

# CHAPTER 11-1

## AQUATIC INSECTS: BIOLOGY

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# CHAPTER 11-1

## AQUATIC INSECTS: BIOLOGY



Figure 1. *Rhyacophila carolina* larva, a free-living caddisfly that occurs commonly on bryophytes. Photo by Bob Henricks, with permission.

### Aquatic Insects

Cascading waterfalls, silt-laden torrents, lurking predators, limited oxygen, unpredictable water levels, icy winters – all these dangers face the insects (Figure 1) that call lakes, and especially streams, their homes. So why do the insects choose to live there, and how do bryophytes help to make life in such unfriendly conditions possible?

The relationship between aquatic insects and bryophytes is a topic dear to my heart. When I was working on my M.S. project on the bryophytes, my roommate was working on aquatic insects. Never passing up an opportunity for a field trip, I accompanied her on all her collecting trips. We both soon realized that in her rocky mountain streams of northern West Virginia, USA, there were typically more insects among the bryophytes than in any other microhabitat in these streams. It was this discovery that led me to my Ph. D. research topic on the insects associated with Appalachian stream bryophytes and the many studies I have done on ecology of aquatic mosses since then.

These wonderful bryophyte-insect communities are not a new discovery. Stream ecologists in particular have observed the importance of mosses as cover for aquatic insects and other aquatic invertebrates and even fish (Thienemann 1912; Carpenter 1927; Percival & Whitehead 1929, 1930; Humphries & Frost 1937; Jones 1941, 1948, 1951; Frost 1942; Badcock 1949; Illies 1952; Hynes 1961; Minckley 1963; Egglisshaw 1969; Arnold & Macan 1969; Lindgaard *et al.* 1975; Hawkins 1984; McKenzie-Smith 1987; Suren & Winterbourn 1992a, b; Gislason *et al.* 2001; Linhart *et al.* 2002; Paavola 2003).

In Idaho, USA, Maurer and Brusven (1983) found that *Fontinalis neomexicana* (Figure 2) housed 5-30x the densities of insects found associated with the mineral substrates; biomass, however, was only 2x as great. The moss did not alter insect densities in the underlying **hyporheic** zone (saturated zone beneath the bed of a river or stream that can support invertebrate fauna). The diversity of functional groups was greater among mosses, but the species richness was similar to that of the mineral substrate.



Figure 2. *Fontinalis neomexicana*, a moss that greatly increases the density of stream insects. Photo by Belinda Lo, through Creative Commons.



The numbers of insects among bryophytes can be extensive (Figure 3). Minckley (1963) found that mosses had the highest densities of insects compared to sand, stones, and tracheophytes in a Kentucky, USA, stream. Lillehammer (1966) found that moss-covered stones had 606 individuals m<sup>-2</sup> compared to 471 m<sup>-2</sup> on stones with no mosses.



Figure 3. This branch of *Palustriella commutata* demonstrates the variety and density of aquatic insects that can occur on aquatic mosses. Photo by Dan Spitale.

When more sophisticated statistical methods became available, bryophyte biomass emerged as one of the factors accounting for the variation in insect fauna among streams, and as we might expect, it has a positive influence on the insect fauna (Gislason *et al.* 2001). Furthermore, bryophytes can occupy deeper waters, forming a zone that is lower than that of tracheophytes, and this zone is able to support fauna that could not otherwise live at those depths (Blackstock *et al.* 1993).

Minshall (1984) considered bryophytes to be a major factor in increasing insect numbers because of the increased surface area offered by them. Egglishaw (1969) found that most species of invertebrates, including insects, were less aggregated in clumps among the mosses than they were under stones. One might interpret that this is due to the complex nature of the mosses and the large space in which they can be distributed. On the other hand, it would seem that the stone habitat would be more homogeneous and thus one might expect less clumping. Another mystery.

Table 1. Orders of insects and their abundances among bryophytes in various locations around the world. NR refers to not recorded, which may mean the researcher(s) didn't look at the group.

	sample size	Collembola	Odonata		Diptera		Coleoptera		Reference
		Ephemeroptera	Plecoptera		Trichoptera				
Straffan, River Liffey, Ireland	200 g	NR	533	NR	22	11446	492	262	Frost 1942
Ballysmuttan, River Liffey, Ireland	200 g	NR	16	NR	310	10482	148	1095	Frost 1942
Cold Springbrook, TN, USA	0.1 m <sup>2</sup>	NR	7.1	NR	8	215	24.6	0.4	Stern & Stern 1969
Bystřice, Czech Republic	10 g dry	NR	1103	NR	18	44762	359	184	Vlčková <i>et al.</i> 2001-2002
Mlýnský náhon, Czech Republic	10 g dry	NR	176	NR	0	11035	13	5	Vlčková <i>et al.</i> 2001-2002
Welsh Dee Tributary, Wales	~300 cm <sup>2</sup>	NR	9.7	NR	513	82.8	0.4	7.4	Hynes 1961
Mouse Stream, Alpine, NZ	1 m <sup>2</sup>	NR	NR	NR	540	61270	730	0	Suren 1991a
Tim's Creek, Alpine, NZ	1 m <sup>2</sup>	NR	NR	NR	270	24580	260	90	Suren 1991a
West Riding, Yorkshire, UK – loose moss	%	NR	13.42	NR	154	65.3	3.1	6.7	Percival & Whitehead 1929
West Riding, Yorkshire, UK – thick moss	%	NR	8.03	NR	0.65	42	8	4.4	Percival & Whitehead 1929
alpine unshaded stream, NZ	%	NR	NR	NR	2.1	581.8	NR	NR	Suren 1991b
alpine shaded stream, NZ	%	NR	NR	NR	2.5	69.9	NR	NR	Suren 1991b
River Sawdde, Wales		rare	NR	NR	very rare	NR	NR	very rare	Jones 1949

## Life Cycle Stages

Life cycle stages play a major role in the occupancy of water habitats by insects. Most of these orders of insects have poor ability to survive freezing, so escape into water can maintain their temperatures above freezing. The flowing part of water generally remains at ~1°C throughout the winter, and lakes and ponds that don't freeze to the bottom have water just above 0 up to 4°C.

Because of the importance of water in the life cycle of the major groups of aquatic insects, we must understand the types of life cycles among them before we can begin a discussion of the biology and ecology of these groups. There are two major groups of classification among the insects, based on life cycles and their developmental stages.

## Collembola

The **Collembola** (Figure 4), or springtails, long considered to be insects, have been kicked out of the **Insecta** by cladistics, due to linkages shown by their DNA and supported by their morphology. Because they have much of their ecology in common with insects, and their earlier inclusion among Insecta, they will be discussed among these aquatic insect subchapters.

The **Collembola** have the simplest life cycle, one in which the hatchling is a miniature of the adult. The immature stage is known as a **nymph**. Their life cycle consists of **egg/embryo**, **nymph**, and **adult**. The **Collembola** hatch from their egg casing and look like the adults, perhaps in somewhat different proportions; they

continue to increase in size without changing their basic form as they become adults.



Figure 4. *Collembola Arthropleona oruarangi*, a group of "pre-insects" that are born looking like little adults. Photo by Stephen Moore, Landcare Research, NZ, with permission.

## Hemimetabolous Insects (Hemimetabola)

### Nymphs

Among the aquatic insects, this group includes the true bugs (order **Hemiptera**), a group that lacks gills in all stages. The **Hemiptera** are **hemimetabolous** insects and thus lack the pupal stage (familiar to most people as the chrysalis of butterflies). Instead, they have only the **egg/embryo** (Figure 8), **nymph** (including **naiads** in the other hemimetabolous orders), and **adult**. [The **holometabolous** insects, on the other hand, have an **egg/embryo**, **larva**, **pupa**, and **adult (imago)**.]

### Naiads

Those orders with obligate aquatic immature stages that do not resemble the adults, but that do not pass through a second stage as a pupa before becoming an adult, have an aquatic stage known as a **naiad**. The **naiad** is a specialized nymph stage known only among aquatic insects and occurs in the orders **Plecoptera** (Figure 5, Figure 73, Figure 74, Figure 77), **Ephemeroptera** (Figure 6), and **Odonata** (Figure 7). The naiad usually differs from the adult in having some form of gills to aid in gaining oxygen in the aquatic environment. When it is time for the adult to emerge, these insects climb to the surface or out of the water, often on an emergent plant, and often hang vertically while they climb out of their naiad **exoskeleton** (Figure 5). The shed exoskeleton is the **exuvia** (pl. **exuviae**; Figure 5). In the **Ephemeroptera**, the emergent stage is a subadult known as a **subimago** (Figure 6). This subimago goes through one additional moult to become the adult (**imago**).

## Holometabolous Insects (Holometabola)

The remaining orders of aquatic insects are **holometabolous** and have what is known as **complete metamorphosis**. These insects have four life cycle stages: **egg/embryo** (Figure 8), **larva** (Figure 1), **pupa** (Figure 9), **adult (imago)** (Figure 10). The larva stage looks nothing like the adult. It is familiar to most people in the moths and butterflies as the caterpillar. The larva is a worm-like

creature, with or without legs, or in some cases with prolegs that are of soft tissues. The aquatic larvae have gills in many taxa, but not in others. Some have fleshy legs with hooks at the posterior end.



Figure 5. **Plecoptera** exuvia. Photo by Jason Neuswanger at <Troutnut.com>, with permission.



Figure 6. *Baetis* male subimago emerging to adult. Photo by Jason Neuswanger at <Troutnut.com>, with permission.



Figure 7. *Enallagma* damselfly naiad. Photo by Tom Murray, through Creative Commons.

The **pupa** is usually a stationary phase (known as a chrysalis in butterflies). As the pupa develops, the larva develops a chitinous outer covering that has the imprint of parts like wings and antennae. The insect is likely to be dormant or in **diapause** (in insects, period of suspended development, especially during unfavorable environmental



conditions) during its pupal stage, providing it reprieve from winter's cold or tropical drought. But during this time the insect goes through a number of changes in both form and physiology. When the insect has matured into an adult and conditions are right for its emergence, it breaks out of the pupa. In most cases, those that spend their larval lives in the water emerge into the atmosphere, spending their adult lives as terrestrial organisms (except in most of the beetles).



Figure 8. Emerald dragonfly with eggs. Photo by Bob Armstrong, with permission.



Figure 9. **Chironomidae** (midge) pupa. Photo by Bob Henricks, with permission.



Figure 10. **Chironomidae** adult male. Photo by Roger S. Key, with permission.

The holometabolous insect orders that live among bryophytes include **Coleoptera**, **Trichoptera**, **Megaloptera**, **Neuroptera**, and **Diptera**.

## Adaptations to Aquatic Bryophyte Life

Bryophyte dwellers might benefit from several behavioral and structural adaptations to make life among the bryophytes easier. They need to be able to gain sufficient oxygen (Hynes 1970), to move about freely, to avoid being pulled out if a predator catches a tail or leg, to avoid being swept away by the current, and to eat the available food. In streams where the water level varies a lot or dries up, they need to have a means to avoid desiccation.

## Life Cycle Strategies

Although I would normally discuss structural adaptations first, the life cycle adaptations appear to be the most important ones among the insects. Differing requirements among life cycle stages permit insects to survive from year to year in changing environmental conditions.

Blackstock *et al.* (1993) found the insects in a clear sequence of bryophyte to herbaceous swamp to woody plant community occupying different depth zones in the basin of Pant-y-llyn, Wales. These changes, on a large scale, require a degree of mobility on the part of the insect inhabitants as the habitat changes from aquatic to terrestrial seasonally. But even more permanent aquatic habitats have their down times. Success for an aquatic insect means having a strategy to survive during stages when the habitat is dry (Blackstock *et al.* 1993), too cold, or too hot.

To understand the role of bryophytes in the life of their insect inhabitants, one must understand these life cycles. Only twelve orders of insects plus the **Collembola** (Figure 4) are generally considered to have aquatic members, but even these aquatic members typically live out of the water during part of their lives (Thorp & Covich 1991; Ward 1992). Since most of the aquatic insects live in the water in immature stages, an understanding of these stages is necessary to understand fully how bryophytes are so important for them.

Danks (1991) points out that we can understand insect life cycle adaptations best by understanding the options. These include the choices (evolutionarily) to develop or to enter **diapause** (period of suspended development) and to grow rapidly or grow slowly. These developmental options respond to photoperiod and temperature, among other things (Danks 1991; Zwick 1996). Because of dependency on these cues, eggs of some stoneflies are able to remain in the sediments for years, providing a "seed bank" (Zwick 1996). The choices that have been programmed into the life cycle impact the life span of the insect.

Eggs (Figure 8) are an important stage for insects with a terrestrial adult stage and aquatic immature stage(s). The term egg is used somewhat loosely, referring to both the unfertilized egg and the embryonic stage that remains within the egg "shell," indicated herein as **egg/embryo**. Most of these insects lay their eggs in the water, so a substrate that anchors and protects them from both flowing water and predation is important. Even such free-swimming insects as the dragonfly *Sympetrum* (Figure 11) in the **Odonata** sometimes lay their eggs in plates on moss



growths, securing the eggs and hatchlings (Figure 12) (Wesenberg-Lund 1943).



Figure 11. *Sympetrum sanguineum* mating. Photo by Qartl through Creative Commons.



Figure 12. *Sympetrum striolatum* egg-laying among grasses and mosses. Photo by Hugh Venables through Creative Commons.

Some of the aquatic insects live in immature stages in the water for more than one year (Danks 1992; Ulfstrand 1968b). These extended lives may result from slow

development, long or repeated dormancy, or adults that live a long time (Danks 1991, 1992). Others, in particular the mayflies (**Ephemeroptera**), may live for only one day as adults (Figure 13), just long enough to mate and lay eggs, but can spend about one year in the naiad stage in the water. The long life cycles are usually coupled with several factors, including cold, unpredictable temperatures, unreliable or low quality food supplies, natural enemies, and large adult size. Life cycle traits relate strongly to the predictability of the environment where the insect lives and the environmental signals that are provided (Danks 2006). But Danks cautions that much more detail is needed to understand these life cycle patterns in insects.



Figure 13. *Callibaetis ferrugineus* subimago. Photo by Jason Neuswanger, with permission.

Radford and Hartland-Rowe (1971) examined the life cycles of stream insects from Alberta, Canada. Several of these represent genera [*Nemoura*/*Zapada*/*Prostoia* (Figure 14), *Ephemerella*/*Drunella* (Figure 15)] that are common among bryophytes. Of these, *Prostoia* (= *Nemoura*) *besametsa* (see Figure 16) and *Drunella* (= *Ephemerella*) *coloradensis* (Figure 17) are characterized as fast seasonal types. But in the same family, *Zapada* (= *Nemoura*) *cinctipes* (Figure 18), *Z. columbiana* (Figure 19), *Z. oregonensis* (Figure 20-Figure 21), and *Drunella doddsii* (Figure 22) are slow seasonal types. None of these species has more than one brood per year except *Zapada cinctipes*, which has two. Temperature is important in determining growth rate in these species.



Figure 14. *Nemoura* sp. naiad, a genus with both fast and slow development. Photo by Bob Henricks, with permission.





Figure 15. *Ephemerella invaria* naiad, a genus with both fast and slow development. Photo by Bob Henricks, with permission.



Figure 16. *Prostoia* naiad, a common bryophyte dweller. Photo by Jason Neuswanger, with permission.



Figure 17. *Drunella coloradensis* naiad, having a fast seasonal type of development. Photo by Bob Henricks, with permission.



Figure 18. *Zapada cinctipes* naiad. Photo by Bob Armstrong, with permission.



Figure 19. *Zapada columbiana* adult on snow, emerging in winter. Photo by Jason Neuswanger, with permission.



Figure 20. *Zapada oregonensis* naiad showing gills. Photo by Jim Moore, through Creative Commons.



Figure 21. *Zapada oregonensis* adult. Photo by Jim Moore, through Creative Commons.





Figure 22. *Drunella doddsii* naiad, having a slow seasonal type of development. Photo by Bob Henricks, with permission.

Since insects have little tolerance for low temperatures (Dunman *et al.* 1991; Moore & Lee 1991), they must spend winter in a way that avoids the dangers of freezing (Ramløv 2000), as will be discussed in more detail below. It is this need to avoid freezing that forces some insects to spend part of their lives in the water. Bryophytes provide a habitat that helps them to cope with this watery habitat.

As Danks (1991) points out, the life cycle strategies provide options that facilitate survival: develop or enter diapause; grow rapidly or grow slowly. These are typically under the control of such environmental parameters as temperature and photoperiod.

### Life Cycle Cues

As already stressed, changes in life cycle phases are often necessary to survive changing weather conditions as the seasons change. Danks (1999) pointed out that life cycles are influenced by climate severity, seasonality, unpredictability, and variability. Some insects solve the unpredictability and variability problems by having flexible life cycles. These modifications can be determined by factors such as food availability and temperature. Danks (1991) points out that various stages in the life cycle are used in combination to adapt the insects to the changes of the seasons in nature.

In cold environments, some of the **Chironomidae** (*Diamesa incallida*; Figure 23) may produce 8-10 generations in a single year, with egg-laying occurring throughout the year (Nolte & Hoffmann 1992). *Diamesa incallida* is a hot-spring-dwelling midge that lives in water at 76-80°C, a community where we are not likely to find bryophytes, but it demonstrates the role of temperature and the wide range of capabilities in a family that is common among bryophytes. Some Arctic **Chironomidae** solve the problem of finding a sexually mature mate by negating the need for mating and being **parthenogenetic** (producing offspring without fertilization) (Langton 1998).



Figure 23. *Diamesa* (Diptera) pupal exuvium, a genus that may produce 8-10 generations in a single year. Photo by Will Bouchard, with permission.

Shama and Robinson (2009) demonstrated that an alpine caddisfly (*Allogamus uncatus*, a bryophyte dweller) in Switzerland responded to late season photoperiod cues by accelerating development, but the species showed adaptive plasticity in response to season length, making responses different among populations with only small geographic differences. Furthermore, the responses of the two sexes can differ (Shama & Robinson 2006).

On the other hand, the bryophyte-dwelling caddisfly *Limnephilus externus* (Figure 24-Figure 26) did not make developmental adjustments in response to diet supplementation, although it did grow to a larger size (Jannot *et al.* 2008). Furthermore, this caddisfly was unable to adjust to pond drying, responding by reduced growth rates and delayed development. This indicates the danger of an unpredictable environment for the aquatic insects.



Figure 24. *Limnephilus externus* larva in case. Photo by Wendy Brown <Gunnison Insects>, with permission.



Figure 25. *Limnephilus externus* adult, a caddisfly that does not adjust its development in response to food supplements. Photo by Jason Neuswanger, with permission.





Figure 26. *Limnephilus externus* larva showing abdominal gills. Photo by Wendy Brown <Gunnison Insects>, with permission.

In unpredictable or unstable environments, flexibility in the life cycle is important (Brittain & Saltveit 1989). Knispel *et al.* (2006) found that the bryophyte-dwelling mayfly *Baetis alpinus* (Figure 27) in the Swiss floodplains has synchronous egg development with high hatching success. By developing faster in warmer habitats it is able to hatch when conditions are favorable in the autumn. Long development time and delayed hatching permit success in unpredictable habitats in the cold glacial conditions. The mayfly *Rhithrogena nivata* (see Figure 28) has a long incubation period; the timing of hatching and glacial discharge conditions determine the success of development. This plasticity permits it to live in the very unstable, cold habitats that are limiting to other species.



Figure 27. *Baetis alpinus* naiad, a mayfly with synchronous egg development that promotes high hatching success. Photo by Andrea Mogliotti, with permission.

Many insects have developmental cues similar to those of plants. These include degree-days (calculated by taking the average of the daily maximum and minimum temperatures compared to a base temperature necessary for growth by the species). As in many plants, degree days may be important in determining the rate of development. For example, the mayfly *Leptophlebia cupida* (Figure 29) in the Bigoray River, Alberta, Canada, has only one reproductive period each year (Clifford *et al.* 1979). Clifford *et al.* (1979) found that degree days of water

temperature was more important than number of days for development, with 34 instars being produced in the laboratory at 20°C. That number is most likely plastic in response to environmental conditions.



Figure 28. *Rhithrogena impersonata* naiad, a genus in which some species have life cycle plasticity that depends on local weather. Photo by Donald S. Chandler, with permission.



Figure 29. *Leptophlebia cupida* naiad, a species with only one reproductive cycle per year. Photo by Jason Neuswanger, with permission.

For aquatic insects, the temperatures are much more tempered than in the terrestrial environment. In a study of 95 aquatic species, Pritchard *et al.* (1996) found that only 4 of 92 possible comparisons among **congenerics** (members of same genus) demonstrated significant differences in degree of cold adaptation. All **Odonata** (damselflies and dragonflies), 71% of **Diptera** (true flies), and 81% of **Ephemeroptera** (mayflies) had significant slopes indicating that they were warm adapted. They suggested that the **Plecoptera** are cold-adapted species that may use the egg stage to survive when the temperatures are too high.

In the stonefly family **Leuctridae**, commonly represented among bryophytes, the length of the naiad stage depends on the temperature. In *Leuctra ferruginea* (Figure 30) those individuals living in the coolest streams required two years for their life cycle, whereas those in the warmest waters were able to complete the life cycle in one

year (Harper 1973). The **Leuctridae** (Figure 30) and **Nemouridae** (Figure 14) are both common at the cooler upstream stations in Southern Ontario. Six species of the stonefly **Isogenoides** (Figure 31) from Colorado, USA, a genus also known from mosses, varied in hatching time both among the species and within some species (Sandberg & Stewart 2004). In one species the eggs hatched over an extended period of time, stopped hatching for the winter, then resumed hatching in May-June the following year. Some eggs even survived and hatched two years later. In one species, a summer diapause was needed before the eggs would hatch. Members of the genus required three months to four years before hatching.



Figure 30. *Leuctra ferruginea* naiad, a stonefly that has modified its life cycle to suit the climatic conditions. Photo by Tom Murray at BugGuide.



Figure 31. *Isogenoides hansonii* naiad, in a genus with moss-dwelling members in which life cycles vary both between and within species. Photo by Bob Henricks, with permission.

### Temperature Relations

As already noted, temperature plays an important role in determining when life cycle stages occur. Freezing, desiccation, and anoxia are all lethal among aquatic insects, from egg to adult (Lencioni 2004). When in the aquatic habitat, these three factors are related, with ice preventing the renewal of oxygen, and ice crystals drawing water from the cells, causing desiccation. Some of the aquatic insects enter **diapause** during winter. This usually requires storage of food as glycogen and lipids, hormonal control, and depression or suppression of oxidative metabolism with mitochondrial degradation.

But the mosses themselves seem to present a relatively constant temperature. Thorup (1963) considered the

temperature among mosses in springs to be so constant that it would not provide the developmental temperature point needed to trigger changes in stages. Correlated with the moss habitats in springs was an insect life cycle with only one generation per year.

### Overwintering

Duman *et al.* (1991) defined two physiological mechanisms by which insects survive winter: freeze tolerance and freeze avoidance or freeze resistance (see also Ramløv 2000). Aquatic insects have only limited ability to survive at temperatures below freezing (Moore & Lee 1991). They can supercool to only  $-3$  to  $-7^{\circ}\text{C}$  and only some members in the order **Diptera** are known to be freeze tolerant. The adults seem to be somewhat more cold tolerant. Thus this is a group of insects for which aquatic habitats that do not freeze provide them with an escape to suitable temperatures for the winter. What is fascinating is the plasticity of their responses. Duman *et al.* (1991) found that not only do different populations of the same species exhibit different overwintering mechanisms, but that even the same population may change its overwintering mechanism from year to year.

Because of their need for warmer temperatures in immature stages than that needed by terrestrial insects, most of the aquatic insects spend their egg and immature stages in the water. In fact, warm-water insects avoid the freezing dangers of winter by surviving as eggs. This is particularly true for the blackflies (**Simuliidae**; Figure 51-Figure 53) (Hynes 1970).

Insects rarely spend their entire lives in the water, but some spend larval stages there, pupal stages on land, then return to the water as adults, as in many **Coleoptera** (beetles). Others, particularly some of the **Trichoptera** (caddisflies) overwinter as adults. In fact, some even emerge mid-winter in cold climates. And the adult stonefly *Zapada cinctipes* (**Nemouridae**; Figure 18) re-enters the water when air temperatures drop below freezing (Tozer 1979). However, the stream chironomid *Diamesa mendotae* (Diptera; Figure 32-Figure 33) does things quite differently – its freeze tolerance is actually greater in the larval (stream) stage (Figure 33). Although it has a larval super-cooling-point (SCP) temperature of  $-7.4^{\circ}\text{C}$  and pupal SCP of  $-9.1^{\circ}\text{C}$ , compared to  $-19.7^{\circ}\text{C}$  for the adults (Bouchard *et al.* 2006), the larvae of *D. mendotae* are freeze tolerant, with a lower lethal temperature (99% dead) of  $-25.4^{\circ}\text{C}$ ,  $\sim 10^{\circ}\text{C}$  lower than their minimum super cooling point ( $-15.6^{\circ}\text{C}$ ). They change from freeze tolerant as larvae to freeze intolerant as adults! Nevertheless, the adults are able to tolerate cold temperatures sufficiently to mate on the snow (Ferrington *et al.* 2010). Furthermore, they can survive under the snow for extended periods of time (Anderson *et al.* 2013).

