 species Todd (1993) studied, 8 were moss consumers, with 7 of these in the same subgenus ***Savtshenkia*** (***Tipula rufina*** (Figure 61), ***T. confusa***, ***T. pagana*** (Figure 62), ***T. staegeri***, ***T. limbata*** (Figure 63), ***T. alpium*** (Figure 64), and ***T. subnodicornis***). Brindle (1960) had earlier observed that all the moss feeders known to him had four pairs of short anal papillae, whereas in wetter environments these papillae were longer. The eighth, ***T. montana*** is in the subgenus ***Vestiplex***. In Great Britain, approximately one-fourth of the 59 (Freeman 1967) members of ***Tipula*** feed on mosses. Even the invasive species ***Campylopus introflexus*** (Figure 65) is ***Tipula*** food in the recently burned *Calluna* heath. ***Tipula montana*** in the upland moors feeds exclusively on mosses.

Figure 60. ***Tipula confusa*** adult; larvae eat mosses, preferring woodland species. Photo by Malcolm Storey, through Creative Commons <www.discoverlife.org>.

Figure 61. ***Tipula rufina*** adult, a species whose larvae eat small particle sizes of bryophytes. Photo by Malcolm Storey, through Creative Commons <www.discoverlife.org>.

Figure 62. ***Tipula pagana*** male adult, a species whose larvae eat small bites of bryophytes. Photo by James K. Lindsey, with permission.

Figure 63. ***Tipula limbata*** adult, a species whose larvae eat bryophytes in small bites. Photo by Derek Sikes, University of Alaska Museum, through Creative Commons.

Figure 64. ***Tipula alpium*** adult, a species whose larvae eat bryophytes in small bites. Photo by Malcolm Storey, through Creative Commons.

Figure 65. ***Campylopus introflexus***, an invasive species that has become a food source for ***Tipula*** larvae in the ***Calluna*** heath. Photo by Michael Lüth, with permission.

The insect **feces** (excrement; waste material discharged from gut) reveal a great deal about the use of mosses as food (Todd 1993). The particle size remains the same in the feces as it was in the cut ingested portion (Pritchard 1983). Interior cells of the pieces are significantly less damaged (Todd 1993). Instead, digestion appears to be limited to the broken cells on the edges, with little or no damage caused by passage through the gut. This inability to obtain nutrients from the interior cells accounts for the consistency in small-sized particles from early to late instars. The particle sizes are significantly smaller for ***Tipula rufina*** (Figure 61), ***T. lateralis*** (Figure 66), and ***T. subnodicornis*** (Figure 59); ***T. paludosa*** (Figure 67) and ***T. oleracea*** (Figure 68) ingest significantly larger particles than any other species. These differences are at least partly explained by mandible size. ***Tipula paludosa*** has significantly larger mandibles and ***T. rufina*** has significantly smaller ones than any other species. In short, those species feeding on grass are generally larger and have longer mandibles than those species feeding on mosses.

Figure 66. ***Tipula lateralis*** adult, a species whose larvae ingest small particle sizes. Photo by James K. Lindsey, with permission.

Figure 67. ***Tipula paludosa*** larva, a bryophyte consumer. Photo by Roger S. Key, with permission.

Figure 68. ***Tipula oleracea***, a bryophyte consumer that ingests large particles. Photo by Malcolm Storey, through Creative Commons <www.discoverlife.org>.

Tipula has both terrestrial and aquatic members. Some of these in both habitats consume bryophytes. But ***Tipula subnodicornis*** (Figure 59) prefers the cottongrass *Eriophorum vaginatum* to the terrestrial moss ***Campylopus paradoxus*** and bog moss ***Sphagnum papillosum*** (Figure 69) (Todd 1993). However, in early winter (10 December to 9 January) the preference changes significantly from cottongrass to ***Sphagnum papillosum***. It is interesting, however, that during the growing season there is a mix of *Eriophorum vaginatum* with ***S. papillosum*** where the larvae spend the most time.

Figure 69. ***Sphagnum papillosum***, a moss that becomes a preferred food in winter for ***Tipula subnodicornis***. Photo by Michael Lüth, with permission.