The often moss-dwelling *Serratella ignita* (Figure 60) overwinters from late summer until late the next spring as an egg (Arnold & Macan 1969). On the other hand, the mayfly *Ameletus inopinatus* (Figure 34) and stonefly *Leuctra hippopus* (Figure 35), a stony bottom dweller, do the most developing in the naiad stage while their stream is iced over, at least in northern Sweden (Ulfstrand 1968b). The low temperatures slow, but usually do not stop, development and growth.





Figure 32. *Diamesa mendotae* adult on snow. Permission to reproduce given by Leonard Ferrington on behalf of the Chironomidae Research Group at the University of Minnesota.



Figure 33. *Diamesa mendotae* larvae alive in Petri dish after freezing. Permission to reproduce given by Leonard Ferrington on behalf of the Chironomidae Research Group at the University of Minnesota.



Figure 34. *Ameletus ludens* naiad, member of a genus where some species develop under the ice in streams. Photo by André Wagner, with permission.

It is interesting that in alpine streams that have snow cover for 6-9 months of the year, taxa richness and abundance of the insects seems to have no seasonal pattern. Nevertheless, the species composition differs significantly from summer to winter. Schütz *et al.* (2001) found two strategies for larval survival. The insects either had to be adapted to the extreme conditions of summer or avoid these by developing during the winter (typical of **Ephemeroptera** and **Plecoptera**).



Figure 35. *Leuctra hippopus*, a stonefly that develops in Sweden while the stream is iced over. Photo by Niels Sloth, with permission.

But ice is also a good insulator, so those insects living on the bottom of lakes and ponds are usually able to avoid lethal low temperatures there. Such insects as the **Chironomidae** (Figure 90) typically live in sediments where oxygen content is low. Cold water holds more oxygen, and since these organisms are adapted to low oxygen conditions, there is sufficient oxygen in the cold water. Some **Chironomidae** and **Trichoptera** (Figure 83) actually occur in ice and frozen sediment, as noted in a north Swedish river (Olsson 1981). Olsson found that 80-100% of these frozen insects survived thawing. **Chironomidae** survived exposure to  $-4^{\circ}\text{C}$  for five months. Danks and Oliver (1972a) found that in the Arctic **Chironomidae** that overwinter are mature larvae and are ready to emerge as soon as the winter season is over. They take advantage of the warm sun by emerging in the middle of the day when the water temperature is highest (Danks & Oliver 1972b).

It is interesting that **Plecoptera**, **Ephemeroptera**, **Trichoptera**, **Diptera**, and **Coleoptera** have all been recovered alive from **anchor ice** (submerged ice anchored to the bottom; Figure 36). Anchor ice can encase bryophytes as well, and when it breaks loose, it can take the entire patch of bryophytes with it. Hence, it would likewise take all the insect inhabitants as well, moving them downstream to a new location.

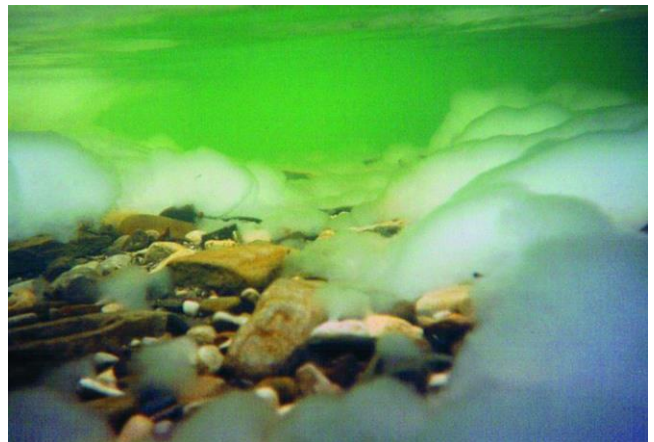


Figure 36. Anchor ice, Alberta, Canada, visible here as cloud-like mounds of ice attached to the rocks under water. Courtesy of Pacific Northwest National Laboratory.



## Structural

Hynes (1970) summarized the adaptations of stream insects to include flattening, streamlining, friction discs, close application to the surface of stones, and in some the presence of hydraulic suckers. But many of these adaptations pertain to a life on rocks or other relatively smooth substrate. Such characters as flattening, friction discs, close application to the surface, and hydraulic suckers are of little value among the chambers of a bryophyte mat. This leaves us with only one adaptation from his list, that of streamlining (Figure 37), present in the stoneflies [Plecoptera: **Leuctridae** (Figure 37), **Capniidae** (Figure 38), **Chloroperlidae** (Figure 39), and some **Gripopterygidae** (Figure 40)], and mayflies [Ephemeroptera: **Leptophlebiidae** (Figure 41) and **Baetidae** (Figure 45)] – all known from bryophytes. Others have retained the dorsi-ventral flattening, but it is better described as compressing (Figure 42) since these insects do not quite fit the definition of flat. And compression is useful among bryophytes. Other bryophyte adaptations include small size, attachment hooks, and gill covers or gills absent (Glime 1968).



Figure 39. **Chloroperlidae** naiad. Photo by Bob Henricks, with permission.



Figure 37. **Leuctra laura** naiad showing streamlining. Photo by Tom Murray at BugGuide, through Creative Commons.



Figure 40. **Zelandobius illiesi**, a stonefly naiad with streamlining. Photo by Stephen Moore, Landcare Research NZ, with permission.



Figure 38. **Allocapnia** sp. naiad showing streamlining. Photo by Bob Henricks, with permission.



Figure 41. **Paraleptophlebia mollis** naiad, a mayfly illustrating streamlining. Photo by Tom Murray through Creative Commons.





Figure 42. *Ephemerella* naiad showing dorsi-ventral compression. Photo by Bob Henricks, with permission.

Bryophyte-dwelling insects therefore do not necessarily have the same adaptations as stream insects in general. Streamlining helps, but does not need to be as severe. Steinmann (1907, in Muttkowski 1929) found that about 30% of the bryophyte-dwelling taxa were streamlined. But in the streams of the Appalachian Mountains, streamlining was not common (Glime 1994). For example, the common bryophyte-dwelling mayfly *Ephemerella* (Figure 42) is neither flattened nor streamlined (Arnold & Macan 1969), but has a shape more like a terrestrial insect – it is dorsiventrally compressed.

Small size is also an advantage and seems to be the most important characteristic of bryophyte dwellers. Bryophytes provide small spaces where invertebrates can hide, but these same small spaces limit the sizes of the organisms that can occur there. This explains why bryophytes tend to harbor small species and hatchling insects (Figure 43).



Figure 43. *Taeniopteryx* naiad on the edge of a Syracuse watch glass, demonstrating the small size of this bryophyte dweller. Photo by Bob Henricks, with permission.

Dudley (1988) suggested that while the complex structure of bryophytes might interfere with attachment by larger larvae, it reduces frequency of encounter between such predators and the small insect inhabitants. In the Appalachian, USA, streams 70% of the bryophyte dwellers were less than 6 mm long (Glime 1994). Egglishaw (1969) found that a higher proportion of smaller animals occurred on mosses than on stones or riffles. In *Leuctra inermis* (see Figure 37, Figure 44), *Baetis rhodani* (Figure 45), and *Isoperla grammatica* (Figure 46) it was the young (small) stages that occurred among the bryophytes.



Figure 44. *Leuctra inermis* adult, a species whose early naiad instars live among mosses in riffles. Photo by James K. Lindsey, with permission.

Frost (1942) remarked that because of the very young and thus small specimens, identification was both difficult and questionable, forcing identification to genus or subfamily only. Glime (1994) found that *Baetis* sp. was present among mosses (10 per gram) in summer, but were absent in later stages when the larger naiads were present among rocks in the stream bed. Others that moved out of the bryophytes when they got larger were the crane fly *Limonia* (Figure 47), stonefly *Taeniopteryx* (Figure 48), and caddisflies *Lepidostoma* (Figure 49) and *Neophylax* (Figure 50). Similar migration of older stages occurs in Europe (Thienemann 1912; Carpenter 1927; Egglishaw 1969).



Figure 45. *Baetis rhodani*, a mayfly that starts its life among bryophytes, but moves out as it grows larger. Photo by J. C. Schou through Creative Commons.



Figure 46. *Isoperla grammatica* naiad showing dorsiventral compression. Photo by Dragiša Savić, with permission.



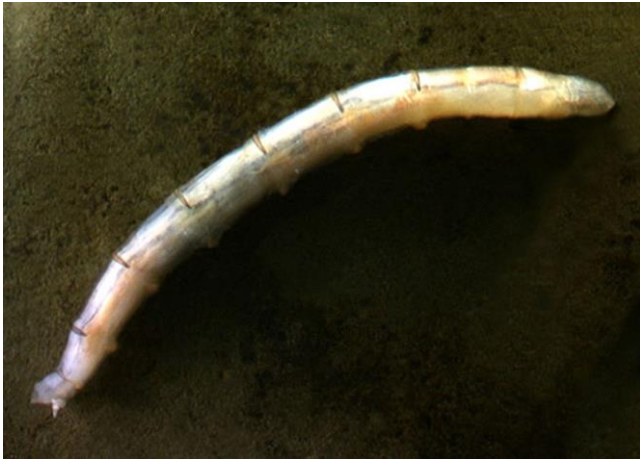


Figure 47. *Limonia* sp., an insect that lives among bryophytes until it gets too large; then it moves out. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 50. *Neophylax atlanta* larva and case, a caddisfly that moves from bryophytes to other substrates as it grows. Photo by Bob Henricks, with permission.



Figure 48. *Taeniopteryx* sp. naiad, a moss-dwelling stonefly that moves to substrates with more space when it gets larger. Photo by Bob Henricks, with permission.



Figure 49. *Lepidostoma* larva and case, a caddisfly that moves out of the bryophytes as it grows. Photo by Bob Henricks, with permission.

### Attachment

While torrents bring much-needed oxygen, they also are treacherous, dislodging the insects and sweeping them downstream. Black flies (**Simuliidae**; Figure 51-Figure 53) are among the best adapted of the aquatic insects for surviving this torrential onslaught, living on the upper surface of the bryophyte mats (Niesiolowski 1979). On both rocks and mosses, they are able to anchor themselves with a circle of hooks on the rear of the abdomen (Figure 51) (Arnold & Macan 1969). Furthermore, they manufacture a silken thread that they lay down on their substrate surface as an anchor. When they do become dislodged by chance or choice, they have a tether that prevents them from travelling too far and helps them to gain a "foothold" on their new downstream substrate. Those hooks, on both the abdomen and the single proleg foot (Figure 52), enable blackfly larvae to grab onto the silken mat (Figure 53) they have made. They are able to use these same two sets of hooks to move along their silken mat like inch worms.



Figure 51. **Simuliidae** larva showing anal hooks. Photo by Bob Henricks, with permission.





Figure 52. *Prosimulium mixtum* larva showing single proleg. Photo by Tom Murray at BugGuide, through Creative Commons.



Figure 55. *Rhyacophila fuscata* larva showing anal hooks that serve as anchors. Photo by Jason Neuswanger, with permission.



Figure 53. Simuliidae larvae on leaf where silken threads form a mat, aiding in attachment. Photo by Bob Henricks, with permission.

The net-spinning caddisflies (**Hydropsychidae**) accomplish anchorage by a pair of hooks on the posterior end (Figure 54), a modification of many caddisflies for pulling themselves into their cases. But among the free-living caddisflies like the **Hydropsychidae** and **Rhyacophilidae** [e.g. *Rhyacophila dorsalis* (Badcock 1949)], these hooks (Figure 55) serve as anchors among the bryophytes. Other insects have hooked claws that help them to clamber among the bryophytes, including the beetles (e.g. **Elmidae**, Figure 56) and some mayflies (e.g. **Ephemerellidae**, Figure 60) and stoneflies [e.g. *Nemoura* (Figure 57) and *Acroneuria* (Figure 58)]. Others, like the **Chironomidae**, achieve anchorage by nestling at the leaf bases (Figure 59) where little flow occurs.



Figure 54. *Hydropsyche* larva showing posterior prolegs with hooks that provide anchorage. Photo by Bob Henricks, with permission.



Figure 56. **Elmidae** adult showing clawed feet that help it climb among mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 57. *Nemoura* sp. naiad showing hooked claws. Photo by Bob Henricks, with permission.





Figure 58. *Acroneuria abnormis* naiad showing hooked claws. Photo by Tom Murray, through Creative Commons.

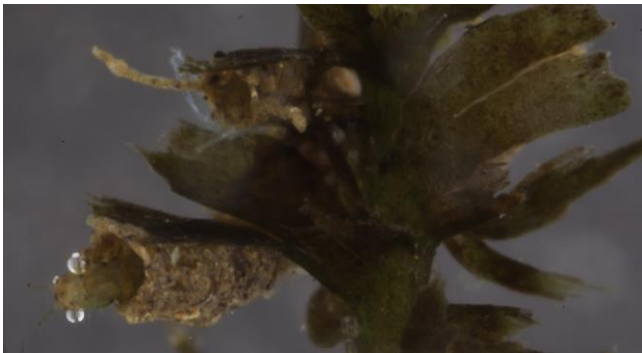


Figure 59. *Rheotanytarsus exiguus* (Chironomidae) group nestled in leaf bases. This species makes a tube where it lives. Photo by D. N. Bennett, with permission.

Hora (1930) and Ward (1992) suggested that backward pointing dorsal spines (Figure 60-Figure 64) of some moss dwellers, e.g. the **Gripopterygidae** (Figure 61), are adaptations to reduce chances of being swept downstream. Illies (1961) reported large dorsal spines on a moss-dwelling stonefly from Chile. Similar (but smaller) spines are known on the common moss-dwelling mayfly *Ephemerella ignita* (Figure 60; Hynes 1970). Even **Diptera** larvae [e.g. **Psychodidae** (Figure 62), **Tipulidae** (Figure 63-Figure 64)] can have backward-directed spines. But the tipulid larvae of *Phalacrocer* (Figure 63) and *Triogma* (Figure 64-Figure 65) have such projections and live mostly among semiaquatic mosses where there is no flow to dislodge them. This suggests the spines may serve either as camouflage or as trapping devices to prevent would-be predators from pulling them out of the moss mat.



Figure 60. *Serratella ignita* naiad showing spinelike structures on the dorsal side of the abdomen. Photo by J. C. Schou through Creative Commons.



Figure 61. *Zelandobius illiesi* (Gripopterygidae) showing backward-pointing dorsal spines. Photo by Stephen Moore at Landcare Research, NZ, with permission.



Figure 62. *Clogmia albipunctata* (Psychodidae) larva with backward pointing spines. Photo by Ashley Bradford through Creative Commons.



Figure 63. *Phalacrocer replicata* larva showing green color and projections that help to camouflage it among mosses. Photo from Wikimedia Commons.





Figure 64. *Triogma* larva showing backward pointing spines. This larva also has cryptic coloration that makes it difficult to detect among the bryophytes. Photo by Janice Glime.



Figure 67. *Serratella* gills showing gill covers and fibrillate gills on successive abdominal segments. Photo by Bob Henricks, with permission.



Figure 65. *Triogma trisulcata* larva among *Sphagnum* showing appendages that mimic moss leaves. Photo by Walter Pfliegler, with permission.

**Gill covers** help to keep silt from accumulating among the gills, since the mosses often reside where they collect large amounts of silt. The gill covers can also be used to fan the fills, hence moving the water and facilitating oxygen exchange. Gill covers are common among the **Ephemeroptera**, especially in the **Ephemerellidae** (Figure 66-Figure 67) and **Caenidae** (Figure 68).



Figure 68. *Caenis latipennis* naiad showing large gill covers over the dorsal abdomen. Photo by Donald S. Chandler, with permission.

## Behavioral

Behavior often permits organisms to change their locations, providing the best location available to them as the season changes and required resources are in new locations. Behavioral adaptations can help them capture prey, avoid being prey themselves, gain sufficient oxygen, avoid being swept away by the current, and escape cool or freezing temperatures.

Bryophytes provide a series of zones (Figure 69) that permit insects to live in the flow regime they require. As will be seen, oxygen can be a limiting factor, requiring some insects to live near the surface of the bryophyte where torrential waters trap oxygen from the air. Hence, these insects require a means of anchorage lest they themselves become part of the torrent. Others are well adapted to the low oxygen levels and live at the base where detritus accumulates and predators seldom venture. But it is advantageous that they can move about and seek the zone within the stream or lake and within the bryophyte community that best meets their needs.



Figure 66. *Drunella grandis* naiad showing raised gill covers and fimbriate gills. Photo by Bob Newell, with permission.

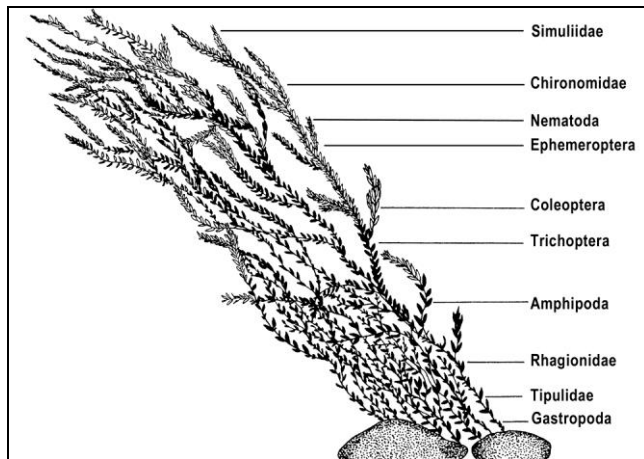


Figure 69. *Fontinalis* zonation of insects. Redrawn from Niesiolowski 1979.

Aquatic insects tend to avoid light, exhibiting negative phototaxis (Moon 1940; Shelford 1945). Mayflies, in particular, demonstrate a negative phototaxis, preferring darker locations (Wodsedalek 1911; Gros 1923; Percival & Whitehead 1926). This may account for the presence of some taxa among the darker spaces of mosses, particularly in rapid water where rock surfaces may be highly exposed to light. Others may avoid light to be less conspicuous to their prey. On the other hand, *Baetis harrisoni* (Figure 70) chose illuminated stones 112 times compared to 14 for shaded stones, exhibiting strong positive phototaxis (Hughes 1966).



Figure 70. *Baetis harrisoni* naiad, a mayfly that prefers illuminated stones. Photo by Helen James through Creative Commons.

Insects often escape adverse conditions in their environments by modifying the environments themselves. Such modifications may include making shelters (Figure 71), excavating, aggregating (Figure 53), forming colonies, and parental actions (Danks 2002). Although all of these actions may be found among aquatic insects, not all of these occur among those living among bryophytes. The bryophyte itself sometimes makes such actions as excavating and making shelters unnecessary. For example, several families of caseless caddisflies live among bryophytes. But the very tiny **Hydroptilidae** may take advantage of the bryophytes for case-building materials.



Figure 71. *Helicopsyche* case, made by the caddisfly as a shelter. Photo by Mike Quinn, through Creative Commons.

### Oxygen Conditions

Ponds can become quite anoxic in winter when the surface is frozen (Nagell & Brittain 1977). Streams are less likely to become anoxic, but within the bryophyte mat water can be quite quiet and oxygen can be used up quickly by decaying organisms. However, insects have a wide array of adaptations to help them through places and times of anoxia (Hoback & Stanley 2001). For example, 10 Arctic species of **Collembola** (springtails) are known to survive anoxia at 5°C for up to 36 days (Hodkinson & Bird 2004). The mayfly *Cloeon dipterum* (Figure 72) is able to survive 3-4 months in anoxic ponds, and naiads survived up to 155 days at 0°C in the lab (Nagell 1977).



Figure 72. *Cloeon dipterum*, a mayfly that can survive 3-4 months in anoxic pond water. Photo by Malcolm Storey, through Creative Commons.

As is obvious from previous studies, oxygen relations in the insects are dependent on temperature (Jacob & Walther 1981). More oxygen can dissolve at low temperatures. In fact, oxygen limitations due to temperature are so important that they set the thermal limits in at least some species of aquatic insects (Verberk & Bilton 2011). Furthermore, since smaller insects use less oxygen, large insects may have been an adaptation to excess oxygen in the Carboniferous Era (Verberk & Bilton 2011). Oxygen limitations may explain in part the presence of small insects among the bryophytes, whereas



the larger stages move to rock faces where flow is uninterrupted and able to replenish the oxygen more easily.

Knight and Gaufin (1966) measured oxygen consumption as a function of temperature in two stonefly naiads that associate with bryophytes: *Hesperoperla pacifica* (Figure 73) and *Pteronarcys californica* (Figure 74). These insects followed the general trend of consuming more oxygen at higher temperatures. This relationship is problematic because gasses are lost from the water at higher temperatures, thus limiting the most available oxygen to winter.



Figure 73. *Hesperoperla pacifica* with its pompom-like gills peeking out from the ventral thorax. Photo by Arlen Thomason, with permission.



Figure 74. *Pteronarcys californica*, probably the largest insect inhabitant of bryophytes. Photo by Bob Henricks, with permission.

Among the common bryophyte dwellers, the mayflies (**Ephemeroptera**) are the least tolerant of low oxygen (Gaufin *et al.* 1974), making them good indicator organisms. These are followed by stoneflies (**Plecoptera**), then caddisflies (**Trichoptera**), flies (**Diptera**), and damselflies (**Odonata**) in that order. Of course there are exceptions within the orders.

Insects living in low oxygen conditions may be adapted by developing enlarged respiratory organs (Figure 75) (Dodds & Hisaw 1924), including enlargement of tracheal gills (Figure 76) (Golubkov *et al.* 1992). Behavior can play an important role, with most species moving away from the anoxic sediments when oxygen becomes limiting (Kolar & Rahel 1993). But moving is not always a good choice because it can result in being swept into the current and usually means becoming more visible, hence being more obvious to predators. The movement itself attracts attention through the excellent vision in the well developed eyes of other arthropods and fish.

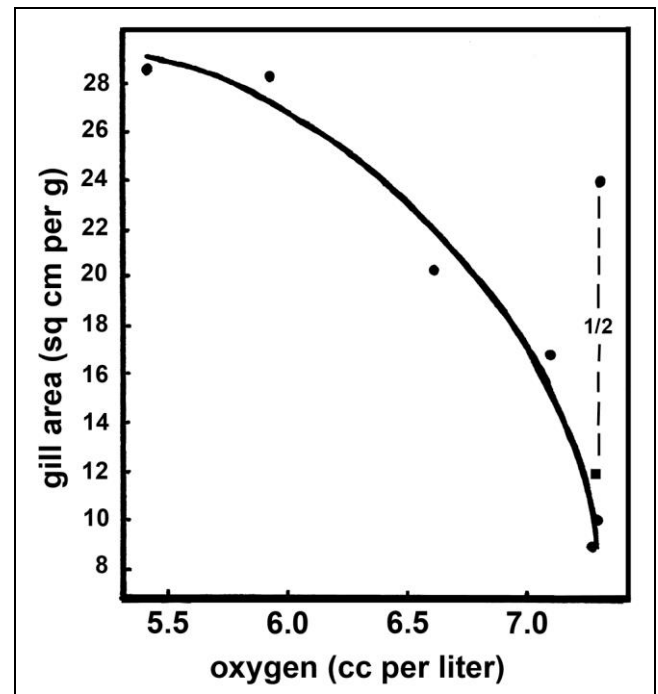


Figure 75. Relationship of gill size in seven species of **Ephemeroptera** to oxygen availability in aquatic systems. The outlier species on the right is the genus *Iron*, a genus for which the gills form a suction cup, preventing one side of the gills from functioning in oxygen uptake. Its position when only half the area is used is shown by the square at the base of the dotted line on the right. Redrawn from Dodds & Hisaw 1924.

Gills are a common adaptation to low oxygen, especially in **Ephemeroptera** (Figure 76), **Plecoptera** (Figure 77-Figure 79), and **Trichoptera** (Figure 80). These are placed in almost every position (*e.g.* Figure 78), depending on the genus or family, and are useful taxonomic characters in some groups. But they also tend to be protected, between legs or under gill covers. Others have cutaneous breathing – providing the expanse of the insect's surface and avoiding the danger of collecting sediments.



Figure 76. *Leptophlebia nebulosa* showing abdominal (tracheal) gills. Photo by Don S. Chandler, with permission.



Figure 77. *Nemoura* sp. naiad showing clusters of white thoracic gills at the "neck." Photo by Bob Henricks, with permission.

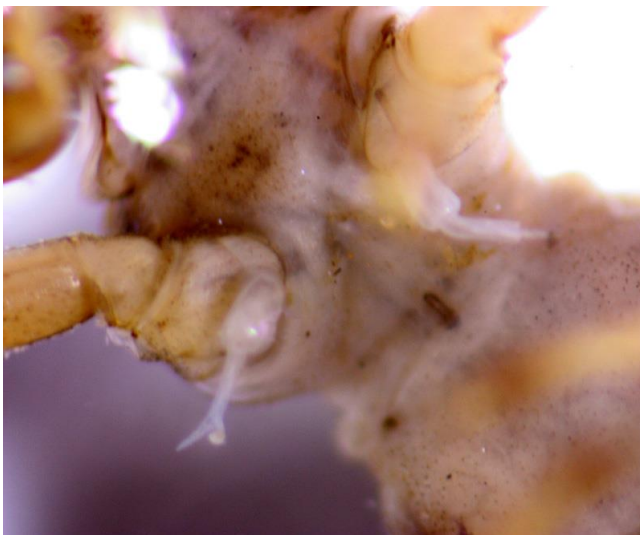


Figure 78. Coxal gills on a winter stonefly. Photo by Bob Henricks, with permission.