Bisang (1996) reports a rather bizarre experience in The Bryological Times. She had several cultures of ***Anthoceros agrestis*** (Figure 70) and ***Phaeoceros carolinianus*** (Figure 71), both hornworts. Using the same techniques as she had used previously, she cultured these in jars, keeping two in Switzerland and taking one to Sweden. To her surprise, one of the cultures in Switzerland and the one taken to Sweden virtually disappeared from the jar. They had not dried and sabotage seemed absurd. Careful examination revealed larvae 1.5 cm long with a breathing apparatus at the posterior end. The cultures were supporting a healthy colony of larvae of ***Tipula*** (Figure 42), craneflies. The hornworts seemed to be a preferred food, as ***Bryum*** (Figure 72) sp. and several seedlings were untouched.

Figure 70. ***Anthoceros agrestis***, food source for ***Tipula*** larvae. Photo by Jan-Peter Frahm, with permission.

Figure 71. ***Phaeoceros carolinianus***, food source for ***Tipula*** larvae. Photo by Michael Lüth, with permission.

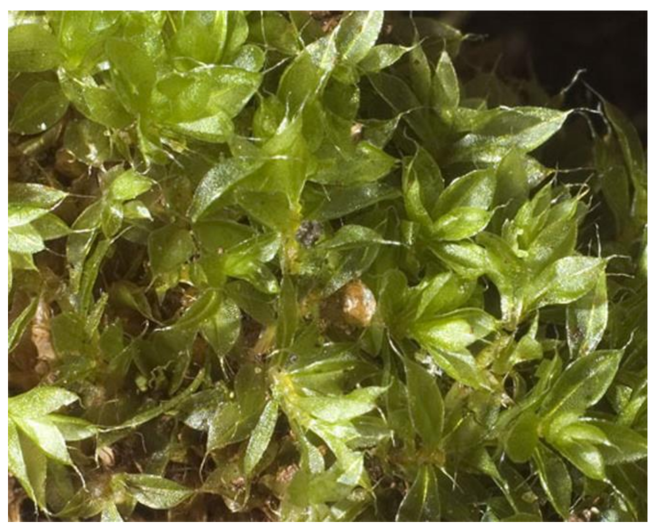

Figure 72. ***Bryum capillare***. A species of ***Bryum*** was refused as food by larvae of a species of ***Tipula***. Photo by Aimon Niklasson, with permission.

The members of ***Tipula*** are among the few documented moss consumers, although there is much more consumption than is generally recognized. Todd (1993) suggested that the presence of cell wall bioflavonoids in bryophytes might function not only to resist fungal invasion (Geiger 1990), but also to discourage insect

browsers. It is also possible that in some cases the fungi are needed to facilitate digestion, making mosses that lack them indigestible. Furthermore, lignin-like compounds in the bryophyte cell walls protect the cell wall compounds (cellulose, hemicellulose, and other kinds of polysaccharides) from **hydrolytic attack** (using a chemical reaction where something reacts with water and is changed into a new substance), preventing the consumers from using hydrolytic attack to extract cell contents, as demonstrated in ***Tipula abdominalis*** (Figure 75) (Martin *et al*. 1980). Nevertheless, in North America the genus ***Tipula*** (Figure 75) is able to hydrolyze proteins from unconditioned maple (*Acer*) leaves (Barlocher & Porter 1986).

Suitable food sources often depend on *p*H of the gut (Martin *et al*. 1980). Very high and very low *p*H levels seem to work best. But Barlocher and Porter (1986) found that the larvae of ***Tipula caloptera*** (Figure 73) have a gut *p*H that is somewhat alkaline. Fungal carbohydrases ingested with the leaves do not remain active in the ***T. caloptera*** gut, but do in the nearly neutral *p*H of the amphipod ***Gammarus tigrinus*** and net-spinning caddis larva ***Hydropsyche betteni*** (Figure 74).

Figure 73. ***Tipula caloptera*** adult female. Larvae of this species have an alkaline gut that may help it digest plant material. Photo by Tom Murray, through Creative Commons.

Figure 74. ***Hydropsyche betteni*** larva, a species with a slightly alkaline gut and ability to keep fungal enzymes alive. Photo by Donald S. Chandler, with permission.