Figure 79. *Acroneuria carolinensis* naiad showing gills on the ventral thorax. Photo by Tom Murray, through Creative Commons.



Figure 80. *Hydropsyche* sp. larva showing gills on ventral side. Photo by Bob Henricks, with permission.

As early as 1907, Babak and Foustka concluded that as the oxygen concentration in the water decreased, movement of the gills of mayflies increased. Dodds and Hisaw (1924) showed a relationship between gill area and oxygen concentration in mayflies. But in the mayfly *Baetis* (Figure 45, Figure 70) used for testing, the gills never beat and it seems that they do not use their gills for oxygen consumption in the range of 5.0 to 8.0 cc L<sup>-1</sup> (Wingfield 1939). Rather, these mayflies live in rapid streams where oxygen concentrations are usually above 4 cc L<sup>-1</sup> and rapid flow keeps fresh, oxygenated water flowing over the gills. Under these conditions their cuticular respiration is sufficient. Macan (1962) reported on the work of Ambühl (1959). He found that *Baetis vernus* was scarce when the current speed was below 10 cm sec<sup>-1</sup> and increased in relative numbers up to 40 cm sec<sup>-1</sup>. *Ephemerella ignita* (Figure 60) was most common at current speeds of 10-30 cm sec<sup>-1</sup>.

Movements of another type – undulating the body (Figure 81) or fanning the gills (Figure 82) – can increase the rate of oxygen movement across the gills. Undulations typically begin as oxygen levels are low and are also used for swimming, a second way to gain more oxygen. These undulations are easily seen when high-oxygen-requiring mayflies are brought to the lab and put in quiet water. **Ephemerellidae** species accomplish water movement over their gills by moving the gill covers (Figure 82) up and down, fanning the gills. **Trichoptera** (caddisflies) are able to pump water through their cases (Figure 83) to renew oxygen. Humps and projections maintain space between the larva and its case, permitting water (and oxygen)



movement through the case. But these activities require energy and the insects cannot sustain prolonged use of these behaviors (Hynes 1970).



Figure 81. *Baetis tricaudatus* naiad showing the tail and abdomen flipped up in an undulation. Photo by Bob Henricks, with permission.



Figure 82. *Ephemerella subvaria* naiad showing four gill covers on each side. Photo by Tom Murray, through Creative Commons.



Figure 83. *Limnephilus* sp. showing spacer hump just behind the thorax. Photo by Jason Neuswanger, with permission.

Most of the bryophyte dwellers do not carry oxygen in the air bubble of a **plastron** (Figure 84) or other form of

bubble (Figure 85), as done by a number of free-swimming species. However, the plastron mechanism is useful to some of the **Elmidae** (Figure 84), tiny beetles that clamber among the bryophytes (Arnold & Macan 1969). The plastron is much like a diving bell. The insect traps a bubble of air and carries it beneath the water surface. As the insect breathes, it exchanges its  $\text{CO}_2$  for the  $\text{O}_2$  in the plastron. Oxygen in the water will diffuse into the bubble as the oxygen is depleted, but as the nitrogen leaves the bubble, the bubble shrinks. The same mechanism applies to other types of bubbles such as the one in Figure 85. Eventually the concentration of oxygen in the bubble is too low and the insect must resurface to grab another bubble, or grab one from a photosynthesizing plant, including bryophytes. The collection of bubbles on plants under water is known as **pearling** (Figure 86).



Figure 84. *Stenelmis crenata* showing plastron (white area under ventral side). Photo by M. J. Hatfield through Creative Commons.



Figure 85. *Lancetes angusticollis* adult from South Georgia clinging to moss. Note the anal air bubble used like a diving bell. Photo by Roger S. Key, through Creative Commons.

### Obtaining Food

Feeding strategies include shredders, gatherers, scrapers, and detritus feeders. Venturing away from the protective bryophyte substrate is dangerous because the insects can easily be swept away by the current in streams. Thus, it is not any surprise that many of the insects have adapted strategies that permit them to obtain food without venturing away from their safe site. Many are detritus

feeders, and if they have adaptations to get enough oxygen, they can live in the silt or sand. Others such as the net-spinning caddisflies (Figure 87) and the blackflies (Figure 88-Figure 89) trap their food as it flows by them. The very effective anchorage permits the **Simuliidae** (blackflies) to hang from the rear and expose the head fans (Figure 89) into the current to trap organic particles, including diatoms, for food. Some eat their surrounding homes – the bryophytes.



Figure 86. *Riccia fluitans* with pearling. Photo through Creative Commons.

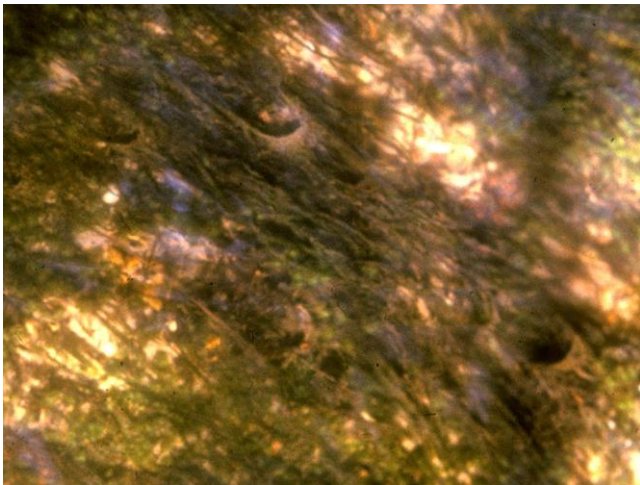


Figure 87. *Cheumatopsyche* nets on *Fontinalis*, trapping detritus and algae that flow by. Photo by Janice Glime.

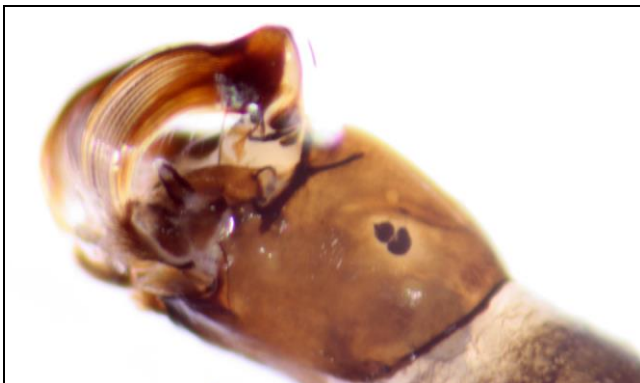


Figure 88. Simuliidae larva head fans closed. Photo by Bob Henricks, with permission.



Figure 89. **Simuliidae** larva showing head fans that are used to capture food. Photo by Bob Henricks.

Others, including some of the net-spinning **Hydropsychidae** (Figure 87), let the bryophytes do the trapping and eat the periphyton and detritus within the bryophyte mat. I base this assumption on finding many more larvae than nets among the mosses. The **Chironomidae** (Figure 90) live in leaf bases where detrital matter accumulates, obtaining both protection and food. In any case, the diet of the aquatic stage is usually quite different from that of the adult.

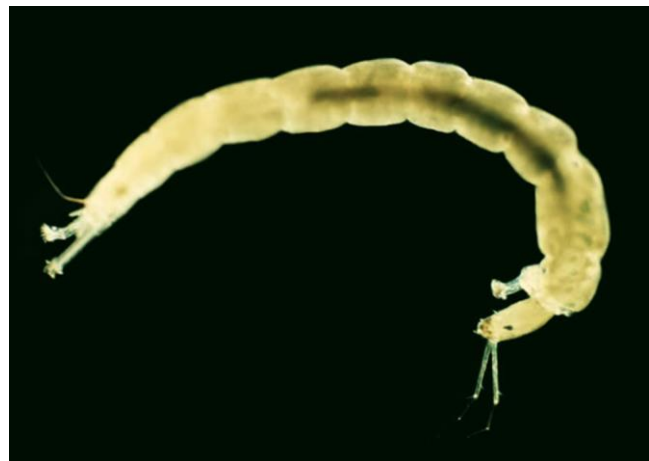


Figure 90. *Coryneura* sp. (**Chironomidae**). Photo by Stephen Moore, Landcare Research, NZ, with permission.

## Who Lives There?

Aquatic bryophytes in mountain streams typically are replete with insects, crawling about and dining on the detritus and algae in the milieu. They find themselves safely out of the torrent above and tucked away from the view of fish and other predators. It seems like they should have a pretty cushy life.

When I began my studies on insects living among bryophytes in Appalachian Mountain, USA, streams, few studies were available for comparison, and most of those



were from Europe. Like the development of keys for bryophytes, the development of keys for aquatic insects lagged way behind what was needed. To further complicate the problem, many of the insects had been described from adults, but studies to link the immature aquatic stages to their adults were lacking for many. It was the insect version of the early *Takakia* classification problem.

As I delved into the many more recent papers to prepare this chapter, I found many unfamiliar names of genera, only to discover that those familiar genera from nearly 50 years ago had gone through reclassification and were now represented under multiple new names, especially at the generic level. To further complicate these changes in generic concepts, the insects, like the bryophytes, comprise many microspecies. Limited dispersal distances for short-lived adult stages, mountain and land barriers, and disconnected stream or lake systems all contributed to the isolation needed for development of differences in physiology, behavior, phenology, and morphology (see for example Hughes *et al.* 1999; Monaghan *et al.* 2002). As bryologists we are well aware of these problems in classifying things separated by great distances, but for these insects the microspecies differences can be manifest over much shorter distances, a phenomenon that has been recognized in some aquatic bryophytes as well (Glime 1987; Shaw & Allen 2000). Nevertheless, there are lessons to learn from the orders, families, and even the genera as we examine who lives among the bryophytes – and why.

Drozd *et al.* (2009) used pitfall traps to compare invertebrate inhabitants related to bryophytes in the mountain areas (384-1200 m asl) of the Czech Republic. In most cases, the **Collembola** were the most abundant group except for the high number of ants at Podolánky. The numbers differed by bryophyte and moisture level (Figure 92). Insects were highest in the dry litter control (within 2

m of moss area). The lowest numbers were in wet *Sphagnum fallax* (Figure 91).



Figure 91. *Sphagnum fallax* with capsules, the species with the lowest number of **Collembola** among bryophytes in the mountainous areas of the Czech Republic. David T. Holyoak, with permission.

Drozd and coworkers (2009) considered several caveats in interpreting their results. Some of the invertebrates move about little and would therefore be poorly represented in the pitfall traps. Others that do move about would move easily between the bryophytes and litter, possibly only passing over the bryophytes in their search for food. Others may reside among the bryophytes as transient visitors, seeking escape from a predator or avoiding the desiccation common in more open areas, but returning to the litter habitat when that environment was safe. In any case, insects that met all their needs within the bryophyte mat would be under-represented in the pitfall traps.

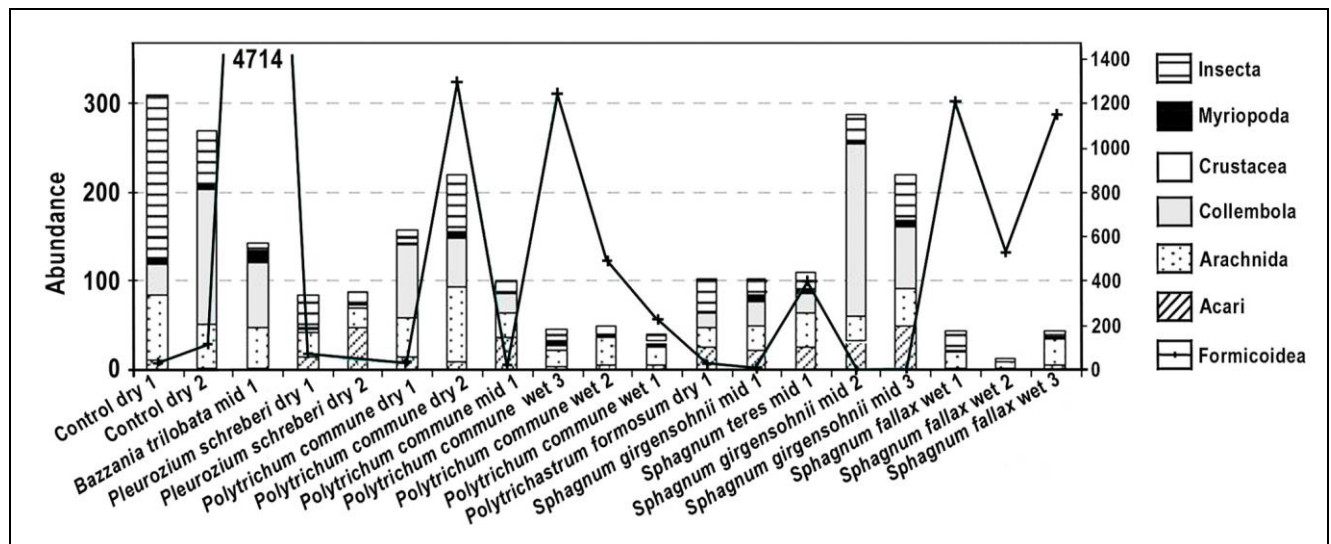


Figure 92. Abundance of taxonomical groups in pitfall traps associated with several species of bryophytes in dry, moist, and wet conditions at five locations in mountains of the Czech Republic. The scale at right is for ant data (**Formicoidea**) from Podolánky. Redrawn from Drozd *et al.* 2009. Controls are litter areas

The insects found among the mosses in streams are mostly **Ephemeroptera** (mayflies), **Plecoptera** (stoneflies), **Trichoptera** (caddisflies), **Diptera** (flies), and

**Coleoptera** (beetles) (Needham & Christenson 1927; Wesenberg-Lund 1943; Cowie & Winterbourn 1979; Glime 1994; Gislason *et al.* 2001). But moving about



among stems and leaves of mosses is not easy for the weak-legged or swimming insects in the small spaces. Hence, as already noted, most of the inhabitants are small (Thienemann 1912; Glime 1994; Amos 1999; Drazina *et al.* 2011). This also means that young, immature naiads of **Ephemeroptera** and **Plecoptera** are common (Stern & Stern 1969).

Many species overwinter as eggs on the mosses, then begin their immature lives there. Among the **Diptera**, *Dicranota* (Figure 93), *Atherix* (Figure 94), and *Simulium* (Figure 51-Figure 53) are common at this time; likewise, young **Elmidae** (larvae; Figure 95) are common among the mosses (Thienemann 1912).



Figure 93. *Dicranota* larva, a common stream moss inhabitant. Photo by Tom Murray, through Creative Commons.



Figure 94. *Atherix* sp. larva, a common dweller among stream bryophytes. Photo by Jason Neuswanger, with permission.



Figure 95. **Elmidae** larva, a common beetle larva among stream bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

In a New Zealand stream, Cowie and Winterbourn (1979) found 44 species of invertebrates, mainly immature stages of insects. The moss *Acrophyllum* sp. (Figure 96) hosted the stonefly *Austroperla cyrene* (Figure 97), a species of beetle in the **Helodidae** (Figure 98), and a triclad, *Neppia montana* (Figure 99); the moss *Fissidens* sp. (Figure 100) hosted the stonefly *Zelandoperla fenestrata* (see Figure 101), the caddisfly *Zelolessica cheira* (Figure 102), a fly in the family **Empididae** (Figure 103), and several species of midges (**Chironomidae**; Figure 90); . The moss *Cratoneuropsis* (Figure 104) had only one common taxon, a terrestrial isopod, *Styloniscus otakensis*, suggesting that the streamside *Cratoneuropsis* habitat is more terrestrial than aquatic. In addition to water saturation and flow rates, the ability of mosses to trap detritus was important in determining invertebrate inhabitants.



Figure 96. *Acrophyllum quadrifarium* from New Zealand, home to beetles in **Helodidae**. Photo by Bill & Nancy Malcolm, with permission.



Figure 97. *Austroperla cyrene* from NZ. Photo by Steve Pawson, permission pending.



Figure 98. **Helodidae** adult, member of a family that lives among leaves of the moss *Acrophyllum* sp. Photo from <www.pybio.org>, with permission.





Figure 99. *Neppia*, an inhabitant of the moss *Acrophyllum* sp. Photo by Stephen Moore, Landcare Research, NZ., with permission



Figure 100. *Fissidens fontanus* with Amano shrimp in an aquarium. Photo through Creative Commons.



Figure 101. *Zelandoperla* sp., an inhabitant of *Fissidens* in New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.

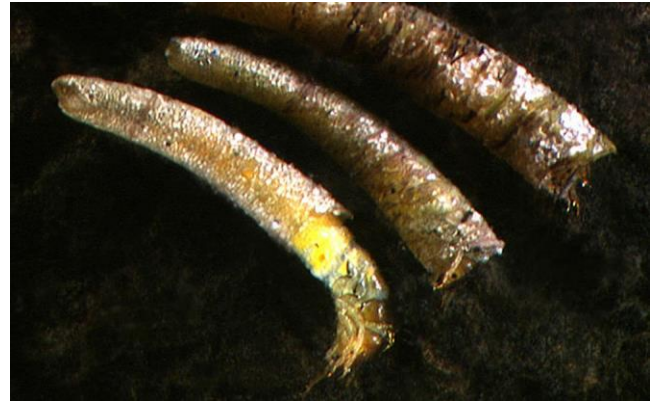


Figure 102. *Zelolessica* sp., an inhabitant of aquatic *Fissidens* in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 103. **Empididae** larva, an inhabitant of aquatic *Fissidens* in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 104. *Cratoneuropsis relaxa*, in a genus that commonly houses isopods but few insects in New Zealand. Photo by Tom Thekathyl, with permission.

Suren (1988) examined faunal assemblages in New Zealand alpine streams, with the stoneflies (**Plecoptera**) *Zelandoperla* (Figure 101) and *Zelandobius* (Figure 105) and midge larvae (**Chironomidae**; Figure 90) being dominant. The mosses supported 5-15 times as many invertebrates as did the rocky habitats. In addition to these dominant insects, several non-insect invertebrates were dominant.





Figure 105. *Zelandobius illiesi*, a stonefly genus that is common among alpine stream mosses in New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.

One of the interesting questions about bryophyte fauna is whether any species has a unique fauna. So far we have seen little specificity among the other invertebrates. Nevertheless, differences may exist dependent upon the niches of the bryophytes themselves. Some bryophytes occupy fast flow, some occupy areas where they spend part of the year above water, some are deep, and certainly differences exist among growth forms that create differences in the protection they afford. And some **Trichoptera** use liverworts or mosses to construct their cases, forcing them to live with certain species. Coinciding with these differences are the kinds of food the bryophyte habitats provide, again affecting who can survive there.

Paavola (2003) examined the concordance among the macroinvertebrates, bryophytes, and fish to look for possible **surrogates** to describe the system and its state of health. **Surrogates** are groups of organisms that can be used to assess suitability of a habitat for another group of organisms such as fish. When considered across drainage systems, there was strong concordance, but within a single river system that concordance was weak.

Bryophyte locations in the Paavola (2003) study were mainly related to nutrient levels and in-stream complexity, whereas macroinvertebrates correlated with stream size and fish correlated with oxygen levels, depth, and substrate size. But macroinvertebrates also relate to in-stream complexity (Allan 1975; Hart 1978; Trush 1979; Wise & Molles 1979; Williams 1980; Vinson & Hawkins 1998) and to substrate texture (Glime & Clemons 1972). And bryophytes add to that complexity. Some of the genera that inhabit bryophytes are also common in leaf packs – a substrate that provides cover and detritus for food. These include *Baetis* (Figure 45), *Leuctra* (Figure 30), and **Chironomidae** (Figure 90) (Robinson *et al.* 1998).

Due to differences in growing season, ice-free season, winter severity, available food, and flow regime changes from year to year, the fauna assemblage can also change from year to year. This can result in the temporary disappearance of an entire species, or even an entire order (Milner *et al.* 2006). This disappearance is particularly true for **Plecoptera**. Channel stability is important in determining faunal stability, but a normally stable channel can suffer from heavy rains or flooding during snow melt.

And channel stability likewise determines the stability of bryophytes, hence playing a role in the bryophyte fauna.

In my study of the insects inhabiting the bryophytes of mid-Appalachian Mountain streams, I identified 141 species occurring among 10 species of bryophytes in 28 streams, and that does not include the species of the **Chironomidae** (Figure 90), which were identified only to family (Glime 1994). The smallest of the insects occurred on the leafy liverwort *Scapania undulata* (Figure 106) and the largest could be found on various species of *Fontinalis* (Figure 107). As in many other studies, the most abundant insects were midges (**Chironomidae**), the stoneflies *Leuctra* (Figure 30) and *Isoperla bilineata* (Figure 108), and the blackflies (*Simulium tuberosum*; Figure 109).



Figure 106. *Scapania undulata*, home for the smallest aquatic insects. Photo by Michael Lüth, with permission.



Figure 107. *Fontinalis antipyretica*, a large moss that houses the largest moss dwellers. Photo by Bernd Haynold Wikimedia Commons.



Figure 108. *Isoperla bilineata*, a common stream moss dweller in the Appalachian Mountains, USA. Photo by Bob Henricks, with permission.





Figure 109. *Simulium tuberosum*, a common inhabitant of bryophytes in Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

Heino and Korsu (2008) questioned the species-area concept in aquatic systems, examining rocks and bryophyte cover in two river sites. They found only a weak species-area relationship on stream stones. On the other hand, bryophyte biomass was important both in supporting species richness and in increasing number of individuals of stream macroinvertebrates. They suggested that cover was important in increasing number of individuals and that the species richness was a subsequent passive response. The bryophyte biomass can be expected to increase with time, whereas the area of stones will not. The mechanisms that promote these species-area relationships need to be demonstrated experimentally. These could involve food relationships, sampling methods, niche space, flood disturbance, predation refugia, or flow regime.

### Specificity

Many streams have only one dominant bryophyte, and others have the species intermingled. These conditions complicate any attempts to determine insect preference. Nevertheless, some specificity seems to exist, but keep in mind that it might be a preference of both insect and bryophyte for the same stream conditions. The caddisfly *Rhyacophila* cf. *invaria* (Figure 110) was present in 36% of the collections (Figure 118) of *Platyhypnidium riparioides* (Figure 111) in mid-Appalachian Mountain, USA, streams, but totally absent among *Hygroamblystegium fluviatile* (Figure 112), despite the frequent occurrence of these two mosses in the same streams, often on the same rocks (Glime 1994). *Rhyacophila carolina* (Figure 1) reached its greatest abundance in clumps of the leafy liverwort *Scapania undulata* (Figure 106; Figure 118).

Less distinct preferences occurred in the elm mid beetle larva *Optioservus* sp. (Figure 113; Figure 118) [36% of *Hygroamblystegium fluviatile* (Figure 112), 7% of *Platyhypnidium riparioides* (Figure 111)] (Glime 1994). The stonefly *Pteronarcys proteus* (Figure 114) occurred in 24% of the *H. fluviatile*, 7% of the *P. riparioides*, and never in any of the other species, including *Scapania undulata* (Figure 106), *Fontinalis dalecarlica* (Figure 115), and *Hygrohypnum* spp. (Figure 116) (Figure 118).



Figure 110. *Rhyacophila invaria* larva, a common free-living caddisfly among *Platyhypnidium riparioides* in Appalachian Mountain, USA, streams. Photo by Donald S. Chandler, with permission.



Figure 111. *Platyhypnidium riparioides*, a common moss in Appalachian Mountain, USA streams. Photo by David T. Holyoak, with permission.



Figure 112. *Hygroamblystegium fluviatile*, a common moss for insect fauna in Appalachian Mountain, USA, streams. Photo by Michael Lüth, with permission.





Figure 113. *Optioservus* sp., a common beetle larva among *Hygroamblystegium fluviatile* and *Platyhypnidium riparioides* in Appalachian Mountain, USA, streams. Photo by Arlo Pelegrin, with permission.



Figure 114. *Pteronarcys proteus*, a stonefly that seems to have some selection in bryophytes it will inhabit. Photo by Jason Neuswanger, with permission.



Figure 115. *Fontinalis dalecarlica*, a large moss but that did not house *Pteronarcys proteus* in Appalachian Mountain, USA, streams. Photo by Kristoffer Hylander, with permission.

The liverwort *Scapania undulata* (Figure 106) has a different form from that of any of the mosses. This flattened habit seems to favor the fast-water members of *Simuliidae*, with *Prosimulium hirtipes* (Figure 117) in

58% of the collections and *Simulium tuberosum* (Figure 109) in 75% of the collections (Figure 118) of this liverwort in mid-Appalachian Mountain, USA, streams (Glime 1994). But *S. tuberosum* also occurred in 78% of the *Fontinalis dalecarlica* (Figure 115) collections (Figure 118).



Figure 116. *Hygrohypnum luridum*, a moss that is not suitable habitat for the large *Pteronarcys* in the streams of the Appalachian Mountains, USA. Photo by Michael Lüth, with permission.



Figure 117. *Prosimulium hirtipes*, a common blackfly on the liverwort *Scapania undulata*. Photo by Janice Glime.