In ***Tipula abdominalis*** (Figure 75) the midgut has a *p*H near 11.5 in a narrow section where there is extremely high proteolytic activity (Martin *et al*. 1980). In addition to low *p*H created by ***Sphagnum*** (Figure 69) and other mosses, mosses are well known for their antibiotics (McCleary *et al.* 1960; McCleary & Walkington 1966), additional factors that might interfere with gut digestion.

Figure 75. ***Tipula abdominalis*** larva. Larvae have a high *p*H in the midgut. Photo by Tom Murray, through Creative Commons.

Dolichopeza (Figure 77) is a genus known from mosses in various parts of the world. ***Dolichopeza americana*** is generally considered to be a terrestrial larva (Byers pers. comm.), but in the Appalachian Mountain streams it occurs among the leafy liverworts (***Scapania undulata***; Figure 30) in small waterfalls in March and December (Glime 1968). ***Dolichopeza albipes*** (see Figure 77) is a white-footed ghost cranefly whose larvae live among the mosses and liverworts of the Ghyll woodlands in Sussex, UK (Roper 2001). But this genus also chooses mosses for home in South Africa (Harrison & Barnard 1972). Members of this genus are known to lay their eggs among bryophytes, giving these larvae their start in life among the bryophytes.

Dolichopeza barnardi, ***D. hirtipennis***, and ***D. peringueyi*** larvae live beneath and within cushions of wet mosses and liverworts at the sides of waterfalls in South Africa (Harrison & Barnard 1972). And in North America, the genus feeds on terrestrial mosses (Byers 1961). In the coastal tundra near Barrow, Alaska, ***Prionocera recta*** (Figure 76) is restricted to mossy depressions.

Figure 76. ***Prionocera turcica*** adult, relative of ***P. recta*** restricted to mossy depressions in the Alaskan tundra. Photo by Andre Vrigens, through Creative Commons.

Figure 77. ***Dolichopeza carolus*** adult. Larvae of several species in this genus live among mosses, including at the sides of waterfalls. Photo by Tom Murray, through Creative Commons.

Many of the **Tipulidae** that inhabit mosses as larvae do so among terrestrial bryophytes and will be discussed in a separate chapter on Terrestrial Insects.

Anisopodidae – Wood Gnats, Window Gnats

This family is worldwide, but bryophytes are not a usual habitat. Most are small (4-12 mm) (Anisopodidae 2014). Fungi are typical foods, but it appears that at least some feed on micro-organisms, as I have observed.

While looking for mosses one day, I found some (***Philonotis fontana***?; Figure 78) in a seepage area on a cliffside. There on one of its branches was a small larva eating away at the wet moss. But as I watched for awhile, I realized that the mosses were going into one end of the larva covered with detritus and coming out the other end clean and still bright green. I was unable to identify this single larva beyond family.

The larvae of ***Sylvicola cinctus*** (Figure 79) was reported from mosses in Norway (Søli 1992). Perhaps there are other members of this small family hiding among the bryophytes.

Axymyiidae

This is a small family of six known species (Axymyiidae 2014). Its limited distribution is Holarctic and Oriental (Hauser 2008). The larvae live in decomposing wood (Axymyiidae 2014).

Figure 78. ***Philonotis fontana*** similar to seepage area where a member of **Anisopodidae** was eating and defecating bits of moss. Photo by Michael Lüth, with permission.

Figure 79. ***Silvicola cinctus*** male adult, a species whose larvae live among bryophytes in Norway. Photo by Walter Pfliegler, with permission.

I have seen only one record from this little-known family. ***Axymyia furcata*** (Figure 80) is a semi-aquatic fly in its larval stage and is typically a wood inhabitant. However, Wihlm and Courtney (2011) found that the larvae often choose logs that are covered with mosses.

Figure 80. ***Axymyia furcata***, a semi-aquatic larva that lives among mosses on logs. Photo by M. J. Hatfield, through Creative Commons.

Cecidomyiidae – Gall Midges, Gall Gnats

This family is worldwide with most records in the Northern Hemisphere. They are small flies, mostly 1-5 mm (Balaban & Balaban 2004). Most of these are gall makers, with their larvae living on the gall material, but some feed on plants and some on decaying matter. Hence, as one might expect, they are predominantly terrestrial, but there are aquatic exceptions.