Diversity differs little among bryophyte species (Figure 119), although richness can be higher in the larger *Fontinalis* (Figure 115) species (Glime 1968, 1994). *Fontinalis* species are also the only ones that typically house larger insects. *Scapania* (Figure 106), on the other hand, housed the smallest insects in the Appalachian Mountains, USA, streams.



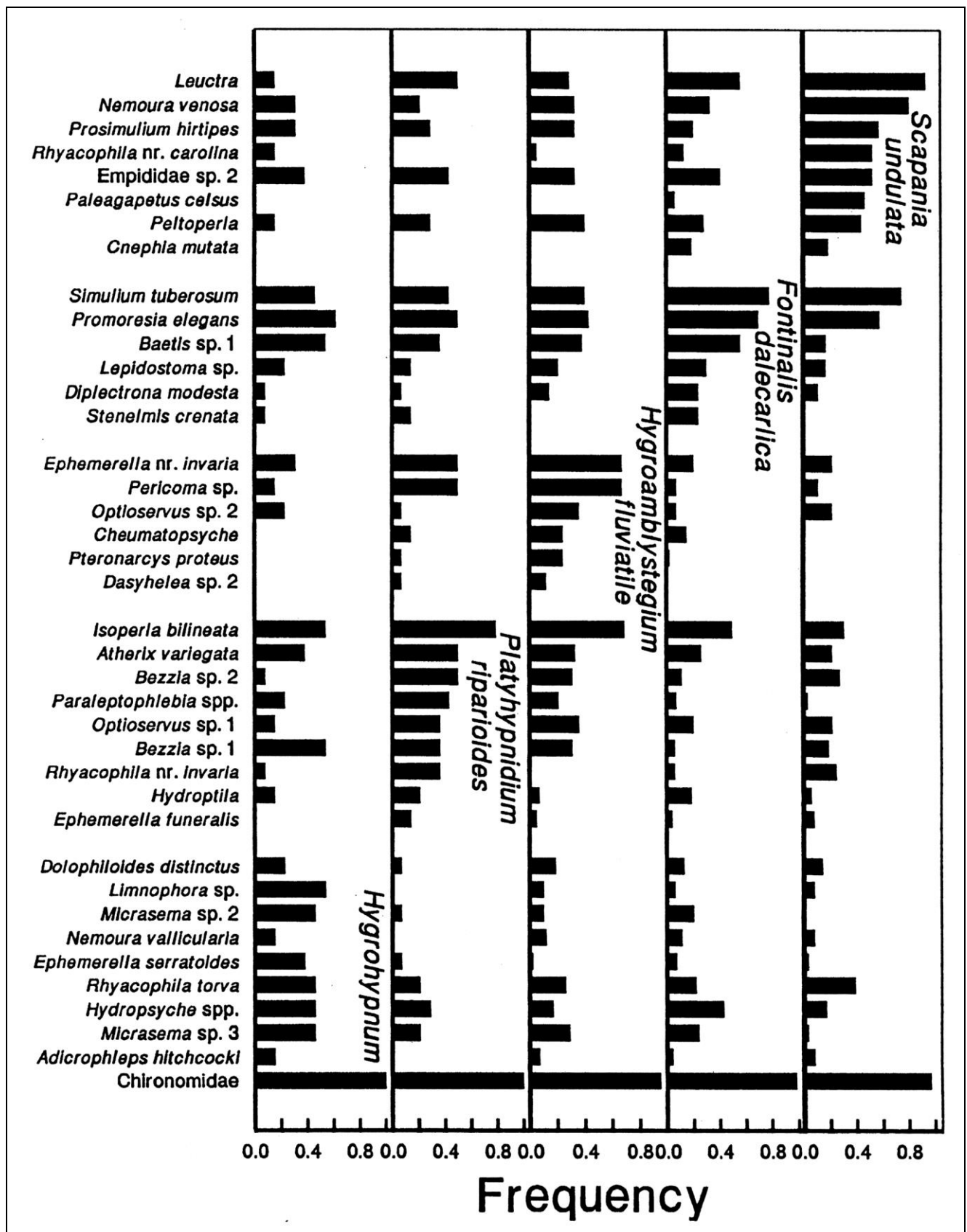


Figure 118. Frequencies of insects on five bryophyte species sampled in 28 streams in the middle Appalachian Mountains, USA. Only insects with at least 10% frequency on at least one species of bryophyte are included. The bryophyte name appears by the group of species that was most abundant on that bryophyte; the name applies to all groups in that frame. From Glime 1994.

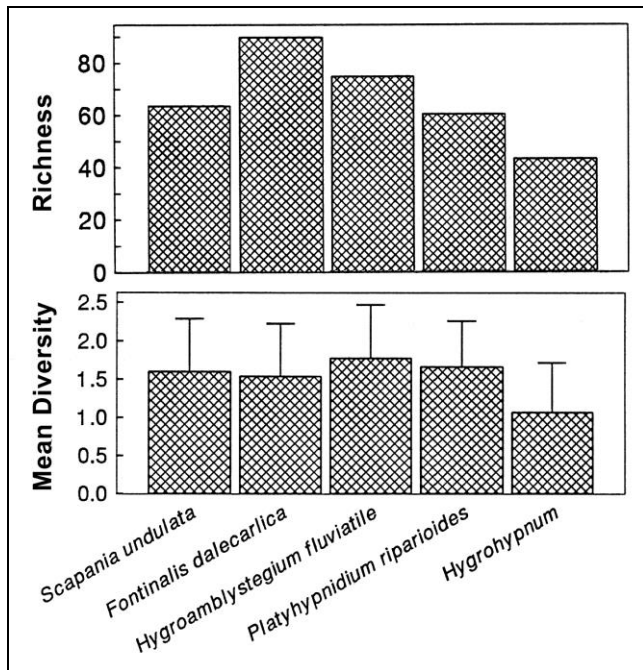


Figure 119. Comparison of mean insect richness and Shannon diversity on a leafy liverwort (*Scapania undulata*) and four species of mosses in 28 mid Appalachian Mountain streams, USA. Redrawn from Glime 1994.

Perhaps the greatest specificity is among some of the case-making caddisflies (**Trichoptera**). Several species in the **Hydroptilidae** make their cases exclusively from bryophytes, including *Palaeagapetus celsus* from leafy liverworts (Flint 1962; Glime 1978, 1994). The flat leaves of *Scapania undulata* seem to be ideal for their method of cutting nearly circular pieces that they cement together for the cases, apparently causing these larvae to live almost exclusively among leafy liverworts (Glime 1978, 1994). Likewise, in the **Brachycentridae** *Adicropheps hitchcocki* (Figure 120) uses bits of *Fontinalis* (Figure 107) leaves or other mosses to construct its cases (Flint 1965; Glime 1994). When it uses *Hygroamblystegium fluviatile* (Figure 112) it may use only costae to make the case, sometimes leaving the ends of the costae dangling from the case (Glime 1994). The **Chironomidae** (Figure 90), as a family, was present in 98-100% of the collections of all species (Figure 118), but these comprised multiple species that could have differed among bryophytes and streams.

The acidity may affect the inhabitants, causing an appearance of bryophyte specificity. Frost (1942) found that the **Plecoptera** and **Coleoptera** were less important in the calcareous stream than in the acid stream, whereas the **Ephemeroptera** and **Trichoptera** reached their greatest density in the more calcareous stream.

### Seasons

One reason for insects to live among bryophytes is to escape the cold of winter. To this end, some insects are more abundant in streams in the winter, but many spend the winter as pupae or eggs.

Thienemann (1912) found that young fauna were especially common among mosses in summer. Seasons can

partition niches, with different sizes of insects occupying different niches. This means that larger members of a genus or family can occupy the same moss clump as younger members of other species in that family feeding group because they have different feeding niches. In some cases this niche partitioning is done by a seasonal migration to a different substrate. Hildrew and Edington (1979; see also Muotka 1990) found that early instars of *Hydropsyche siltalai* (Figure 121) and *H. pellucidula* (Figure 122) occupied the same rocks. However, in spring *H. siltalai* migrates to moss beds, but *H. pellucidula* was totally absent among the mosses at that time.



Figure 120. *Adicropheps hitchcocki* showing case made with *Hygroamblystegium*. Note costae protruding near opening. Photo by Bob Henricks, with permission.



Figure 121. *Hydropsyche siltalai*, a caddisfly larva that moves to moss beds as it gets older, avoiding competition with *H. pellucidula*. Photo by Urmas Kruus, with permission.



Figure 122. *Hydropsyche pellucidula*, a net-spinning caddisfly that avoids niche competition with *H. siltalai* by avoiding moss beds when the latter migrates there. Photo by Niels Sloth, with permission.



In the Appalachian Mountain streams, the total numbers diminish in the winter (Glime 1968), but some insects, like the blackfly *Prosimulium hirtipes* (Figure 51-Figure 53; Figure 123), hatch in late fall and spend the winter in the water, emerging as adults in spring.

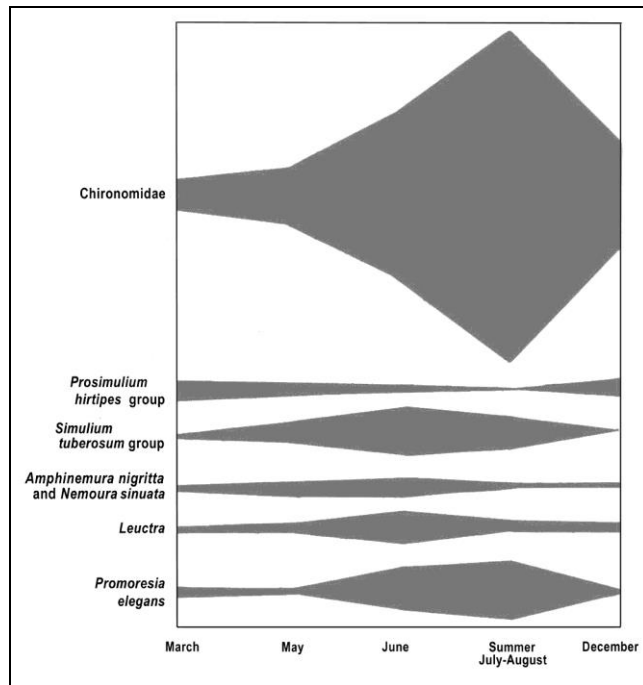


Figure 123. Relative abundance of the six most common insects among bryophytes in five collecting seasons in Appalachian Mountain, USA, streams. Based on Glime 1968.

In these Appalachian streams, counts do not always track diversity and richness (Figure 127; Glime 1994). What is more interesting is that **Shannon diversity** (following Patten 1962) and species richness do not always agree. This may be the result of the differences in counts, which are reflected in the **Shannon diversity**:

$$H' = -\sum_{i=1}^R p_i \log_2 p_i$$

where  $p_i$  = the proportion of individuals belonging to the  $i$ th type, or count of the species divided by total count of all species

$R$  = richness, or total number of species

**Richness**, on the other hand, is simply the number of species present. In these streams, Shannon diversity was highest in March, but richness was highest in July. It is also interesting that these seasonal differences can be different among bryophyte species (Figure 124-Figure 127).

The ever-present **Chironomidae** (Figure 90) often peak among the mosses in winter (Frost 1942), but in the Appalachian Mountain, USA, streams the peak is mid-summer (Figure 123) (Glime 1968). Whitehead (1935) suggested that this might be a behavioral attribute in which the insects seek shelter among the mosses to avoid or respond to the ravages of flooding. But clearly the insects differ among orders, families, and seasons, as seen in these Appalachian Mountain streams (Figure 125-Figure 126).

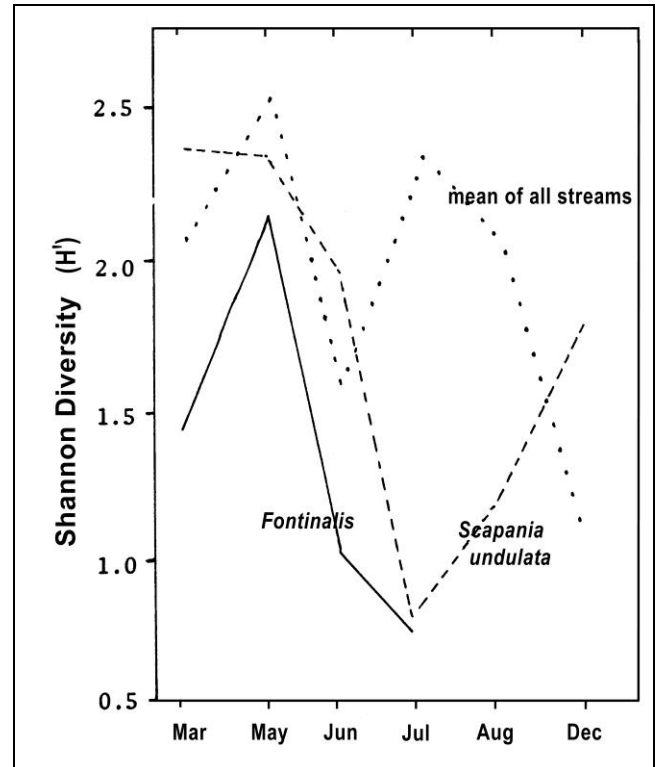


Figure 124. Seasonal changes in species diversity ( $H'$ ) among mosses (*Fontinalis* spp. —) and liverworts (*Scapania undulata* --) in Appalachian Mountain, USA, streams.

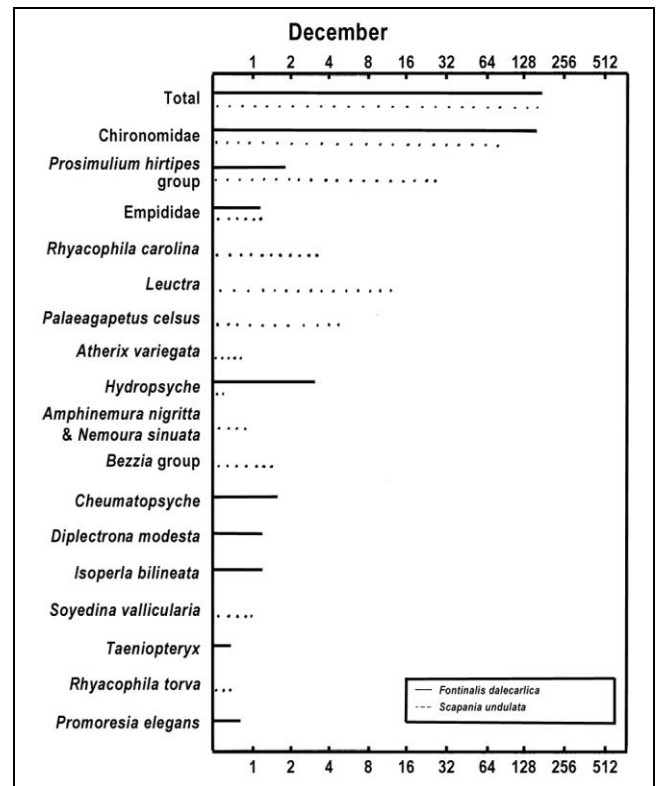


Figure 125. Relative numbers of the most abundant species (>3 occurrences) of insects per gram dry weight of bryophyte in December in Appalachian Mountain, USA, streams. Frequencies appear at right end of each bar. Based on Glime 1968.

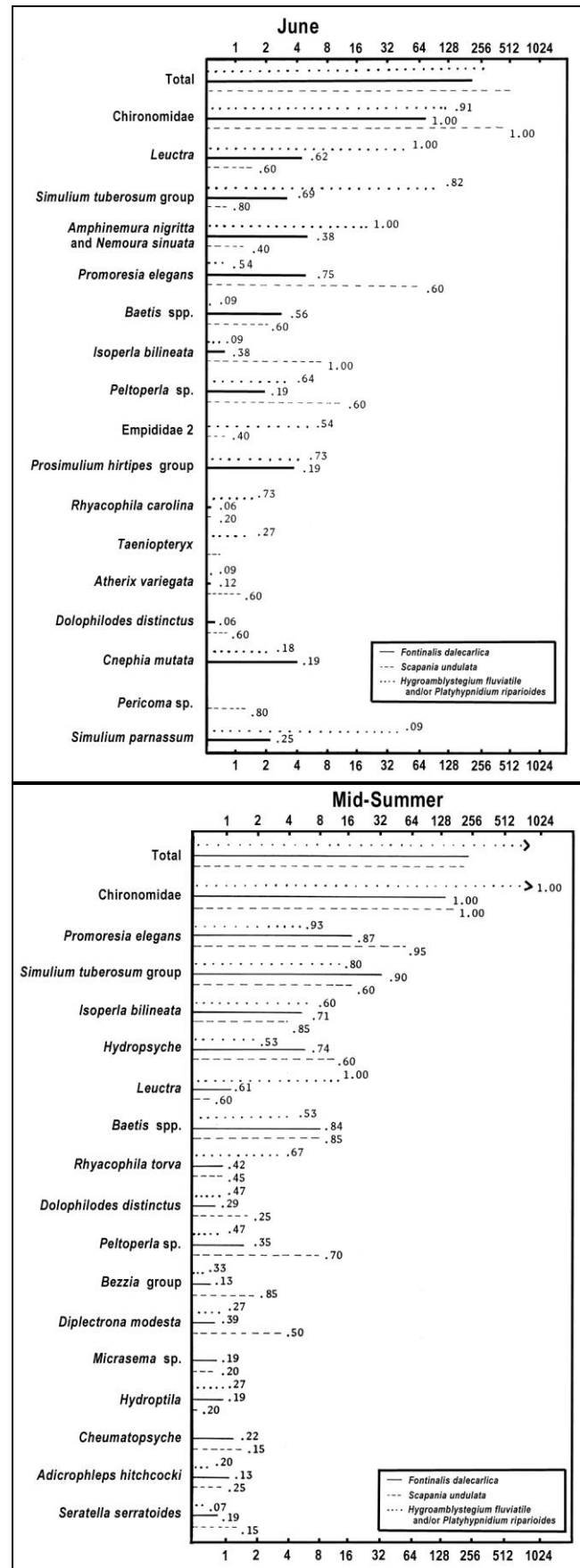
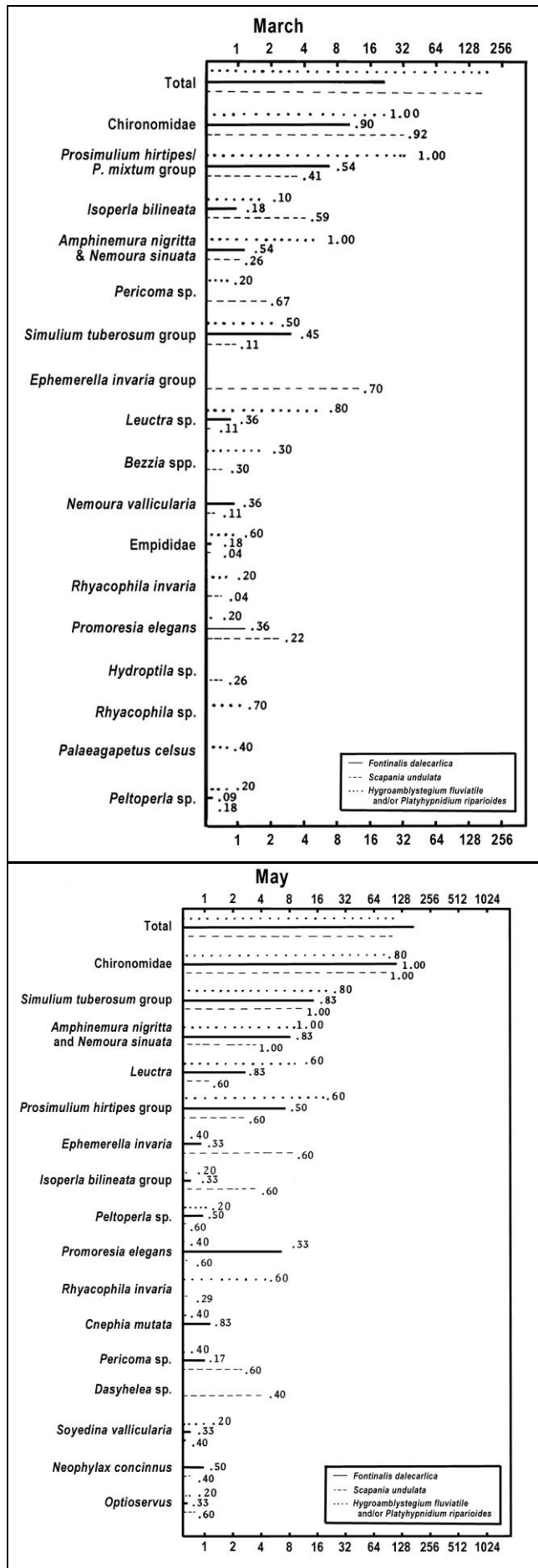


Figure 126. Seasonal relative numbers of the most abundant species (>3 occurrences) of insects per gram dry weight of bryophyte in Appalachian Mountain, USA, streams. Frequencies appear at right end of each bar. Based on Glime 1968.



Table 2. Common genera of bryophyte-dwelling aquatic insects. Numbers refer to references: (1) Percival & Whitehead 1930 (UK); (2) Glime 1994 (Appalachian Mountains, USA); (3) Thienemann 1912 (North Rhine-Westphalia); (4) Suren 1988 (alpine NZ); (5) Muttkowski & Smith 1929 (Yellowstone USA); (6) Frost 1942 (UK); (7) Tada & Satake 1994 (Japan); (8) Krno 1990 (Slovakia). Only studies that included all insect groups are included; note that most studies did not identify genera of the Chironomidae.