Although the **Cecidomyiidae** (Figure 81) are not typical bryophyte inhabitants, some do prefer mosses in torrents (Thomas 1980). ***Porricondyla ramadei*** was described as a new species from tufts of mosses in the turbulent waters of high Pyrénées streams. This is a poorly known fauna, and it is likely more insects may be discovered among the bryophytes there.

Figure 81. **Cecidomyiidae** larva; some members of this family live among mosses in torrents. Photo by M. J. Hatfield, through Creative Commons.

Mycetophilidae – Fungus Gnats

As the name implies, these flies live among fungi, hence making them most common in damp or sometimes wet habitats (Mycetophilidae 2014). They are worldwide, especially in forested areas (Kits 2005a). Although they are worldwide, most records are in the Northern Hemisphere (Mycetophilidae 2015). They typically feed on the fruiting bodies of the fungi (Mycetophilidae 2014). But some live among mosses and liverworts.

Fungi are often moist, so it may not be so surprising that some of these fungus gnats have found bryophytes to be suitable habitats. ***Gnoriste apicalis*** (Figure 82) is a semi-aquatic species. The larvae are able to live in saturated moss clumps on lake shores (Lenz 1927; Johannsen 1969). The pale green coloring may help it to be inconspicuous as it feeds on detritus. It may also make a dense but delicate white web in which it lives in such habitats, with the web offering further camouflage.

Sciaridae – Dark-winged Fungus Gnats

As you might expect of a fungus gnat, these flies prefer moist sites and eat the fruiting bodies of mushrooms and various parts of other fungi (Sciaridae 2014). They are worldwide in distribution, including such extremes as deserts, sub-Antarctic islands, and altitudes over 4000 m. Because they live among litter and fungi, they are frequent in flower pots. They are small, up to 7 mm long.

Figure 82. ***Gnoriste*** sp. adult; larvae of ***Gnoriste apicalis*** live in saturated mosses. Photo from Biodiversity Institute of Ontario, through Creative Commons.

In Korea, Japan, China, and other parts of Asia, the shiitake mushroom business is important. To this end, studies on the pests of this delicacy are common. And sometimes we find that mosses are involved. Shin *et al*. (2012) found that one of the mushroom pests, ***Bradysia difformis*** (Figure 83), also occurs in moorland on peat moss.

Figure 83. ***Bradysia difformis***, a shiitake mushroom pest whose larvae sometimes live on peat mosses of moorlands. Photo by David Pilling, with permission.

Ceratopogonidae – Biting Midges, No-see-ums, Sand Flies, Punkies

Their small size (<3 mm) has earned the **Ceratopogonidae** such names as no-see-ums and the adults can be quite a nuisance along lakes in June and July (Moisset 2005). Their distribution is worldwide in salt and freshwater marshes, forests, edges of ponds, and streams.

Usinger (1974) lists mosses among the usual habitats for larvae in the **Ceratopogonidae** and Krno (1990) found them to be representative of bryophyte habitats in the River Rajcianka in Slovakia. In addition to those aquatic

members, ***Forcipomyia*** (Figure 84) species live among damp mosses, including building nests in ***Sphagnum*** species (Figure 69) (Oldroyd 1964). The larvae in this family are elongate, wider in the middle, and most of them lack legs (Usinger 1974).

Figure 84. ***Forcipomyia*** sp larvae – inhabitants of damp mosses. Photo by Tom Murray, through Creative Commons.

In Germany, ***Kolenohelea calcarata*** occurs among mosses in a spring and ***Serromyia femorata*** (Figure 85) occurs among damp mosses (Strenzke 1950).

Figure 85. ***Serromyia femorata*** adult, a damp moss dweller. Photo by James K. Lindsey, with permission.

In the Atlantic Forest of the coastal area of South America, **Ceratopogonidae** were second in dominance during the rainy season among mosses in a first-order stream (Rosa *et al*. 2011). Living among the bryophytes minimizes the downstream loss in fast-moving water.

In European alpine areas, ***Dasyhelea modesta*** (see Figure 86-Figure 87) and ***Bezzia xanthocephala*** (see Figure 88) use mosses for their pupal site (Thienemann 1936). ***Dasyhelea*** (Figure 87) larvae likewise can spend their lives among mosses. The species known to Thienemann as ***Culicoides neglectus*** (*nom. dub*. – a name without valid publication) lived as pupae among mosses in small alpine waterfalls. (This name is now excluded, so I can't be sure what species he found.) Species in ***Culicoides*** as it is currently known are the ones that bite humans (Moisset 2005).

Figure 86. ***Dasyhelea flavifrons*** adult, member of a genus that is frequent among stream bryophytes. Photo by Walter Pfliegler, with permission.

Figure 87. ***Dasyhelea lithotelmatica*** larvae, member of a genus that frequents stream bryophytes. Photo by Roger S. Key, with permission.

Figure 88. ***Bezzia*** larva, a frequent inhabitant of stream bryophytes. Photo from California Department of Wildlife, through public domain.

In my Appalachian Mountain, USA, streams, I found at least two species of ***Bezzia*** (Figure 88), two of ***Dasyhelea*** (Figure 86-Figure 87), and one each of ***Alluaudomyia*** (Figure 89) and ***Atrichopogon*** (Figure 90)

among the bryophytes. These were mostly among ***Hygroamblystegium fluviatile*** (Figure 91) – ***Platyhypnidium riparioides*** (Figure 6), but also occurred among ***Fontinalis dalecarlica*** (Figure 92) and ***Scapania undulata*** (Figure 30).

Figure 89. ***Alluaudomyia paraspina*** adult female, a genus with some species whose larvae live among bryophytes in Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

Figure 90. ***Atrichopogon*** larva, a genus with some species whose larvae live among bryophytes in Appalachian Mountain streams. Photo courtesy of the State Hygienic Laboratory at the University of Iowa, with permission.

Figure 91. ***Hygroamblystegium fluviatile***, home for multiple species of **Ceratopogonidae**. Photo by Michael Lüth, with permission.

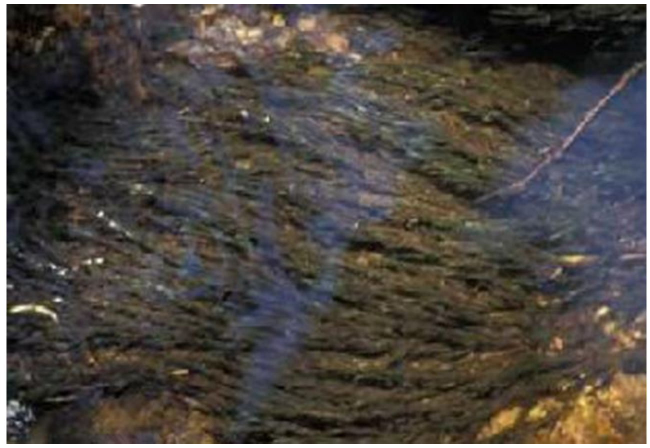

Figure 92. ***Fontinalis dalecarlica***, home for a number of genera of **Ceratopogonidae**. Photo by Kristoffer Hylander, with permission.

Summary

The **Nematocera** are primarily aquatic as larvae and a number of species and genera live among bryophytes. Adaptations to the bryophyte habitat, differing little from those needed for aquatic living, include claws and hooks to hold them in place, cutaneous breathing and/or gills, small size, often slender, and a detritus feeding habit. In return for the hospitality of the bryophyte, they may disperse bits of the plants or their spores to other suitable locations.

The dominant **Diptera** among bryophytes are **Chironomidae** and **Simuliidae**, with **Tipulidae**, **Limoniidae**, and **Ceratopogonidae** being less abundant. The **Chironomidae** can reach 1000's in a single handful of moss.

The **Cylindrotomidae** are among the few bryophyte mimics. They live among mosses in wet areas and bogs and the projections from their bodies resemble moss leaves.

In the genus ***Tipula*** (**Tipulidae**), a high gut *p*H may facilitate digestion of bryophytes.

Acknowledgments

George W. Byers verified my identifications of Tipulidae and Julian P. Donahue verified some of the remaining Diptera from my mid-Appalachian Mountain study.

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