<b>COLLEMBOLA</b>	2	<b>Pediciidae – <i>Dicranota</i></b>	3,6
<b>Isotomidae – <i>Isotoma</i></b>	2	<b>Psychodidae – <i>Pericoma</i></b>	2,3,6,8
<b>EPHEMEROPTERA</b>	1,2,3,5,6,7,8	<b>Simuliidae</b>	2,6,7,8
<b>Baetidae</b>	1,2,3,6,7,8	<i>Cnephia</i>	2
<i>Baetis</i>	1,2,3,6,7,8	<i>Odagmia</i>	8
<b>Baetiscidae – <i>Baetisca</i></b>	2	<i>Prosimulium</i>	2,8
<b>Caenidae – <i>Caenis</i></b>	6,8	<i>Simulium</i>	2,6
<b>Ephemerellidae</b>	1,2,5,6,7,8	<b>Tipulidae</b>	1,2,6,7
<i>Drunella</i>	5,7	<i>Hexatoma</i>	1,2
<i>Ephemerella</i>	1,2,6,7,8	<b>Limnobiinae</b>	6
<i>Torleya</i>	8	<i>Limnophora</i>	2
<b>Heptageniidae</b>	1,5,7,8	<i>Tipula</i>	2,6
<i>Cinygmula</i>	7	<b>COLEOPTERA</b>	1,2,3,6,8
<i>Heptagenia</i>	1,5	<b>Dytiscidae – <i>Ilybius</i></b>	2
<i>Rhiithrogena</i>	8	<b>Elmidae</b>	1,2,3,6,8
<i>Stenacron</i>	2	<i>Dubiraphia</i>	2
<b>Leptophlebiidae</b>	2,6,8	<i>Elmis</i>	1,8
<i>Habroleptoides</i>	8	<i>Esolus</i>	3,6
<i>Leptophlebia</i>	6	<i>Limnius</i>	3,6
<i>Paraleptophlebia</i>	2,6	<i>Optioservus</i>	2
<b>ODONATA</b>	2	<i>Promoresia elegans</i>	2
<b>Gomphidae – <i>Gomphus</i></b>	2	<i>Stenelmis crenata</i>	2
<b>PLECOPTERA</b>	1,2,4,5,6,7,8	<b>Gyrinidae – <i>Gyrinus</i></b>	6
<b>Chloroperlidae – <i>Chloroperla</i></b>	6,7	<b>Hydraenidae</b>	3
<i>Chloroperla</i>	6	<i>Hydraena</i>	3
<b>Gripopterygidae</b>	4	<i>Limnebius</i>	3
<i>Zelandobius</i>	4	<b>TRICHOPTERA</b>	1,2,3,5,6,7,8
<i>Zelandoperla</i>	4	<b>Brachycentridae</b>	2,3,7,8
<b>Leuctridae – <i>Leuctra</i></b>	1,2,6,8	<i>Adicrophleps</i>	2
<b>Nemouridae</b>	1,2,4,5,6,7,8	<i>Brachycentrus</i>	5,8
<i>Amphinemura</i>	6,7,8	<i>Micrasema</i>	2,3,7
<i>Nemoura</i>	2,8	<b>Hydropsychidae</b>	1,2,3,8
<i>Protonemura</i>	6,7,8	<i>Arctopsyche</i>	7
<b>Perlidae</b>	5	<i>Cheumatopsyche</i>	2
<i>Acroneuria</i>	5	<i>Diplectrona</i>	2
<b>Perlodidae</b>	2,6,7,8	<i>Hydropsyche</i>	1,2,3,6,8
<i>Megarcys</i>	7	<i>Parapsyche</i>	2
<i>Isoperla</i>	2,6,7,8	<b>Hydroptilidae</b>	1,2
<b>Peltoperlidae – <i>Peltoperla</i></b>	2	<i>Agapetus</i>	1,6
<b>Pteronarcidae – <i>Pteronarcys</i></b>	2,5	<i>Agraylea</i>	2
<b>Taeniopterygidae – <i>Taeniopteryx</i></b>	2,6	<i>Hydroptila</i>	1,2,3,6
<b>HEMIPTERA</b>	2	<i>Ithytrichia</i>	1,2,3,6
<b>Veliidae – <i>Microvelia</i></b>	2	<i>Oxyethira</i>	2,3,6
<b>DIPTERA</b>	1,2,3,4,6,7,8	<i>Paleagapetus</i>	2
<b>Athericidae – <i>Atherix</i></b>	2,3	<b>Leptoceridae – <i>Leptocerus</i></b>	1,6
<b>Ceratopogonidae</b>	2,8	<b>Lepidostomatidae – <i>Lepidostoma</i></b>	1,2,6
<i>Bezzia</i>	2	<b>Limnephilidae</b>	7,8
<i>Dasyhelea</i>	2	<i>Allogamus</i>	8
<b>Chironomidae</b>	1,2,3,4,6,7	<i>Drusus</i>	8
<i>Corynoneura</i>	3	<i>Parachiona</i>	8
<i>Cricotopus</i>	3	<i>Pseudostenophylax</i>	7
<i>Dactylocladius</i>	3	<b>Philopotamidae</b>	1,2,3
<i>Diamesa</i>	3	<i>Chimarra</i>	2,6
<i>Orthocladius</i>	3,7	<i>Dolophiloides</i>	2
<i>Tanytarsus</i>	3	<i>Philopotamus</i>	1,3
<i>Thienemanniella</i>	3	<b>Polycentropodidae – <i>Polycentropus</i></b>	1,2,6
<b>Empididae</b>	2	<b>Psychomyiidae – <i>Psychomyia</i></b>	1,6
<i>Clinocera</i>	6	<b>Rhyacophilidae – <i>Rhyacophila</i></b>	1,2,3,6,7,8
<i>Hemerodromia</i>	6	<b>Uenoidae</b>	2,5
<b>Limoniidae – <i>Antocha</i></b>	7	<i>Neophylax</i>	2
<b>Muscidae – <i>Limnophora</i></b>	1,3,6	<i>Thremma</i>	5

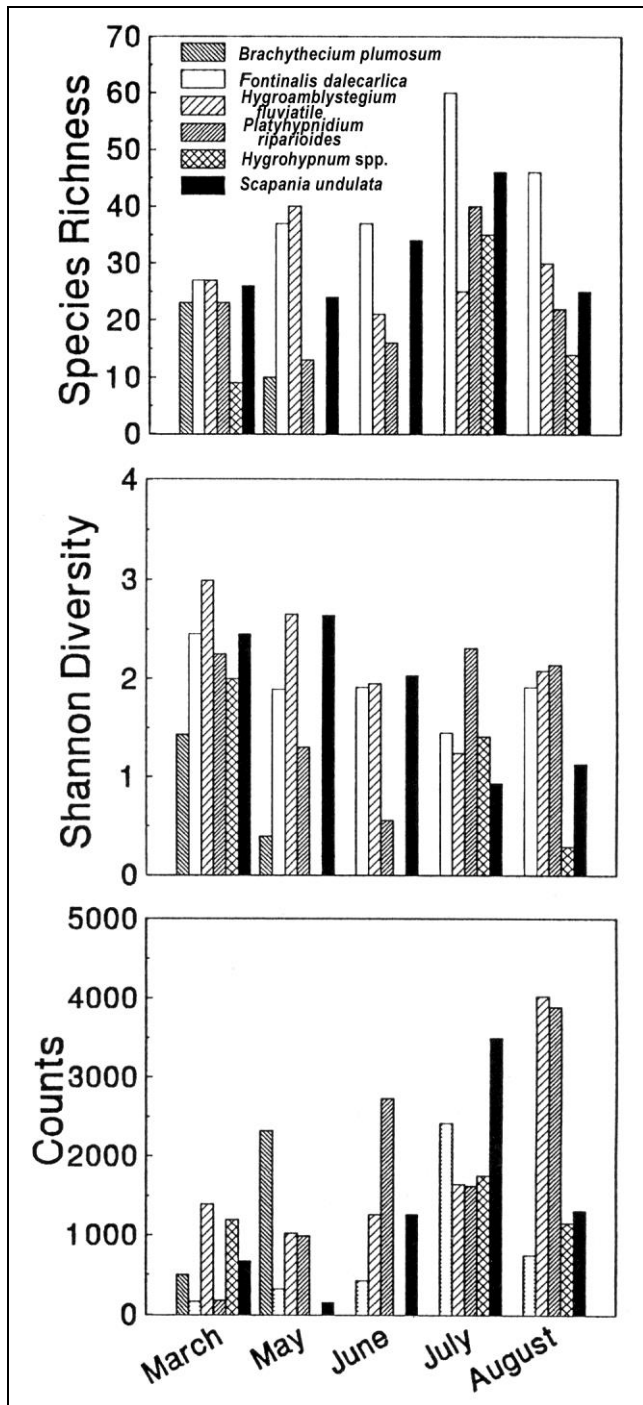


Figure 127. Bryophyte-dwelling insect seasonal richness, species diversity, and counts from handful samples. Redrawn from Glime 1994.

## Sampling

Sampling of the fauna of aquatic bryophytes can be a time-consuming process. And sampling used for most terrestrial or stream habitats can introduce strong biases for these sheltered species.

My own methods were to use hand grabs, then determine the dry weight of the bryophytes after the fauna had been removed. This sampling kept the internal fauna intact, and to test for surface losses, I initially placed a net just downstream from my collections. Very few

invertebrates landed in the net, so I proceeded with my hand collections. These were placed in baby food jars with 95% alcohol and a few drops of glycerine added to prevent predation and decay until the jars reached the lab. I removed the insects with microforceps while systematically searching through a dissecting microscope at 10 X.

Frost (1942) was one the early surveyors of bryophyte fauna. Her sample size was 200 g of wet moss. Kamler (1967) cut 10x10 cm samples under water. Maurer and Brusven (1983) were particularly careful. They surrounded the moss with a nylon organdy net of 250  $\mu$ m mesh while removing the moss from the stream, then used several washes and hand picking to extract the insects.

Armitage (1961) used the modified square foot sampler, similar to the Surber sampler (Figure 128) used by Gurtz and Wallace (1984), to catch insects from rocks, mosses, sticks, and under rubble in streams. However, most bryophyte dwellers are adapted to clinging to the bryophyte and require more than a little disturbance to free them. This leads to underestimates of the bryophyte fauna relative to those among the rubble of the stream bottom and also to species bias. Wulforst (1994) modified this method slightly, using a box sampler to cut a square of 14  $\text{cm}^2$  to sample mosses in an acid stream. The moss samples were quantified by volume using displacement of water in a graduated cylinder.

In his New Zealand studies, Suren (1988) likewise used a Surber sampler (Figure 128) with 100  $\mu$ m mesh to sample 0.01  $\text{sq m}$ . Rocky areas were sampled with a 0.02  $\text{sq m}$  sampler that had a thick foam flange around the bottom to provide a seal with the substrate. Mosses were scraped into the sampler with a razor blade. This method permitted the same area to be sampled in both rock and moss areas.



Figure 128. Surber sampler being used as drift net for winter stream drift sampling. Photo by Janice Glime.



## Preservative

It is important to understand the role of the preservative. Not only does it keep the organisms from decaying and being eaten by cohabitants during the period until the sample can be examined, but it increases the extraction efficiency for flotation techniques (discussed below), at least in a sucrose solution of 1.12 specific gravity (Pask & Costa 1971). In samples preserved for 14 days in 10% formalin compared to those not preserved but examined the same day, the preserved insects had a recovery of 91% whereas those with no preservation had only an 83% recovery rate.

Since any collection of bryophytes will bring significant water with it, it is necessary to use a higher concentration than that used when preserving just insects. I added 95% alcohol to my bryophyte collections (with insects), hoping to achieve a concentration of around 70%.

## Extraction

The least bias in extraction can be achieved by careful hand picking while observing through a dissecting microscope. When I first tried to publish my Ph. D. work, the reviewer wanted to know what method I had used to "estimate" the numbers of **Chironomidae**, which could reach thousands in a single handful of moss. But I had removed and counted every single one of them at 10X magnification! Gurtz and Wallace (1984) also hand-picked invertebrates from the mosses at 7X under a dissecting microscope, using a count per dry weight of moss.

There are simpler and less time-consuming methods for those who don't want to spend three years searching among the bryophytes with a microscope. But, these each have their biases. The Tullgren funnel (Andrew & Rodgers 1999) creates a temperature gradient over the sample, typically with a tungsten light bulb above it. Mobile organisms will move away from the higher temperatures and fall into a collecting vessel with alcohol or mixed preservative. But not all insects move quickly, and some may die from the heat and desiccation before falling to their death in the alcohol below. Furthermore, some will die before reaching the lab due to the reduced oxygen.

Fairchild *et al.* (1987) developed a behavioral method for extracting invertebrates from *Sphagnum* (Figure 91). The method includes a vertical temperature gradient coupled with dissolved oxygen gradients in a column of water containing the *Sphagnum* sample. They determined the overall extraction to be 85% efficient ( $n=4$ ). I do have concerns about bias in the species extracted.

Teskey (1969) developed a method especially for sampling the small flies of the family **Tabanidae**. He used a combination of a specially designed sieve with a multiple Berlese funnel (similar to the Baermann funnel in Figure 129) or by using hand searching to sample these larvae. But to identify the larvae, as in many of the aquatic taxa, they had to be reared to adults. Cochrane (1913) used sieves to collect larvae of *Culicoides furensoides* (Diptera: **Ceratopogonidae**) from *Sphagnum* (Figure 91).

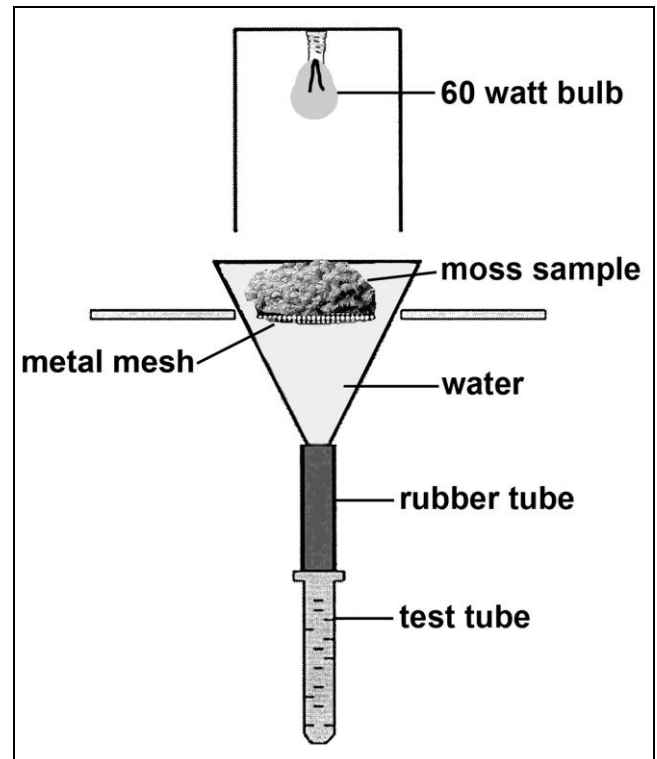


Figure 129. Baermann funnel using moss sample and modified from the Berlese funnel setup, using water instead of air. Modified from Briones 2006.

## Flotation

Any flotation technique requires that the density of the flotation liquid be greater than that of the insects but less than that of the debris (Lackey & May 1971). The 1.12 specific gravity sucrose solution of Pask and Costa (1971) works well in this regard. The kerosene phase separation extracts more total individuals than those extracted by sugar flotation or the Tullgren funnel, particularly more **Acari** (mites) and **Collembola** (springtails) (Andrew & Rodgers 1999).

Fast (1970) pointed out that calling the flotation techniques "flotation" was a misnomer. While the sugar solution is important, many of the organisms remain lodged at leaf bases or caught among the leaves and stems. He preserved samples with 10% formalin. To separate the organisms, he used 360 g sucrose per liter of water and gave the samples only one immersion in the sugar solution. He then sorted at 3.5X magnification. One problem I found with the flotation method was that tiny creatures like the Chironomidae got trapped in the surface tension. They were almost impossible to pick up, so they needed to be trapped on a filter. By the time you have then picked them off the filter, you might as well sort them directly from the moss and learn about their hideouts and spatial relationships at the same time.

Hribar (1990) reviewed ten methods for sampling biting midge larvae. Some of these will work for aquatic bryophytes. Hribar was successful in extracting larvae of **Ceratopogonidae** (*Alluaudomyia*, *Atrichopogon*, *Bezzia*, *Culicoides*, *Dasyhelea*, and *Forcipomyia*) from *Fontinalis*

(Figure 107) and aquatic liverworts by using a Berlese funnel (see Figure 129). He found that sugar flotation and salt flotation provided similar results, but the sugar flotation caused less mortality. Magnesium sulfate is a slower process but results in fewer deaths than salt solutions. Nevertheless, he considered agar extraction and salt flotation to be the most effective for collecting larvae. Sieving, sieving plus salt flotation, and Berlese funnels worked well for mosses.

In short, unbiased sampling to determine numbers of insects living among bryophytes requires time and patience.

## Artificial Mosses

Several researchers have attempted to explain the role of aquatic bryophytes by using artificial mosses. Glime and Clemons (1972) used strips of plastic and bundles of string (Figure 130) as artificial mosses. The plastic permitted colonization by **periphyton** (attached organisms) but lacked the chambering found among mosses; only 13 species occurred on the 33 samples. The string offered a soft substrate with limited chambers; 23 species of aquatic insects occurred on the 35 samples, some of which were not present on the real mosses. The real mosses [*Fontinalis novae-angliae* (Figure 131) & *F. dalecarlica* (Figure 115)] had 25 species among the 46 samples, differing little in overall richness from that of the string mosses. It appeared that density of insects was higher among real mosses, but there was no common base upon which to compare them. It is interesting that the Shannon diversity differed little among the three substrata (1.8 on moss, 1.9 on string, and 1.7 on plastic). Nevertheless, the Shannon diversity (d) on plastic was significantly different from that on mosses or strings. The lack of complexity and smaller surface area of the plastic may have accounted for the limited diversity.



Figure 130. Artificial mosses made of cotton string. Photo by Janice Glime; see Glime & Clemons 1972.

Suren (1988) used nylon twine (5 cm long, 1 mm thick) to weave squares 0.01 m<sup>2</sup> thick with a pore size of 4

mm. He found no differences in the fauna between artificial and real mosses in a New Zealand stream. The artificial mosses even had abundant periphyton growth [especially *Epithemia* (Figure 132) in winter and spring], but their accumulation of detritus and silt was sparse. This perhaps explains the significantly lower numbers of detritus feeders such as **Acarina** (mites), **Collembola** (springtails), **Tardigrada** (water bears), **Dorylaimoidea** (nematodes), and **Ostracoda** (seed shrimp) on the artificial mosses.

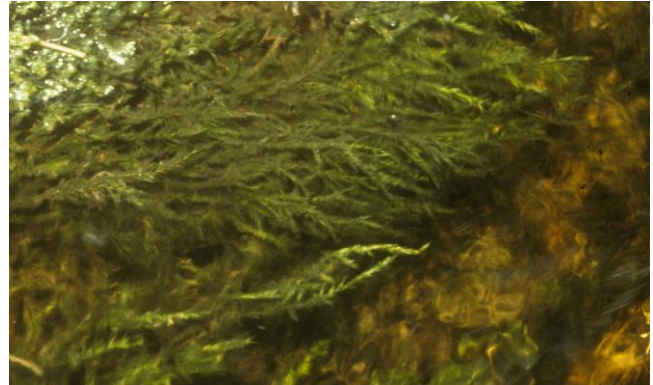


Figure 131. *Fontinalis novae-angliae*, a moss with around 25 species of insects in a New Hampshire, USA, stream. Photo by Janice Glime.



Figure 132. *Epithemia* sp., a common diatom genus on mosses, on a filamentous alga. Photo by Jason Oyadomari, with permission.

## Summary

Aquatic insects are those insects that spend part of their life cycles in the water, usually as a means of escaping the harsher environment on land during one or more seasonal conditions. For most, the immature stages are those requiring such an escape.

Aquatic bryophyte dwellers include the **Collembola** (no longer considered to be insects) that look like miniature adults when born. The **hemimetabolous** insects include the **nymphs** of **Hemiptera** that look like their parents from birth and simply grow larger. The **naiads** of **Ephemeroptera**, **Odonata**, and **Plecoptera** are likewise hemimetabolous, but the naiads often differ from the adults in having gills, different mouth parts, and wing



pads instead of wings. Their life cycle goes from egg/embryo to naiad to adult. The **holometabolous** insects have four distinct stages in the life cycle – **egg/embryo**, **larva**, **pupa**, and **adult**. These orders, among bryophytes, include **Coleoptera**, **Neuroptera**, **Megaloptera**, **Trichoptera**, and **Diptera**. Some have gills as larvae but not as adults.

As an escape from unfavorable conditions, the life cycle stages often respond to environmental cues, including photoperiod, temperature, or available food. Aquatic insects are especially sensitive to temperature, and many of them are in the water for winter to escape the below-freezing temperatures in the terrestrial environment. Some overwinter as dormant eggs or pupae, others as active larvae, naiads, or adults.

Structural adaptations include streamlining, small size, gills, hooks or silk for anchoring, gill covers, and cases or tubes. They move about in the bryophyte clumps to achieve the best oxygen and flow conditions, often leaving as they grow larger. Oxygen may be obtained through gills, cuticle, or a **plastron** that carries an air bubble from the surface or from photosynthesizing plants or algae. Bryophyte dwellers include shredders, gatherers, scrapers, and detritus feeders that prey upon smaller organisms, including periphyton, or eat the detritus gathered by the bryophytes. Some eat the bryophytes. Some make nets to trap food. A few species have a specific requirement for bryophytes for case building, but most simply need a refuge with adequate oxygen, food, and cover.

Sampling is often done with nets, but is best by hand grabs and hand sorting. The faster methods such as nets are commonly used, but they have biases against interior and clinging organisms. Sorting by flotation or Berlese funnels has similar biases. Artificial mosses can sample colonizers but they may not provide the food sources needed and require somewhat lengthy colonization times.

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# CHAPTER 11-2

## AQUATIC INSECTS: BRYOPHYTE ROLES AS HABITATS

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# CHAPTER 11-2

## AQUATIC INSECTS: BRYOPHYTE ROLES AS HABITATS



Figure 1. Habitat for stream bryophyte dwellers, Wolf Brook, NY, USA. Photo by Jason Neuswanger, with permission.

### Potential Roles

Ulfstrand (1967) astutely stated that aquatic insects select their habitats on the basis of factor combinations. While some minimal levels of factors are important – oxygen, temperature, space, stability – the most important factor determining location within this medley of minimums is usually food. And that food works in two directions: enough food to maintain nutrition and avoidance of becoming food themselves. To satisfy both food factors, Ulfstrand found that substrate is especially important; bryophytes are often important choices among those substrates.

Bryophytes are major components in several types of ecosystems, including peatlands, mountain streams (Figure 1), high latitudes, and boreal forest floor. Many researchers have found that bryophytes are important substrata for insects (Percival & Whitehead 1929). Arnold and Macan (1969) found the greatest species richness and number of individuals among mosses, citing their role as cover and source of food by trapping particles.

Bryophytes, both mosses and liverworts, often form extensive cover in rocky and stony reaches of streams (Macan & Worthington 1951). These can have profound effects on the fauna by providing footholds against the current. Mosses with moderate thickness are suitable for the mayflies *Baetis* (Figure 2) and *Ephemerella* (Figure 3) and **Plecoptera** (stoneflies; Figure 20). Fish benefit as well, with the greatest production of fish-food organisms where there are either rooted plants or mosses. For example, **Chironomidae** (Figure 9) are in greatest numbers among thick mosses. And fish certainly eat **Chironomidae** (Mousavi *et al.* 2002). Based on gut contents, Frost (1939) considered moss-dwelling insects to be an important constituent of the diet of trout (Frost 1939) and young salmon (Frost & Went 1940) in the River Liffey, Ireland. Likewise, Minnows appear to crop the moss fauna (Frost 1942). On the other hand, Brusven *et al.* (1990) found that at least in the daytime when salmonid fish feed, the insects drifting in the moss-covered channel (*Fontinalis neomexicana* – Figure 4) did not provide any greater biomass for fish food than in channels where mosses were absent and insect faunal density was much less. Bowden *et*



*al.* (1999) likewise questioned whether fish actually benefit from the increased abundance of insects in streams where bryophytes are present, citing a lack of evidence.



Figure 2. *Baetis rhodani* on sand, a mayfly that also lives among mosses. Photo by J. C. Schou, with permission.

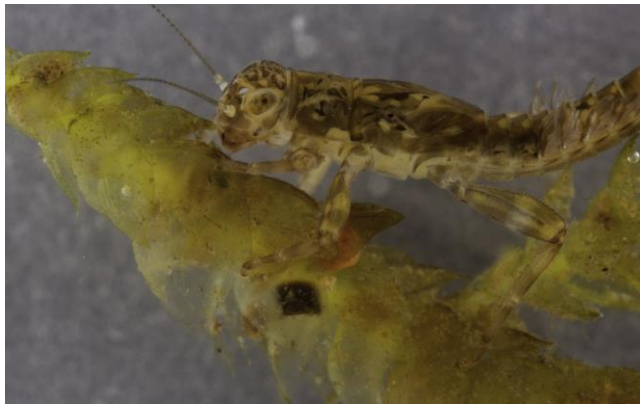


Figure 3. *Ephemerella dorothea* on moss (*Platyhypnidium riparioides*) in Virginia, USA. Photo by D. N. Bennett, with permission.



Figure 4. *Fontinalis neomexicana*, a slightly amphibious species that provides shelter for moss dwellers. Photo by Belinda Lo, through Creative Commons.

I am aware of no study that demonstrates quantitatively that the increase in number of insects in moss mats benefits fish. It appears that insects may have evolved to drift at night precisely to avoid predation by day-feeding

fish. Bryophytes are a difficult place for fish to locate and catch the insects, perhaps reducing the catchable food from what might have been available if rock-dwelling insects were present instead. The hypothesis that bryophyte dwellers increase available fish food needs to be tested.

Corona (2010) suggested that immature insects in streams stayed together because that behavior would increase survival, a concept already suggested for vertebrates by Elgar (1986), Robinette *et al.* (1995), and Brown and Brown (2004). Bryophytes that provide a stable, protected habitat would facilitate such behavior.

Nearly fifty years after Macan and Worthington (1951) expressed the profound contribution of bryophyte-dwelling insects, Bowden *et al.* (1999) summarized that bryophytes "can profoundly influence both the abundance and community structure of stream invertebrates." But they further stated that "the number of fundamentally important roles of bryophytes in stream ecosystems remain unexamined." I will attempt to pull together what various scattered studies around the world have revealed about the roles of stream bryophytes.

Paddling a Kayak to gain first-hand information, Yamamura (2009) observed the adaptations of aquatic insects to various flow regimes in the rivers of Idaho, following up on studies by Rosentreter (1984). In their studies, Yamamura and Rosentreter found that aquatic insects benefit by having aquatic bryophytes because:

1. Bryophytes **decrease stream velocity** on the rock's surface layer.
2. Bryophytes **trap more detritus** (Figure 5; product of disintegration, especially organic matter produced by the decomposition of organisms) than smooth rock (food for shredder insects).
3. Bryophytes provide hiding cover (**refuges**) from predators.
4. Bryophytes provide better background coloration for **camouflage**.
5. Bryophytes provide **greater surface area**, providing a greater amount of habitat area.
6. Bryophytes provide **more food** since algae can grow upon the greater surface area created by the three dimensions of the moss surface.
7. Bryophytes provide greater **algae retention** and protection when stream flow regimes are low enough to create dry surfaces. The bryophytes **retain water longer** than other substrata in the stream, permitting the algae to dry slowly and acclimate to the encroaching desiccation.
8. Perennial bryophytes such as *Scouleria aquatica* (Figure 6) can provide **long-term stability** to an ephemerally dry rock surface, permitting survival of algae, insect larvae, and eggs.

Yamamura (2009) concluded that insect larval data support the interpretation that larvae in spring-fed streams (streams containing aquatic moss) are larger compared to those in runoff-dominated streams (streams that lacked mosses). He concurred with Rosentreter (1984) that spring-fed (mossy) streams have three cohorts present while most run-off (non-mossy) streams have two cohorts. This raises the question, do mosses in runoff-dominated streams benefit insects enough to produce larger larvae and another generation (cohort) per year? Perhaps the insects benefit

from the added cover of bryophytes – insect predators in Idaho streams include other insects, fish, shore birds, and the American dipper. Mosses provide cover in which to hide from all these predators.

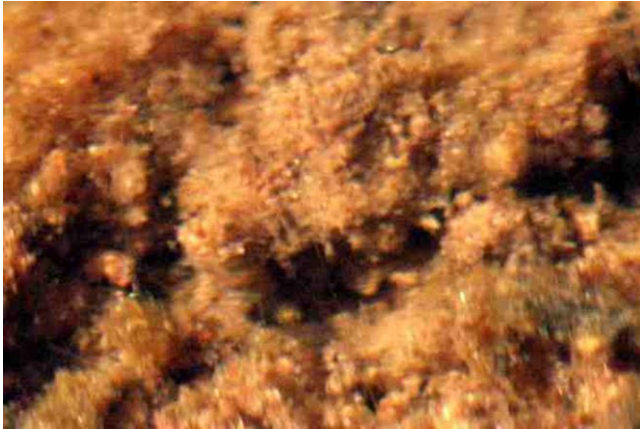


Figure 5. **Detritus**, a common food for aquatic insects and typically accumulated at plant and leaf bases among bryophytes. Photo by James K. Lindsey, with permission.



Figure 6. *Scouleria aquatica* on rock near stream water. Photo by Matt Goff, with permission.

## Refuge

Bryophytes serve as refuges in both moving water and lentic systems such as lakes and ponds. In streams, they provide a refuge against the torrents of rapidly flowing water, permitting insects to live where they can take advantage of the higher oxygen and suspended food sources available in flowing water while remaining safely anchored within the moss or clinging to its surface. In both habitats, the bryophyte provides a hiding place from predators, especially fish, but also larger insects, crayfish, and birds.

The importance of bryophyte-dwelling insects as fish food is a subject for speculation. While the bryophytes provide homes for numerous insects, there is no direct evidence that these insects are available as increased fish food. Greig and McIntosh (2008) examined the effect of brown trout (*Salmo trutta*) predation on the caddisfly *Zelandopsycha ingens*, a bryophyte dweller in New Zealand. They determined that these trout can have

positive effects on the size and fecundity of the adult caddisflies by reducing competition among the larvae through predation. The striking revelation of this study was that despite the detritus-based diet of these caddisflies, reduction in the number of larvae still had a positive effect on the adults of the species when compared to those in fishless streams. The adults were larger and the females had 33% more eggs, but the egg size was unchanged. Nevertheless, the increase in number of eggs did not compensate for the loss of larvae.

The study by Greig and McIntosh (2008) suggests that fish have an impact on insects that typically live among the bryophytes, many of whom are detritus feeders. Thus, the bryophyte cover potentially increases the number of insects surviving and the number of adults reproducing, but we are left with the question of whether the bryophytes ultimately produce more available fish food.

## Habitat Diversity and Substrate Variability

Habitat diversity offers more niches, hence making the area suitable for more species. Clenaghan *et al.* (1998) identified ecological factors that contribute to macroinvertebrate community composition. Local ecological factors include acidic water, moss, shading, agricultural runoff, longitudinal trends in stream physico-chemistry (distance from headwaters, geology, land use) and season (related to life history patterns of the invertebrates). In their study of a conifer-afforested catchment in Ireland, macroinvertebrate density and richness increased with the distance from the headwaters and the concomitant increases in pH, water hardness, and available nutrients.

Douglas and Lake (1994) demonstrated that habitat diversity was important in increasing species richness in streams. Bryophytes not only add to that diversity, but increase available surface area. Based on a review of the literature, Smith-Cuffney (1987) reported that stream mosses in low order, high elevation streams have a structurally unique community. Measured as respiration rates, the communities among *Fontinalis* (Figure 4) had three times the rates found in the stone community and five times that of the **hyporheic** community. Arnold and Macan (1969) found the largest number of species and individuals of insects inhabited mosses in a Shropshire Hill stream in the UK, where the mosses provided both shelter and trapped food.

Pardo and Armitage (1997) demonstrated the importance of environmental variables in the spatial distribution of aquatic insects based on eight mesohabitats. They found that water velocity and flow dynamics, together with the nature of the substrate were the major determinants of **benthic** (bottom) communities. Heino (2009) looked at the environmental variables somewhat differently, attempting to explain why such things as the influence of altitude varied with geography. He found pH, stream size, and moss cover were the most important variables, with functional diversity increasing with moss cover. These two approaches are not that different, with pH and water velocity both influencing moss cover and moss cover providing safe sites in areas of high flow rates.

Špoljar *et al.* (2012) likewise found that flow velocity and pH had the greatest effect on community structure. In two springs in Papuk Nature Park, Croatia, the



macroinvertebrate taxa numbered only 25. Where the bryophyte cover was dense (90% cover), the community structure was most affected by flow velocity and pH; macroinvertebrate diversity and abundance were higher than in the stream with only 50% bryophyte cover. In the latter stream, algae, protozoa, and **meiofauna** (minute animals living in small spaces in soil or aquatic sediments) reached higher abundance, apparently resulting from suspended organic matter and epiphytes.

Bryophyte communities exemplify the species-area relationship (Gleason 1922). Increased bryophyte cover means an increase in available substrate due to its three-dimensional structure. Heino and Korsu (2008) found a strong relationship between species richness and number of individuals, and both of these were significantly related to the bryophyte biomass. They attributed the relationship to the increased cover provided by greater bryophyte coverage. Heino *et al.* (2005) found that despite the highest congruence between bryophytes and macroinvertebrates among the stream biological groups, that congruence was nevertheless weak. This seems to relate to differences in the stream factors that determine bryophyte locations. Bryophyte diversity followed water color, habitat stability, and stream size, in that order. Macroinvertebrate diversity instead was determined in the order of stream size, water color, and acidity.

## Nutrients

Nutrients can affect moss growth in some cases and limit it due to competition for light by encrusting algae in others. In their study of the Kuparuk River, Alaska, USA, Lee and Hershey (2000) found that fertilization with phosphorus increased the growth of mosses (*Hygrohypnum* – Figure 7), but that insects did not respond as extensively as one might expect. Invasion by mosses resulted in an increased density of the mayfly *Ephemera aurivillii* (Figure 8) and **Chironomidae** (midges; Figure 9), but had no effect on densities of the mayfly *Baetis* spp. (Figure 2) or **Simuliidae** (blackflies; Figure 22). Both *Baetis* and *Ephemera* grew larger in fertilized areas, but Lee and Hershey suggested that this was most likely due to the increase in epiphytic diatoms. Only *Ephemera* seemed to be affected by substrate type (bare rock, natural moss, artificial moss), with the greatest densities among the mosses, presumably due to increased habitat complexity. Clenaghan *et al.* (1998) compared several factors and found that mosses were one of the factors explaining the diversity of insects in a catchment stream in Ireland, and that both density and richness increased with moss weight. Voelz and McArthur (2000) likewise concluded that habitat complexity was one of the most important factors in determining species richness in streams.

In my own culturing studies, I have found that enrichment was often detrimental to the mosses. These mosses lost their green color and were covered by algae that presumably intercepted the light – and CO<sub>2</sub>. While the bryophytes remained intact, even if dead, this enrichment could benefit the insects by increasing food sources, but such enrichment most likely would make establishment of new mosses or increased coverage by existing ones less likely.



Figure 7. *Hygrohypnum alpinum*, home of many aquatic insects. Photo by Michael Lüth, with permission.



Figure 8. *Ephemera aurivillii* naiad, a species whose density increases when there are mosses. Photo by Tom Murray, through Creative Commons.



Figure 9. **Chironomidae** larva, an insect that increases in abundance when greater moss growth occurs. Photo by Bob Henricks, with permission.

## Substrate Size

The biodiversity of macroinvertebrates typically increases linearly with the substrate suitability index [suitability of sediment, **periphyton** (freshwater organisms attached to or clinging to plants, but also used to include other objects projecting above the bottom sediments; *Aufwuchs*), and benthic organic materials] (Duan *et al.* 2009). In large rivers in China (Yangtze River, Yellow River, East River, Juma River), Duan *et al.* found that the macroinvertebrate community was not dependent upon macroclimatic conditions or latitude, but rather responded to the commonality of instream habitat conditions of substrate composition and flow conditions in these rivers.



They found that taxa richness was highest on cobble covered with hydrophytes, high on moss-covered bedrock, and low on clay or cobble where there were no plants. Sandy beds were unstable and thus devoid of benthic macroinvertebrates. As in many stream studies, the EPT insects [**Ephemeroptera** (Figure 8, **Plecoptera** (Figure 20), **Trichoptera** (Figure 13)] dominated the cobble, gravel, and moss-covered bedrock. But contrasting with most stream studies (see Chapter 11-9, Holometabolous Insects – **Diptera**), the **Chironomidae** larvae (Figure 9) reached greatest dominance in the clay beds.

But substrate size apparently does not act alone and importance differs among types of insects (see for example Ulfstrand 1967). Contrasting with other studies, Wise and Molles (1979) found that small substrates supported more insect individuals than did the larger stones. And mixed sizes supported numbers between the small and large sizes.

### Stability

I love the expression "A rolling stone gathers no moss," because it so perfectly describes the situation of stability. This expression can be traced to Erasmus' Adagia, first published around 1500, and has since taken on wide usage with somewhat conflicting interpretations. Nevertheless, in the context of a stream, its meaning is clear.

Bryophytes themselves indicate a stable substrate (Yamamura 2009). Such stable areas are present due to stream channel geometry. Rapids can focus the ice scraping at the center of the river, away from the sides where bryophyte populations are able to grow. Hence, some invertebrates may live in those mossy areas simply because they, too, only survive where the substrate is stable and the water has a reduced shearing effect.

Stability is most important for eggs and many pupae that cannot move to a more favorable location when the need arises. Bryophytes will only become well established on stable rocks and boulders, so they signal a stable habitat. Furthermore, as water levels recede, bryophytes maintain water content well beyond the time that a rock can do so, creating a moisture stability. And when the young insects hatch from the eggs, these tiny animals are not only easy prey for larger animals, but they are poor swimmers unable to navigate in the flowing water. The bryophytes provide cover and protection in their small-chambered labyrinth that prevents entry to predators such as fish and large insects and that reduces the flow to near-pool conditions (Glime 1978).

### pH Relationships

The **depauperate** (lacking in numbers or variety of species) fauna of some bryophytes may relate more to the preferred habitats of the bryophytes than to the bryophytes themselves. For example, in Wales, Ormerod *et al.* (1987) found that in streams with low pH the bryophytes [liverworts *Scapania undulata* (Figure 10) and *Nardia compressa* (Figure 11)] had few insects; 60% of the *S. undulata* sites had fewer than 20 macroinvertebrate taxa. The pH where Ormerod *et al.* found these liverworts growing was 5.2-5.8. On the other hand, less than 5% of the sites with the red alga *Lemanea* (Figure 12) (pH 5.5-8.5) were so impoverished. In particular, *Hydropsyche*

(Figure 13) was absent at sites with *S. undulata* and *N. compressa*, but present in streams with *Fontinalis squamosa* (Figure 14).



Figure 10. *Scapania undulata*, a leafy liverwort that can serve as food for the mayfly *Ecdyonurus*. Photo by Michael Lüth, with permission.



Figure 11. *Nardia compressa*, a leafy liverwort that can be eaten in some streams by the mayfly *Ecdyonurus* sp. Photo by Des Callaghan, with permission.



Figure 12. *Lemanea* sp. covered with blackflies. Photo by Janice Glime.





Figure 13. *Hydropsyche* larva, a net-spinning caddisfly that frequents *Fontinalis antipyretica* (Figure 18) and *Platyhypnidium riparioides*. Photo by Guillaume Doucet <<http://guillaume.doucet.free.fr/>>, with permission.



Figure 14. *Fontinalis squamosa* above and below water on rocks, home to several stonefly genera. Photo by Janice Glime.

Research by Willoughby and Mappin (1988) suggests that the insect avoidance of the two leafy liverworts that Ormerod *et al.* (1987) observed may not have been a response to pH, but rather the result of the liverwort terpenes and terpene alcohols in the oil bodies. On the other hand, some insects such as the mayfly *Ecdyonurus* (Figure 15) feed on such acid-tolerant bryophytes as *S. undulata* (Figure 10), but are unable to live in the acid streams at the lower end of the pH tolerance range of this liverwort. Ormerod and coworkers (1987) considered that these mayflies are therefore physiologically restricted from acid streams.



Figure 15. *Ecdyonurus venosus* naiad, a mayfly genus in which some members feed on *Scapania undulata* (Figure 10) when the pH is not too low. Photo by Guillaume Doucet <<http://guillaume.doucet.free.fr/>>, with permission.

Other factors may affect the choices of many insects to avoid colonizing these acid-tolerant bryophytes. For example, one possibility that Ormerod *et al.* (1987) considered was that the diatom *Eunotia* (Figure 16) that grows in the leaf axils of leafy liverworts (acid-loving) is inaccessible to grazing *Baetis* (Figure 2), whereas the diatom *Cocconeis* (Figure 17) grows on the leaf lamina of the moss *Hygrohypnum* (Figure 7; growing at a higher pH) where it is easily grazed (Sutcliffe *et al.* 1986).



Figure 16. *Eunotia* sp., a diatom that grows in leaf axils of leafy liverworts where *Baetis* is unable to reach it. Photo by Janice Glime.

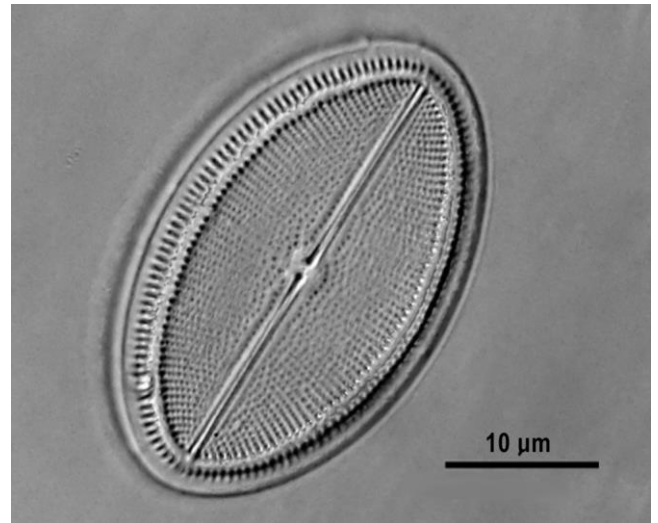


Figure 17. *Cocconeis placentula*, an epiphytic diatom that cements itself to aquatic bryophyte leaves. Photo by Ralf Wagner at <<http://www.dr-ralf-wagner.de/>>, with permission.

Heino (2005) likewise found that functional richness of macroinvertebrates increased with increased pH, with total nitrogen, water color, and substrate particle size also varying with moss cover in 111 boreal headwater streams in Finland. The functional structure depended on these same variables with its dominant pattern being related to increase of shredder-sprawlers and decrease of scraper-swimmers in acidic conditions.

Frost (1942) compared the fauna on the mosses in acid and alkaline streams in her survey of River Liffey, Ireland. *Chironomidae* (Figure 9) constituted 40-54% of the fauna in these streams. In the carboniferous limestone sites,



*Fontinalis antipyretica* (Figure 18) and *Platyhypnidium riparioides* (Figure 19) dominated in a pH range of 7.4 to 8.4. The stonefly fauna of these mosses was comprised of predominantly *Isoperla* (Figure 20). The dominant caddisfly genus was *Hydropsyche* (Figure 13). Mayflies included *Ephemere*llidae (Figure 8) (mean 533 per sample of 200 g wet weight), *Baetis* (Figure 2), and *Caenis* (Figure 21). The blackfly *Simulium* (Figure 22) was common. In the acid streams (peat bog drainage), the pH ranged 4.4-6.8, and the bryophytes were dominated by *Fontinalis squamosa* (Figure 14) with a small coverage by the leafy liverwort *Scapania undulata* (Figure 10). The stonefly fauna was comprised of *Protonemura* (Figure 104), *Amphinemura* (Figure 105), *Leuctra* (Figure 49), and *Chloroperla* (Figure 23). *Polycentropus* (Figure 24) was the predominant caddisfly.



Figure 18. *Fontinalis antipyretica*, home to the stonefly *Isoperla* and net-spinning caddisfly *Hydropsyche*. Photo by Andrew Spink, with permission.

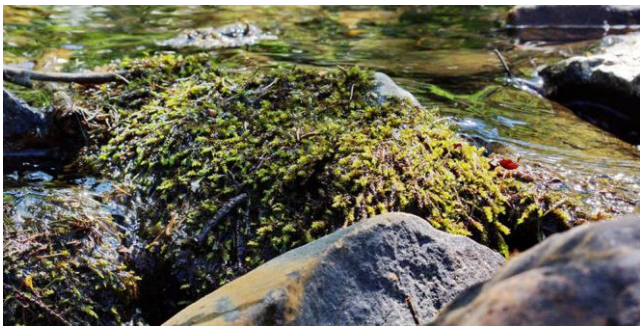


Figure 19. *Platyhypnidium riparioides*, home to the stonefly *Isoperla* and net-spinning caddisfly *Hydropsyche*. Photo by Andrew Spink, with permission.



Figure 20. *Isoperla similis* naiad, member of a genus that inhabits *Fontinalis antipyretica* (Figure 18) and *Platyhypnidium riparioides*. Photo by Donald S. Chandler, with permission.



Figure 21. *Caenis youngi* naiad, member of a genus that sometimes inhabits *Fontinalis antipyretica* (Figure 18) and *Platyhypnidium riparioides*. Photo by Bob Newell, with permission.



Figure 22. *Simulium* (blackfly) larvae showing the large numbers that can occupy one rock – or moss. Photo by F. Christian Thompson, through USDA public domain.



Figure 23. *Chloroperlidae* naiad, a detritus inhabitant, including mosses. Photo by Bob Henricks, with permission.



Figure 24. *Polycentropus* larva, a dominant caddisfly among *Fontinalis* in acid streams. Photo by Jason Neuswanger, with permission.



In a similar study, Willoughby and Mappin (1988) found that growth of the mayfly *Serratella ignita* (Figure 25) was similar when fed on food from acid or alkaline streams. In acid streams they fed on the leafy liverwort *Nardia compressa* (Figure 11) with the filamentous alga *Klebsormidium subtile* (Chlorophyta; see Figure 26), whereas in the alkaline streams they ate the moss *Platyhypnidium riparioides* (Figure 19) with the epiphytic diatom *Cocconeis placentula* (Figure 17). But if the alga *Klebsormidium subtile* was absent in the acid streams, they were unable to subsist on the liverworts alone.



Figure 25. *Serratella ignita* naiad, a mayfly species that can subsist in both acid and alkaline streams, feeding on bryophytes and associated algae. Photo by J. C. Schou, with permission.



Figure 26. *Klebsormidium flaccidum*, a green alga associated with *Nardia compressa* in acid streams, providing food for *Serratella ignita*. Photo by Sarah Kiemle, with permission.

### Bryophyte Structure

Not all bryophytes are created equal, despite their frequent treatment as one entity in ecological studies. Their structures can differ greatly, and this has a strong influence on which organisms can live there. This structure is seldom considered in describing the habitat and the influences of the bryophytes on the inhabitants. Let's consider a few and the differences they offer.

### *Scapania undulata*

This is a leafy liverwort whose chemical components of terpenoids have already been mentioned. Its growth form is somewhat layered (Figure 27), and its leaves are **conduplicate** (Figure 28). That is, the leaf is folded over so that the smaller portion is on top. This fold provides a protected area where several small insects such as the stoneflies *Leuctra* (Figure 49) and *Nemoura* (Figure 40) like to hide (Glime 1968). Its layered effect makes it somewhat more open to the water, permitting predators to penetrate more deeply in search of prey, a problem that is avoided by the small insects that can hide within the folds of the leaves.



Figure 27. *Scapania undulata* showing layered effect. Photo by Hermann Schachner, through Creative Commons.



Figure 28. *Scapania undulata* showing folded leaves with smaller lobes on top. Photo by Florent Beck, through Creative Commons.

### *Hygroamblystegium* spp.

This genus, including *Hygroamblystegium fluviatile* and *H. tenax*, forms thick mats on rocks (Figure 29). Its extensive branching provides an array of spaces within the mat, affording protection from both the current and most larger insects and fish. The leaf has a strong costa (Figure 30) that is used by some caddisflies in the construction of their cases (to be discussed later in the **Trichoptera** subchapter). Its small leaves and branches afford small spaces unavailable to larger insects, thus limiting the species and life stages that can live there.





Figure 29. *Hygroamblystegium tenax* in a dry stream bed. Photo by Janice Glime.



Figure 31. *Platyhypnidium riparioides*, home to many kinds of aquatic insects. Photo by Michael Lüth, with permission.



Figure 30. *Hygroamblystegium fluviatile* showing cupped leaves and strong costa used by some caddisflies in construction of their cases. Photo by Hermann Schachner, with permission.

### ***Platyhypnidium riparioides***

This species occurs in many of the same streams as those of *Hygroamblystegium fluviatile* (Figure 30). It is a widespread species that forms a chambered mat. It has somewhat larger leaves than *H. fluviatile* but creates a similar habitat with many species in common. It is not unusual to find these two species on the same rock, often intermixed. *Platyhypnidium riparioides* (Figure 31-Figure 32) affords somewhat larger spaces within the mat. Its costa is reduced and much thinner than that of *Hygroamblystegium* species and does not seem to be particularly useful for case building.

### ***Fissidens grandifrons***

*Fissidens grandifrons* (Figure 33) tends to prefer alkaline streams. It is a large moss with flat branches that are layered somewhat like those of *Scapania undulata* (Figure 27-Figure 28), an inhabitant of acid streams. It occurs in very cold water and waterfalls, both conditions that provide it access to more CO<sub>2</sub> than would be available in un-aerated warmer water. I never searched this moss for insects, but my collections of it did not reveal any conspicuous fauna. It is a stiff moss and its preference for torrential water may discourage them.



Figure 32. *Platyhypnidium riparioides*, showing leaves where many kinds of insects are able to hide. Photo by John Hribljan, with permission.

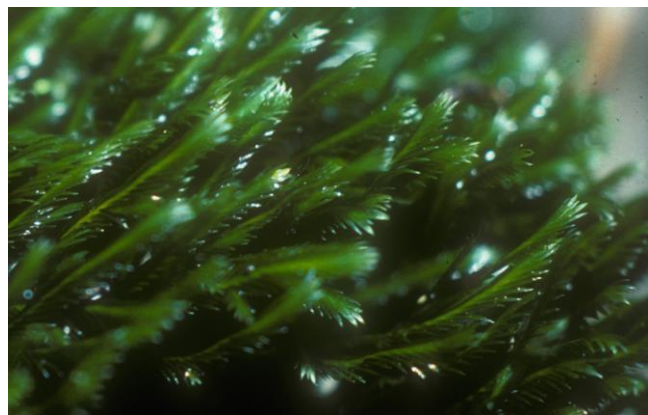


Figure 33. *Fissidens grandifrons* showing the flat branches and accessible spaces between them. Photo by Janice Glime.

### ***Fontinalis* spp.**

*Fontinalis* species are large mosses (Figure 34). They have a **streamer** growth form in which all stems dangle in the same direction as the flow of water, at least where there is a distinct flow. The end portions of the stems are



exposed, harboring **Simuliidae**. The leaf structure varies among species, thus providing differing suitability for the insects. *Fontinalis antipyretica* (Figure 35) has large, keeled leaves that form a 3-sided branch with well protected interior space. However, this space may be somewhat difficult for many insects to enter due to the close **appression** (state of being pressed close to) of leaves. *Fontinalis hypnoides* (Figure 36) has narrow, more or less flat leaves that do not provide much enclosed space. In between these two extremes are various degrees of enclosure and access to that enclosure. The flat surface of the branch of *F. antipyretica* would be ideal for blackfly larvae, but this *Fontinalis* species is often not successful in the very fast flow needed by these larvae. If the moss is in fast flow, the keel is easily worn away and the leaves become tattered. However, in cool streams there is usually sufficient oxygen for both the moss and blackflies to survive.



Figure 34. *Fontinalis dalecarlica*, a refuge for invertebrates during low water levels. Photo by Kristoffer Hylander, with permission.



Figure 35. *Fontinalis antipyretica* demonstrating the folded, overlapping leaves that give little accessibility to the interior leaf space. Photo by David T. Holyoak, with permission.

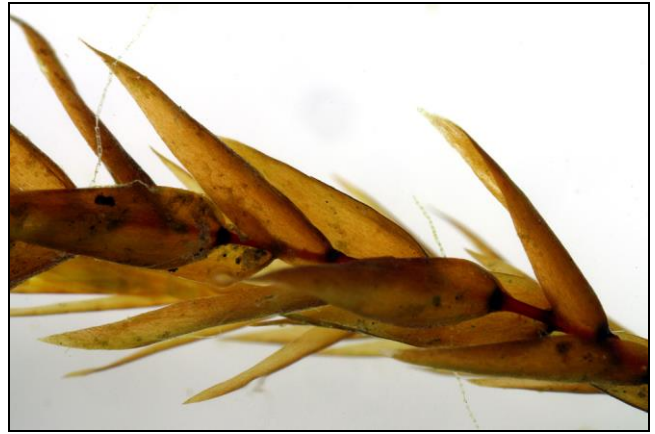


Figure 36. *Fontinalis hypnoides* showing flattened, narrow leaf. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

*Fontinalis squamosa* (Figure 37), a European species, is one of the several intermediate species. Its leaves are concave and provide hiding places within the concavities. Like all *Fontinalis* species, it lacks a costa. This species has been indicated as home to numerous insects in many European stream studies.



Figure 37. *Fontinalis squamosa* showing concave leaves. Photo by Michael Lüth, with permission.

## Flow Regimes

Flow regimes provide another limitation for bryophyte inhabitants. Many bryophytes live in areas of high flow that is too abrasive for the establishment of **tracheophytes** (plants with lignified vascular tissue, *i.e.*, all plants that are not bryophytes). At the same time, many insects require protection from the rapid flow. Furthermore, insects drift in streams for various reasons – searching for food, making a false move that puts them in the current, overpopulation, finding a site for pupation, and dislodgment due to changes in flow.

Baker *et al.* (1996) found that the hydraulic stability of streams over multiple years determined whether a site was dominated by periphyton, bryophytes, or tracheophytes. Variations within the year can control periphyton biomass, with low velocities favoring both periphyton and tracheophytes that serve as additional substrate for them. Bryophytes, on the other hand, are often restricted to areas of high velocity; these same high velocities restrict colonization and accumulation of detritus.

Bryophytes modify the internal flow of water. The arrangement of sedimentary deposits and fauna below the leaves of submerged stream bryophytes supports this concept of internal current modification (Devantery 1995). Using *Platyhypnidium riparioides* (Figure 19) and colored liquid, Devantery was able to demonstrate that a single leaf of this moss caused symmetrical twirling behind it. Between the leaves he observed a retrocurrent in the direction of the leaf. This current was slowed progressively and directed the water toward the leaf insertion, explaining the accumulation of detritus there. The same hydrodynamics also occurred in a second species of bryophyte that had a different leaf morphology.

Certain insects take advantage of refugia, especially during periods of high flow (Lancaster & Hildrew 1993). Bryophytes are able to provide such refugia and are likely to be especially important for such species as *Nemurella pictetii* (Figure 38) and larger naiads of *Leuctra nigra* (Figure 39), both stoneflies known from bryophytes. Lancaster and Hildrew found that seasonal flow conditions affected the distribution of these two species in streams after high-flow events, but that these seasonal differences in flow seemed to have little effect on the *Chironomidae* or the young *instars* (instar is developmental stage between molts of an insect) of *Leuctra nigra*.



Figure 38. *Nemurella pictetii* naiad, a species that uses bryophytes as refugia. Photo by Urmas Kruus, with permission.



Figure 39 *Leuctra nigra* naiad, a species that uses bryophytes as refugia. Photo by J. C. Schou, with permission.

### Flow Rates

One possible role of bryophytes as a habitat for insects and other invertebrates is their ability to provide a refuge with multiple current velocities (Madaliński 1961; Elliott 1967a; Gurtz & Wallace 1984; Suren 1992a, b; Glime 1994). Hence, organisms can migrate within the bryophyte mass to locate the current velocity that meets their needs.

Macan and Worthington (1951) suggested that mosses can "profoundly influence the fauna by providing a foothold for animals which otherwise could be swept away by the current."

Devantery (1987) reminds us of the importance of flow in contributing to the accumulation of food resources in the bryophyte mat. With regard to the moss *Platyhypnidium riparioides* (Figure 19), Devantery considers that the moss increases the spatial uniformity, a perspective that seems to be in contrast with those who consider the moss to increase the complexity of the habitat (Dražina *et al.* 2011). The flow serves as an antagonist with the danger that it can dislodge the bryophytes.

Flow rates approaching the bryophytes influence the insects that make those bryophytes home. The *Chironomidae* (Figure 9) are reduced by higher flow velocities associated with *Fontinalis antipyretica* (Figure 18), whereas the smallest of the *Simuliidae* larvae (Figure 22) are positively influenced (Linhart *et al.* 2002a, b). This may relate to available food, with the Simuliidae trapping fine particles with their head fans and *Chironomidae* living among the detritus that has been trapped by the moss.

### Overturned Rocks

The famous statement, "a rolling stone gathers no moss," applies in its literal sense as well as the figurative. Bryophytes cannot grow under an overturned rock, and rolling is abrasive, damaging new stems and knocking off older clumps. For stream ecosystems, these dangers prevail. Englund (1991) found that 16.7% of the moss-covered stones in North Swedish woodland streams had been overturned in the last few years. Small stones rarely had mosses (See also Slack & Glime 1985), a factor most likely related to their instability. But when stone size exceeded more than 12 cm, mosses were abundant even on rocks that were not embedded into the substrate.

Englund (1991) experimented on the effects of overturning not only on the mosses, but also on their invertebrate fauna. Overturning, as expected, reduced both diversity and abundance of fauna as well as reducing the dry weight of mosses. Nevertheless, 3 out of 16 invertebrate taxa increased, predominantly on the moss-covered underside. For the remaining taxa, peak densities occurred on the upper moss-covered sides of control stones, and these densities decreased on the overturned stones. Despite the introduction of insects through stream drift (see below), recovery was still weak 14 months later, probably because of the slow recovery of the mosses.

### Life History and Flow

For insects living in streams, the habitat is likely to be too fast at times and too dry at others. Yamamura (2009) concluded that the variability of the flow regime can limit the distribution and the life history traits of aquatic insects.

Some have solved this transient habitat problem by life cycle stages that either are dormant or that do not require water. Among these, the egg stage is a suitable stage for surviving drought in some stoneflies, mayflies, and dipterans (Ward 1992). In the case of the stonefly *Nemoura* (s.l.) (Figure 40), a common moss dweller, in a Welsh stream, the adults emerge at the end of the drought (Hynes 1958; Ward 1992). In their short adult life stage,



they may take advantage of newly formed pools in the stream for oviposition before the stream returns to normal flow.



Figure 40. *Nemoura* naiad, a common bryophyte dweller. Photo by Bob Henricks, with permission.

Mosses may often play an important role in providing moist sites for the aquatic insects during fluctuating conditions, but their role at such times has scarcely been investigated. In a Welsh mountain stream, severe flooding transported large quantities of gravel (Hynes 1968). Gravel-dwelling insects were greatly reduced, and the moss cover was reduced by 80%. But the fauna living among the remaining mosses was not significantly decreased. The stoneflies, caddisflies, and **Elmidae** (riffle beetles; Figure 41) recolonized the area before any reproduction could have contributed to their recovery. Hynes hypothesized that these insects migrated to deep within the benthic zone (away from abrasion) during the flood and then reappeared after the water level returned to normal.



Figure 41. **Elmidae** adult, a rapid colonizer of bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

## Water Level

Water level changes bring problems of not only hydration but also food availability for aquatic insects. Open-water carnivores can easily move and will most likely still have access to smaller insects and other

invertebrates for food. But those that feed on periphyton, and most likely on high quality detritus, may depend on the chambered bryophyte clumps for their dinner. Fortunately, these bryophytes help to provide both hydration and food for herbivores and detritus feeders. As the water level decreases, bryophytes can act like a filter to trap detrital matter from the slow water. In a Québec, Canada, stream, Cattaneo *et al.* (2004) found that many of the invertebrates moved to or remained among mosses (*Fontinalis dalecarlica*; Figure 34) at low water levels. Water depth explained 50-80% of the variation in the invertebrate biomass among the mosses and the biomass was lower on shallow mosses that had more frequent exposure. Grazers were more common in the moss habitat than in the gravel, but carnivores such as **Plecoptera** and **Odonata** were in the gravel.

## Stream Drift

**Stream drift** is a natural occurrence among stream fauna, especially insects (Anderson & Lehmkuhl 1968). Waters (1972) emphasized that this is an episodic event and not a continuous phenomenon. The drift organisms are bottom and vegetation organisms. When stream discharge is reduced by seasonal events, **catastrophic drift** can occur. Two primary organisms in such drift in Oregon, USA, are *Simulium* sp. and *Baetis tricaudatus*, both bryophyte dwellers (Corrarino & Brusven 1983).

**Catastrophic drift** (Minckley 1964) occurs from a physical disturbance such as flooding, **anchor ice** (ice anchored to bottom) (O'Donnell & Churchill 1954), pollution (Coutant 1964), drought, and high temperatures (Wojtalik & Waters 1970; Reisen & Prins 1972 for *Simulium* - Figure 22). **Behavioral drift** occurs at a particular time of day or night; it may result from crowding, competition, need for food, predation, making a new case, or attempting to reach land at emergence time (Waters 1972). **Constant drift** is comprised of small numbers that are always present as organisms move about and become dislodged from their substrates (Waters 1972).

Most drift occurs at night (Bishop 1969; Elliott 1965, 1968; Holt & Waters 1967), and it always moves the drifters downstream, at least initially. This night-time drift typically has two peaks: one just after darkness begins and one just before dawn (Waters 1972). But in some species, younger individuals may drift in the daytime and older, larger individuals at night (Anderson & Lehmkuhl 1968). Light often suppresses drifting in night drifters (Holt & Waters 1967); a full moon on a clear night can suppress it (Anderson 1966; Bishop & Hynes 1969).

Brusven (1970) found that the riffle beetle *Optioservus seriatus* (Figure 42) was much more likely to drift as an adult compared to its larval form. This species demonstrated the complexity of the drift phenomenon, with drift relating closely to density in one stream but not in the other in this study.

Larimore (1974) studied a very different kind of stream in the Salt Fork Basin, Illinois, USA. This stream ran through farmland where farm runoff was common and rooted macrophytes and bryophytes were absent. Only **Chironomidae** (Figure 9) among the drift organisms matched those found in cooler streams with rocky bottoms discussed above.





Figure 42. *Optioservus seriatus* adult, an insect more likely to drift as an adult than as a larva. Photo from ISUInsects.org, through Creative Commons.

Drift distances are usually not far. McLay (1970) found that the maximum drift in a New Zealand stream was 45.7 m, with a mean of only 10.7 m. Waters (1965) found that *Baetis tricaudatus* (Figure 43) travelled 50-60 m, but Elliott (1971a) showed that this strong swimmer was also capable of dropping out of the drift rapidly. Elliott (1967a) found that when dense macrophyte vegetation was present the maximum drift distance was only about 10 m. Nevertheless, this is sufficient to redistribute the insects and reduce local population competition.



Figure 43. *Baetis tricaudatus* naiad, a drifter that can travel 50-60 m in the drift, or drop out rapidly. Photo by Bob Henricks, with permission.

Many of the species enter the drift as young naiads and larvae, permitting them to disperse and to reduce population competition (Anderson 1967; Elliott 1967a, b; Waters 1969). But more frequently it is the larger stages later in the life cycle that enter the drift (Anderson 1967; Elliott 1967a; Müller 1966; Ulfstrand 1968). While drifting permits macroinvertebrates in streams to seek a more favorable location and to colonize new habitats, it poses its own set of threats (Brittain & Eikeland 1988). The insects may fall prey to predatory fish or fail to stop at a favorable habitat before reaching a quiet area of the stream where drift can no longer help them to relocate.

Some insects enter the drift to avoid or escape from predators. In experiments the net-spinning caddisfly *Ceratopsyche bronta* (Figure 44) moved from one area to another in an artificial stream when the predator stonefly *Acroneuria lycorias* (Figure 45) was present (Michael & Culver 1987). However, it did not exhibit the same drift response to the predator megalopteran *Corydalus cornutus* (Figure 46). Michael and Culver suggested that the caddisfly might have been unable to detect the megalopteran.



Figure 44. *Ceratopsyche bronta* larva, an insect that drifts in response to the presence of the predator stonefly *Acroneuria lycorias*. Photo by Bob Henricks, with permission.



Figure 45. *Acroneuria lycorias* naiad, predator on the caddisfly *Ceratopsyche bronta* larvae. Photo by Tom Murray, through Creative Commons.



Figure 46. *Corydalus cornutus* larva, a stream predator. Photo by Alan Cressler, with permission.



Researchers were curious about how the upstream positions got repopulated. Elliott (1971b) marked insects and found that some immature insects were able to move upstream on the stream bottom, especially small naiads of stoneflies and mayflies, small larvae of true flies, and beetle larvae. In winter, upstream movement was about 30% of downstream drift; in spring and summer it fell to only 7-10%. Madsen *et al.* (1973) examined upstream movement in adult mayflies and stoneflies and found that the representative of the common moss-dwelling stonefly genus *Nemoura* (Figure 40) did not move upstream, whereas the mayflies *Caenis rivulorum* (Figure 47), *Baetis rhodani* (Figure 2), *B. vernus* (Figure 48), and *Serratella ignita* (Figure 25) all moved upstream; all three of these mayfly genera are known from bryophytes. Furthermore, females migrated upstream more than males.



Figure 47. *Caenis rivulorum* naiad, a mayfly whose adults move upstream to lay eggs. Photo by Urmas Kruus, with permission.



Figure 48. *Baetis vernus* adult, a species in which females fly upstream to lay eggs. Photo by Walter Pfliegler, with permission.

Elliott (1971a) divided the drift invertebrates into three groups based on their ability to return to a substrate. The first group apparently had no control over their return to a substrate and did so at the same rate as dead organisms. This group included the *Chironomidae* (Figure 9). The second group includes several bryophyte dwellers, including *Leuctra* (Figure 49) and *Simulium* (Figure 22). These insects travelled shorter distances and were able to return to the substrate more quickly than dead ones at low velocities (10-12 cm sec<sup>-1</sup>) but not at faster velocities ( $\geq 19$  cm sec<sup>-1</sup>). The third group, which included bryophyte dwellers such as *Serratella ignita* (Figure 25), *Hydropsyche* spp. (Figure 13), and *Baetis rhodani* (Figure 2), returned to the substrate significantly faster and drifted significantly shorter distances at all velocities tested; *Baetis* and *Simulium* are usually the insects with the highest numbers in the drift (Waters 1972). Caddisflies with cases fall out of the drift very quickly.



Figure 49. *Leuctra* sp. naiad. Photo by Guillaume Doucet <<http://guillaume.doucet.free.fr/>>, with permission.

Elliott (2003) examined dispersal in nine genera of aquatic invertebrates, most of which occur among bryophytes. He found that dispersal of invertebrates in the streams was not density dependent. Rather, it was a constant percentage of the initial number of each species. The most rapid dispersers, with 70-91% dispersing within 24 hours, were the carnivores *Perlodes* (Figure 50), *Rhyacophila* (Figure 116), and *Isoperla* (Figure 20), travelling up to 13.5 m per day. *Protonemura* (Figure 104) and *Rithrogena* (Figure 51) exhibited about 50% dispersal within 24 hours and travelled only about 8 m per day. The third group, *Ecdyonurus* (Figure 15), *Hydropsyche* (Figure 13), *Gammarus* (Figure 52), and *Baetis* (Figure 2, Figure 48), only had about 33-40% dispersal in 24 hours and travelled only 5.5-7 m per day. All of these genera dispersed upstream. These examples do not answer the question of why drift, but they suggest that some of that downstream drift is compensated by upstream movement.



Figure 50. *Perlodes microcephala* naiad, a genus in the high dispersing insects of Elliott 2003. Photo by Niels Sloth, with permission.



Figure 51. *Rithrogena impersonata* naiad, a genus with 50% dispersal in 24 hours. Photo by Donald S. Chandler, with permission.



Figure 52. *Gammarus pulex*, a genus in the dispersing invertebrates of Elliott 2003. Photo by Niels Sloth, with permission.

Lehmkuhl (1969) found that the six mayfly species in his study, including the sometimes moss-dweller *Baetis tricaudatus* (Figure 43), were displaced by winter flooding. He found that in these species drift was not related to habitat. Two of the species that were abundant in the riffle areas were scarce in the drift. In the lab, drift rate did not correlate with ability of a species to hold to its substrate.

Lehmkuhl and Anderson (1972) demonstrated that drift of individual species is seasonal. Within the four species of *Ephemeroptera* studied, some species had peak drift in October and others in May. Winter floods accounted for lesser peaks in drift. Periods of low drifting occur when a species is in its egg state, suggesting that life cycle stages are among the determinants of who is drifting.

Some insects enter the drift at the time of emergence, not by choice, but because they must at that time break through the water-air interface and penetrate the surface tension. If there is no suitable emergent rock or vegetation, this becomes a nearly impossible task. Bryophyte-covered rocks can afford a better place to climb out than a smooth rock. However, there is thus far no study to determine if any insect group might seek out bryophytes as opposed to just rocks for this dangerous endeavor.

The behaviors of the *Hydropsyche* spp. (Figure 13) are worthy of note. This net-spinning caddisfly must live near the water surface where it can trap food in its nets (Edington 1968). When released into the water, larvae would swim with side-to-side movements toward the surface (Edington 1965; Elliott 1971a). When the velocity was slow, they returned to the bottom (Elliott 1971a). When they encountered mosses in swift-flowing areas they made "firm contact." It appears that bryophytes may have a role in catching these drifters.

Elliott (1967a) suggested that aquatic plants served as a natural net for drifting insects. Previously Elliott (1965) examined invertebrate drift in a Norwegian mountain stream where bryophytes formed a dense bottom cover. He did not show a direct link between the bryophyte fauna and drift, but did list the dominant insects in both. Using 400 cm<sup>2</sup> samples, he found *Baetis* sp. (Figure 2), *Simulium* spp. (Figure 22), *Rhyacophila* sp. (Figure 79), *Polycentropidae* (Figure 24), and *Plecoptera* (Figure 49). When he

calculated those insects in the water column above a square meter of bottom at any time, he found that the values were extremely low, although all the insects among the top taxa in the mosses except *Polycentropidae* were also in the drift.

At least some of the bryophyte dwellers are drift organisms, including *Simulium* (Figure 22), *Isoperla* (Figure 20), and *Ephemerella* (s.l.) (Figure 8) (Minshall & Winger 1968). In these three genera, the drift is suppressed by light, including that of a full moon on a clear night. Density may play a role in the number of individuals entering the drift, as in *Capniidae* (Figure 109), *Ephemerella* sp., and *Hydropsyche* sp. (Figure 13) in a South Carolina, USA, stream (Reisen & Prins 1972; see also Waters 1962, 1966). And, to my surprise, Minshall and Winger (1968) found that reductions in flow cause an increase in drift. The latter may relate to the need for a new location to gain suspended food or oxygen. To this end, *Simulium* larvae may drift at least 100 m (Carlsson 1967). Elliott (2002) calculated the rate of drift and found that most of the organisms had a very constant amount of time spent in a drifting event. For *Serratella ignita* (Figure 25) the mean drift time was 28.8 s, whereas for *Baetis rhodani* (Figure 2) it was 9.4 s, the same drift time as for the amphipod *Gammarus pulex* (Figure 52). For the blackfly *Simulium* it was only 6.4 s, with their choice of rapid water accounting for the 100 m drifting they can accomplish.

In Oregon, USA, Anderson and Lehmkuhl (1968) likewise found known moss dwellers in the drift: the mayflies *Paraleptophlebia* (Figure 53) and *Baetis* (Figure 2), the stoneflies *Nemoura* (Figure 40), *Capnia* (Figure 109), and possibly *Leuctra* (Figure 49) (small *Capnia* and *Leuctra* are difficult to distinguish), dipterans *Chironomidae* (Figure 9) and *Simuliidae* (Figure 22). Dendy (1944) likewise found *Baetis*, *Nemoura*, *Simuliidae*, *Chironomidae*, and *Hydropsychidae* (Figure 13) in the drift in a stream in Michigan, USA, but added significant numbers of the mayfly *Ephemerella* (s.l.) (Figure 8) and caddisfly *Brachycentrus americanus* (Figure 54) to those found by Anderson and Lehmkuhl. To these, Reisen and Prins (1972) added the stoneflies *Isogenus* (probably now *Isogenoides*; Figure 55) and *Isoperla* (Figure 20).



Figure 53. *Paraleptophlebia bicornuta* naiad, a moss-dweller genus that enters the drift. Photo by Bob Newell, with permission.





Figure 54. *Brachycentrus americanus* larva, moss dweller that enters the drift. Photo by Donald S. Chandler, with permission.



Figure 55. *Isogenoides frontalis* larva, a moss-dweller that enters the drift. Photo by Donald S. Chandler, with permission.

Bryophytes may provide safe sites for drifting organisms, primarily insects. There is a periodicity in stream drift, with light, even strong moonlight, suppressing activity (Albrecht 1968). Numerous organisms, particularly stoneflies, mayflies, and caddisflies, become detached from their substrate and join the water current (Bishop & Hynes 1969). Diptera are day-active and contribute significant numbers to daytime drift. Lest they travel ultimately to a lake or even the distant sea, these drifting organisms must find a suitable substrate where they can cling against a sometimes raging current. Furthermore, it is during these excursions that they are most visible and vulnerable to predation by birds and especially fish.

Bryophytes would seem to provide an ideal location for regaining their composure and taking a more leisurely approach to locating a suitable settling place. The 3-d surface of the bryophyte provides numerous "handles" for hanging on in the current and gives the insects either an instant home or one that can be traversed while maintaining a safe hold to something permanent. On the other hand, one theory for the cause of drift is to decrease population numbers (Müller 1954; Waters 1961, 1962; Pearson & Franklin 1968; Bishop & Hynes 1969). If such is the case, a rock with both smooth surface area and bryophyte cover

would support such loss by forcing at least some individuals to the smooth rock as the bryophyte itself becomes overpopulated. This would seem to eventually provide a selection factor against those organisms that did not do their nightly foraging among the mossy safe site. Is there really a selection factor involved in moss-seeking behavior?

Glime and Clemons (1972) set out to determine the relative importance of bryophytes in catching such insects and constructed artificial mosses to determine how the new colonizers compared to the organisms in the drift. Clemons (unpubl data; Glime & Clemons 1972) used string mosses to determine the use of substrata similar to mosses as a catching net for drifting organisms and compared this substrate to that of real mosses and Visqueen (polyethylene plastic sheeting) strips. In the 24 hours following the placement of 7 of these artificial mosses, insects were found on the strings. These included the mayfly *Baetis* sp. (Figure 2), stoneflies *Amphinemura nigritta* (= *Nemoura venosa*) (Figure 56) and *Leuctra* sp. (Figure 49), blackflies *Cnephia* sp. (Figure 57) and *Prosimulium mixtum* (Figure 58), midges *Chironomidae* (Figure 9), and the caddisfly *Lepidostoma* sp. (Figure 59) occurring in more than one of the string habitats. The Visqueen strips had a smaller and less diverse fauna. While this experiment provides evidence that insects can settle on such substrates rather quickly from the drift, much more study is needed to determine the importance of bryophytes in providing safety nets for drifting insects. Gurtz and Wallace (1984) found that following a major disturbance that dislodged many of the insects, it was moss-covered rock faces that increased in insect density more than any other substrate. Furthermore, they considered that the mosses may enhance the stability of the substrate on which they reside.



Figure 56. *Amphinemura nigritta* naiad, a rapid bryophyte colonizer. Photo by Donald S. Chandler, with permission.



Figure 57. *Cnephia* adult, a genus that sometimes lives among bryophytes and enters the drift. Photo by Sam Houston, with permission.



Figure 58. *Prosimulium mixtum* larva, a blackfly that lives among bryophytes and enters the drift. Photo by Tom Murray, through Creative Commons.



Figure 59. *Lepidostoma* larva, a drifting caddisfly that sometimes lives among bryophytes. Photo by Jason Neuswanger, with permission.

In alpine streams the drift pattern may differ. Hieber *et al.* (2003) found no night-day differences in these streams. They found that **Chironomidae** (Figure 9) were the dominant drifting organisms, so one might look at this group in alpine streams as creating more food for fish in streams with mosses than in those without.

The complex structure of bryophytes may not only catch drift, but it may also deter stream drift. Holomuzki *et al.* (1999) found that resettlement choices after drifting by hydropsychid caddisfly larvae depended on the complexity of the algal community. Drift entry of hydropsychids due to stonefly predation increased on rocks with a biofilm, but not on rocks with a thick periphyton mat or macroalgae such as *Cladophora* (Figure 60), with drift inversely related to the amount of *Cladophora* on the rocks. Since bryophytes are even more complex in structure, it is reasonable to assume that they reduce drift.



Figure 60. *Cladophora crispata*, a filamentous alga that keeps **Hydropsychidae** from entering the drift in the presence of predatory stoneflies. Photo by Yuuji Tsukii, with permission.

It is interesting that when Perić *et al.* (2014) sampled the invertebrate drift in a moss-rich **karst** (landscape underlain by limestone that has been eroded by dissolution, producing characteristic landforms) stream system, they did not find the **Chironomidae** (Figure 9) (3.9%) to be the most abundant. Rather, the most abundant insects were the beetles in **Elmidae** (Figure 41) (13.2%) and blackflies **Simuliidae** (Figure 58) (12.2%).

So let's revisit the possibility that other bryophyte dwellers besides **Chironomidae** do not enter the drift as readily as insects on other substrates. Brusven *et al.* (1990) found that in a channel of the South Fork Salmon River, Idaho, USA, the 20% moss-covered portion (*Fontinalis neomexicana*, Figure 4) had 1.6-7.2 times the diversity of the moss-free channel and 1.4-6.1 times the biomass. But the mossy portion did not have any greater numbers in the drift than did the moss-free channel. This, however, does not offer us much on which to base a conclusion because the study only included daytime drift. Their drift organisms were more than 50% **Chironomidae** (Figure 9), a group that drifts equally in day and night (Anderson & Lehmkuhl 1968). The implications for fish are that the bryophytes do not benefit them because the food organisms they house do not increase the daytime drift, at least in this one example.

## Safe Sites

For many insects, the mosses offer a safe site, a pool-like environment in which they can forage for food without danger of being swept away by rapidly flowing water. Beetles (**Coleoptera**), scuds (*Gammarus*; Figure 52) and mites occupy only sheltered niches and mosses in the Welsh Dee (Badcock 1949). On vertical faces of waterfalls, the dipteran *Limnophora* (Figure 61) can be found only in moss (Badcock 1949).



Figure 61. *Limnophora* larva, sometimes a bryophyte dweller. Photo by Stephen Moore, Landcare Research, NZ, with permission.

In aquatic habitats, fish are a major predator on insects. The result is that fishless lakes have a higher insect species richness and diversity than lakes inhabited by fish, as demonstrated for chironomids (midge larvae) (Mousavi *et al.* 2002). Bryophytes are typically inhabited by many **Chironomidae** (Figure 9) and when present in lakes or streams they can provide safe sites with loads of detrital food.



Several studies have alluded to the possibilities of bryophytes in providing a **refuge**, a location in the stream where the small organisms can escape predation by larger ones. For example, Parker *et al.* (2007) found twice as many insects on *Fontinalis novae-angliae* (Figure 62) as on *Podostemum ceratophyllum* (Figure 62). One possibility is that the insects are avoided because the moss provides an unpalatable location – an **enemy-free space**. Parker *et al.* (2007) remind us that a number of studies have shown that small herbivores that use plants as both a habitat and a food source may be protected by living on hosts that are chemically defended against wood-be insect consumers. Aquatic mosses may be just such safe sites. To test this hypothesis, Parker and coworkers observed the feeding habits of the Canada goose (*Branta canadensis*, Figure 63-Figure 64) and a crayfish (*Procambarus spiculifer*, Figure 65). In a riverine system where both the riverweed *Podostemum ceratophyllum* (Figure 62) and the moss *Fontinalis novae-angliae* (Figure 62) occurred, both animals consumed riverweed in preference to the moss. This was despite the fact that the moss comprised 89% of the plant biomass. At the same time, there were twice as many macroinvertebrates among the mosses as associated with the riverweed. Examination of the moss chemistry revealed the presence of C<sub>18</sub> acetylenic acid, octadeca-9,12-dien-6-ynoic acid, a compound that deterred the crayfish from eating it. Some invertebrates, on the other hand, had different connoisseurial preferences; the amphipod *Crangonyx gracilis* (Figure 66) and the isopod *Asellus aquaticus* (Figure 67) rejected the riverweed, but consumed significant quantities of *Fontinalis novae-angliae*. For periphyton-consuming insects, the same chemical deterrents could protect them without affecting their food source.

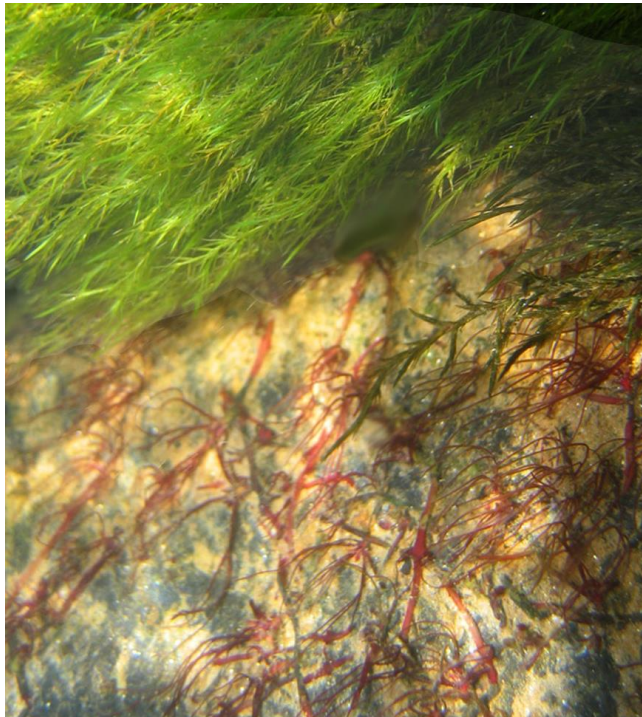


Figure 62. *Podostemum ceratophyllum* (red) and *Fontinalis novae-angliae*, the latter protecting invertebrates from grazing by geese. Photo by John Parker, with permission.



Figure 63. Canada Goose (*Branta canadensis*) searching for food. Photo by Eileen Dumire, with permission.



Figure 64. Canada Geese (*Branta canadensis*) grazing on *Podostemum ceratophyllum*. Photo by John Parker, with permission.

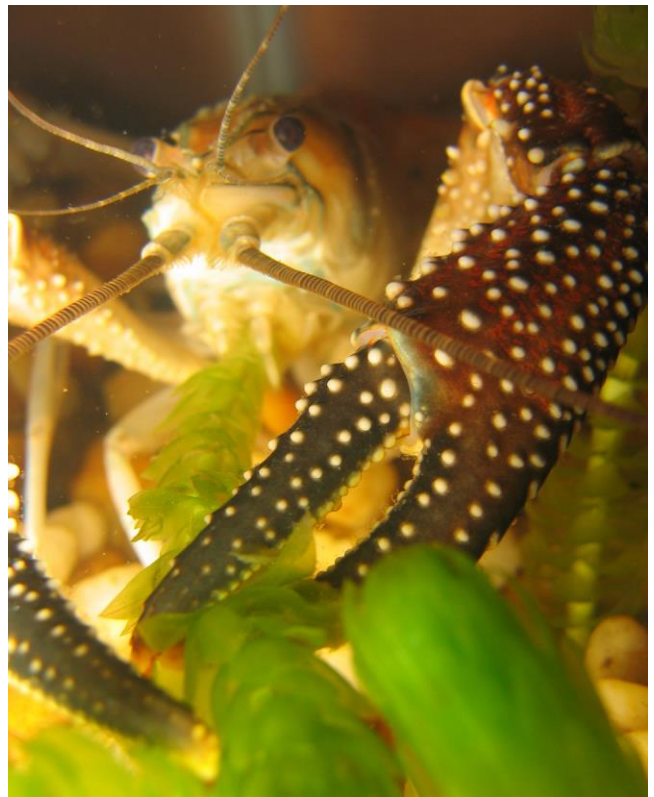


Figure 65. *Procambarus spiculifer* eating *Egeria*. Photo by John Parker, with permission.





Figure 66. *Crangonyx* sp., an amphipod *Fontinalis* consumer. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Figure 67. *Asellus aquaticus*, an isopod *Podostemum* avoider and *Fontinalis* consumer. Photo by Niels Sloth, with permission.

But bryophytes are not always selected for their provision of shelter. Using experimental reduction of bryophyte stem density in New Zealand alpine streams, Suren and Winterbourn (1991b) found that only two out of 22 taxa of invertebrates selected the bryophytic home based on shelter as the primary factor in the shaded site; none of them selected it based primarily on its offer of shelter in the sunny site. Rather, periphyton or detrital biomass were the primary influencing factors.

Winterbottom *et al.* (1997) cleverly tested the importance of refugia against the effect of reduction of shear stress during periods of peak flow by creating artificial refugia using cages of different mesh sizes to restrict the flow within cages. They compared a 1.1 mm mesh size that created a reduced flow within the cage with that of a 15 mm mesh size that did not restrict flow. They found that during periods of high flow the invertebrates accumulated more in the flow-restricted refugia than they did there during low-flow periods or in the unrestricted cages. By contrast, in a second stream with lower flow rates generally and during the experimental period, the number of invertebrates did not increase in the refugia during natural spates of increased flow (but less flow than in the first stream), suggesting that the reduced flow in the 1.1 mm mesh cages enabled them to serve as refugia in the first stream during periods of rapid flow. However, the researchers were unable to determine if the accumulation of invertebrates was by active movement to the refugia or by passive collection. Nevertheless, this experiment

demonstrates that bryophytes with different mesh sizes could provide differential refugia for insects during periods of high flow rates.

## Biomass and Richness

Many insects hang out among the riffles, taking advantage of the flowing water that brings food and oxygen. Dodd (2011) found that in a river community 516 out of 521 individuals collected occurred among riffles and mosses. These are the sites where biomass and richness usually reach their peaks.

Clenaghan *et al.* (1998) concluded that macroinvertebrate density and richness increased with moss weight. Wulforst (1994) compared the biomass of insects among mosses with those in the interstitial spaces of the substrate (Figure 68). In general, they were orders of magnitude higher (100's of times) in biomass among the mosses. These included **Ephemeroptera**, **Plecoptera**, **Trichoptera** and **Coleoptera** (EPTC).

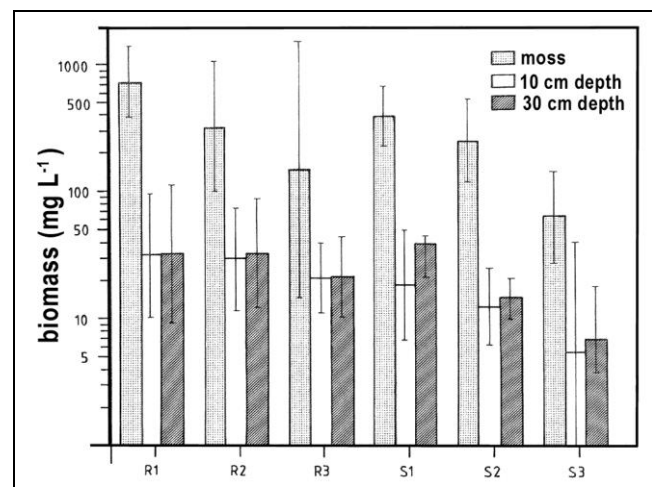


Figure 68. Combined biomass ( $\text{mg L}^{-1}$ ) of **Ephemeroptera**, **Plecoptera**, **Trichoptera**, and **Coleoptera** at six stations of two brooks in the Harz Mountains in mosses and interstitial spaces of the hyporheic zone at 10 and 20 cm depth. Bars show 95% CI.  $N = 14$  for mosses, 28-36 for interstitial spaces. Redrawn from Wulforst 1994.

Linhardt *et al.* (2002a, b) examined the **meiobenthos** (meiofauna; between .1 mm and 1 mm in size) of two low-order streams (*i.e.*, small feeder streams) and found that these bryophytes harbored ten times as many organisms as the surrounding mineral bed. In this case, the **Chironomidae** (midge larvae, Figure 9) were the dominant organisms, but a number of other aquatic insects and other invertebrates call this location home, at least in the early stages of their lives.

Brusven *et al.* (1990) studied the effect of bryophyte biomass on macroinvertebrate density in the South Fork of the Salmon River, Idaho, USA. They compared the insect densities on sand, pebbles, cobbles, and the moss *Fontinalis neomexicana* (Figure 4). Insect densities in moss clumps were 4-18 times as great as those in adjacent mineral substrata. Although mosses occupied only 20% of the channel, insect density was 1.6 to 7.2 times as great, with 1.4 to 6.1 times as much insect biomass as the moss-free channel, thus accounting for nearly 50% of the insects in the stream. Midges (**Chironomidae**, Figure 9) typically comprised over 50% of the insect community, whereas



annelids were the primary non-insect invertebrates. The moss seemed to provide a safe site, at least during the day, because despite the greater number of insects present, daytime drift was not greater. Hence, the salmonid fish that feed primarily on drifting invertebrates during the day derive little benefit from the increased numbers in the bryophytes.

On the other hand, Tada and Satake (1994) found that in a cool mountain stream in Japan macroinvertebrates from *Platyhypnidium riparioides* (Figure 19) had 11-13 taxa (species), whereas bare rock bottoms had 13-14. Nevertheless, the caddisfly *Micrasema* sp. (Figure 69) exceeded 100,000 individuals per m<sup>2</sup> of mosses in November, a level that ranged 2.8-16.3 times as high as that on the bare rock bottom.



Figure 69. *Micrasema charonis* larva, a common genus on bryophytes. Photo by Robert G. Henricks, with permission.

Chantha *et al.* (2000) found that the invertebrate communities of bryophytes and algae in a Quebec, Canada, stream were dominated by **Chironomidae** (especially **Orthocladinae**; Figure 9). The algae and invertebrates formed stable communities during the summer, even sustaining during strong mid-summer flooding. Like many other northern streams, the **Ephemeroptera** and **Coleoptera** were important components. The relative importance of the various taxa changed with the seasons as sizes and life cycle stages changed. Moss biomass explained 43% of the algal spatial variation, but surprisingly the periphyton did not increase proportionally with increase in moss biomass. The epiphytes were less dense per unit of bryophyte biomass as the bryophyte biomass increased in density. Insects in this system became more abundant, but smaller, as the moss biomass increased, with a net result of little change in insect biomass per moss biomass. This may be a function of decreased light for algal growth and decreased oxygen for insects in deeper parts of the moss mat.

Matthaei *et al.* (2006) found that runoff from land use could reduce both aquatic mosses and invertebrate density. The greatest decrease in richness occurred in **Ephemeroptera**, **Plecoptera**, and **Trichoptera**, the three most abundant moss-dwelling orders that move among the open spaces of the bryophyte mats.

## Food Sources

Bryophytes harbor a wide variety of invertebrates that can serve as food for the larger members of the bryophyte fauna. Dražina *et al.* (2011) reported 100 taxa of meiofauna among bryophytes in a European study. For example, rotifers averaged 219 individuals per cm<sup>3</sup>.

Bryophytes are usually predominate in the upper reaches of streams where the flow rate is greater and the stream is shaded. Shredders likewise predominate among the bryophytes in these reaches. Hawkins and Sedell (1981) found that functional groups characterized different stretches of the river continuum. Upstream in shaded reaches the shredders were dominant. Scrapers were most important in the intermediate sections. Collectors increased in importance progressively downstream. Predators were represented equally throughout the stream.

Mosses seem to afford ideal feeding locations for some kinds of insects. In particular, filterers and scrapers can be more common there than elsewhere in streams, showing a positive correlation with such habitats, whereas shredders are negatively correlated, *i.e.*, are moss avoiders (Ely 2005). On the other hand, Zalewski *et al.* (2001) found a significant correlation between **CPOM** (coarse particulate organic matter), bryophytes, and shredders. Smith-Cuffney (1987) found that mosses in streams of a clearcut community supported collector-gatherers, whereas in the forested streams the shredders formed a much larger proportion of the moss fauna.

Cattaneo *et al.* (2004) found that in a Québec stream grazers were more abundant in mosses than among gravel, suggesting that they used the periphyton. The reduction of periphyton when shallow water mosses are exposed may explain why deeper mosses might house more invertebrates.

Wallace *et al.* (1988) found that the mosses retained large amounts of detritus, providing abundant food for collector-gatherers. Like Ely, they found that scrapers reached greatest abundance on cobbles and pebbles that were free of mosses. Smith-Cuffney (1987) found that in a southern Appalachian Mountain stream, mosses in a clearcut community of a forested watershed supported predominantly collector-gatherers with shredders as a minor component. Shredders were a much larger component in the stream that drained the clearcut. Scrapers were more common in the clearcut system where periphyton were abundant. Collector-filterers such as *Parapsyche cardis* (see Figure 70) benefited from the physical environment provided by the mosses.

Although aquatic mosses are seldom eaten by their inhabitants (Haefner & Wallace 1981), they can provide a rich food source through the other inhabitants. Fontaine and Nigh (1983) considered the periphyton (Figure 71) on bryophytes to be an important food source. In New Zealand, periphyton and detritus were primary food sources (Suren 1993). Unfortunately, bryophytes tend to be shade plants and periphyton tends to prefer the sun, so the periphyton is not at its max. Nevertheless, invertebrate densities were higher among mosses containing periphyton than among those with detritus, most likely reflecting the higher food quality of periphyton. Ogbu and Akinya (2001) likewise found that mosses in Nigeria provided a suitable substrate for periphytic algae, especially diatoms.



Figure 70. *Parapsyche apicalis* larva, member of a genus known to seek shelter in bryophytes. Photo by Donald S. Chandler, with permission.



Figure 71. Stream mosses in Tucquan Creek, Lancaster County, Pennsylvania, USA, laden with a detrital-periphyton complex. It is likely that the schist bedrock is contributing to the light color. Photo by Keith Williams, with permission.

McWilliam-Hughes *et al.* (2009) found *Fontinalis* sp. (Figure 4) abundant in headwater streams and *Drepanocladus* (*s.l.*) sp. (Figure 72) abundant in low-order streams. The scrapers living in low-order streams seemed to depend more on *Fontinalis* as a food source than did scrapers in high-order streams depend on *Drepanocladus* (*s.l.*). They suggested that in low-productivity, nutrient-limited rivers primary consumers might switch to marginal food sources such as bryophytes when more preferred food is limited or unavailable.

The feeding guilds change with the seasons. Habdija *et al.* (2004) found that current velocity and food supply affected the composition of insects inhabiting bryophytes in karst streams. Those inhabiting the bryophytes were predominantly small forms of oligochaetes, **Diptera** (Figure 58), and **Coleoptera** (Figure 41), comprising 64.1-98.7% of the total macroinvertebrate individuals. **Collector-gathers** dominated in spring and summer, whereas in autumn it was **collector-filterers**, and in winter

**scrapers** reached their maximum. Gregg and Rose (Gregg 1981; Gregg & Rose 1985) found that among the **tracheophytes** (plants with lignified vascular tissue, *i.e.*, all plants that are not bryophytes), shredders, scrapers, and predators were the primary guilds in the autumn and that all guilds had their highest abundances in spring. Bryophytes offer the advantage of being present year-round, and their extensive periphyton growths provide a good winter food source for those insects that remain active in the winter. It is interesting that Gregg found that *Hydropsyche* (Figure 13), *Simulium* (Figure 22), *Baetis tricaudatus* (Figure 43), *Glossosoma velona* (Figure 73), and *Helicopsyche borealis* (Figure 74) avoided macrophytes, whereas all of these genera are known from bryophytes (though *Helicopsyche* is rare there). One problem for these insects was that the tracheophytes reduced the velocity, creating problems for these high-oxygen taxa. The advantage in the presence of tracheophytes seemed to be that of increasing heterogeneity, an advantage also offered by bryophytes.

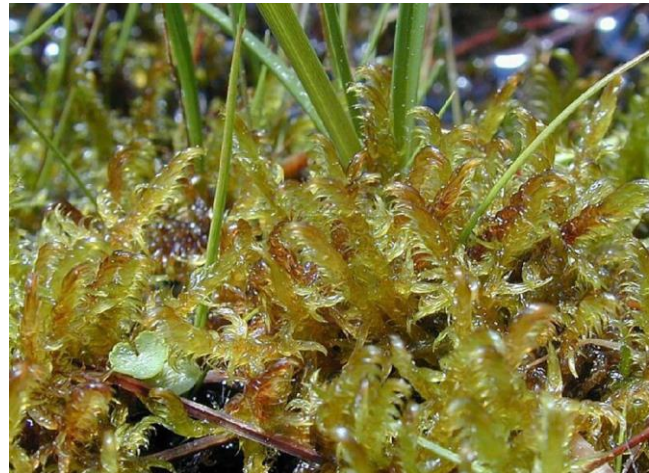


Figure 72. *Drepanocladus exannulatus*, a less desirable food source than *Fontinalis* for insect scrapers. Photo by Michael Lüth, with permission.



Figure 73. *Glossosoma* sp. larvae, a tracheophyte avoider that lives among bryophytes. Photo by Jason Neuswanger, with permission.





Figure 74. *Helicopsyche* sp. larva & case. *Helicopsyche borealis* avoids tracheophytes, but the genus is known from bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Thus, we have seen that the reduced water velocity within a bryophyte mat (Devantery 1987; Suren 1991) makes the bryophytes suitable safe sites not only for insects, but also for the periphyton and detrital food components, as shown in New Zealand (Suren 1991), as well as for the insect prey species, as shown in the North Temperate Zone (Elliott 2005).

### Bryophytes as Food

Early reports indicated that bryophytes were ingested, but the food value remained in question. Nevertheless, *Fontinalis* (Figure 4) was found in gut contents (Gaevskaya 1969). Jones (1949, 1950) found *Fontinalis* in the guts of the stoneflies *Amphinemura* (Figure 105), *Chloroperla* (Figure 23), *Dinocras* (Figure 75), *Leuctra* (Figure 49), and *Protonemura* (Figure 104), the mayflies *Ecdyonurus* (Figure 15) and *Ephemerella* (s.l.) (Figure 8), as well as in the caddisflies *Hydropsyche* (Figure 13) and *Philopotamus* and the beetle *Oreodytes* (Figure 76).



Figure 75. *Dinocras cephalotes* naiad, a stonefly genus that eats mosses. Photo by Guillaume Doucet <www.guillaume.doucet@yahoo.fr>, with permission.

Jones (1951) considered *Fontinalis antipyretica* (Figure 18) to be one of the main foods for herbivorous insects in his study of the River Towy, Wales. But Dangles (2002) cautions us against categorizing food habits by

generic or higher levels. In his study of four streams in northeastern France he found that two species in the same genus with very similar mouthparts had different diets, one feeding on bryophytes and the other on detritus, including leaf litter.



Figure 76. *Oreodytes septentrionalis*, a genus including bryophyte consumers. Photo by Brian Eversham, with permission.

Caddisflies *Pycnopsyche guttifera* (Figure 77) and *Philocasca alba* both feed on mosses. In an interesting study, Mutch and Pritchard (1984) found that the late-instar larvae of *Philocasca alba* had significantly higher growth rates if their diet of detritus or leaf litter was supplemented with mosses.



Figure 77. *Pycnopsyche guttifera* larva, a consumer of mosses. Photo by Donald S. Chandler, with permission.

Tada and Satake (1994), working with insects on mats of the moss *Platyhypnidium riparioides* (Figure 19) in a cool mountain stream in Japan, found the mayflies *Baetis* (Figure 43) and *Ephemerella* (s.l.) (Figure 8), the stoneflies *Acroneuria* (Figure 45) and *Isoperla* (Figure 20), and the caddisflies *Micrasema* (Figure 69), *Rhyacophila* (Figure 79), and *Palaeagapetus rotundatus* not only live among the bryophytes, but also feed on the leaves of the leafy liverwort *Chiloscyphus polyanthos* (Figure 78) and *Scapania undulata* (Figure 10). Interestingly, they do not feed on leaves of the moss *Platyhypnidium riparioides*, suggesting the possibility of antifeedant compounds in that species.





Figure 78. *Chiloscyphus polyanthos* in the fluctuating water level zone where several kinds of insects eat the leaves. Photo from <www.aphotofauna.com>, with permission.

Even the free-living carnivore caddisfly *Rhyacophila dorsalis* (Figure 79) apparently eats mosses (Slack 1936). One out of nine had *Fontinalis antipyretica* (Figure 18) leaves in the gut. For the mayfly *Ephemerella* (s.l.) (Figure 8), *Fontinalis* is a common food (Jones 1949). *Ephemerella* (s.l.) feeds on the green alga *Ulothrix* when it is available, but feeds on the ever-present moss when the alga is scarce or absent (Jones 1949). On the other hand, in a different study, Jones (1950) found that beetles and mayflies did not eat *Fontinalis* (Figure 18), but the moss was in the gut of *Chloroperla* (Figure 23), *Leuctra* (Figure 49), *Protonemura* (Figure 104), and *Amphinemura* (Figure 105), all stoneflies, and in the gut of the net-spinning caddisfly *Hydropsyche* (Figure 13) – a genus that traps its food with a net. In addition to using the moss for housing, the caddisfly *Micrasema* (Figure 69) eats mosses and associated periphyton (Chapman & Demory 1963; Decamps & Lafont 1974). Chapman and Demory (1963) found that in its preferred food was *Platyhypnidium riparioides* (Figure 19). It is possible that many insects eat the mosses primarily for their associated periphyton, but for *Micrasema* it appears that the primary target is the mosses themselves. Even the filter-feeding blackflies such as *Simulium tuberosum* (Figure 80) will feed on aquatic mosses (Jones 1949), but we need to check to see if they are really digested.



Figure 79. *Rhyacophila dorsalis* larva, a moss consumer. Photo by Walter Pfliegler, with permission.



Figure 80. *Simulium tuberosum* larva, known to have mosses in its gut. Photo by Tom Murray, through Creative Commons.

Most members of the caddisfly genus *Rhyacophila* (Figure 79) are carnivores, although some of these bryophyte dwellers eat bryophytes. Perhaps more importantly is their ability to hide among the mosses to ambush their prey at dusk and dawn [e.g. *Baetis* (Figure 43), *Gammarus* (Figure 52)]. Elliott (2005) found most of the *Rhyacophila dorsalis* (Figure 79) among clumps of the leafy liverwort *Scapania* (Figure 10) and the mosses *Platyhypnidium riparioides* (Figure 19) and *Fontinalis antipyretica* (Figure 18). Although most of the *Rhyacophila* species are carnivores, most of their guts had fragments of bryophytes, but these appeared to be undigested, exhibiting chlorophyll. Older individuals fed primarily at night and diatoms occurred in 29% of the guts of 4th instars; bryophytes occurred in 25%. However, in the 5th instar, only 9% contained diatoms and 7% contained bryophytes. The *Rhyacophila* larvae would disappear into the moss colony to search for food, then return to the bryophyte surface to eat it. These observations suggest that the bryophytes may have been eaten inadvertently when capturing prey.

The inadvertent consumption of bryophytes by carnivores is a likely occurrence in a number of insects. For example, Jones (1950) found *Fontinalis* (Figure 14) in the guts of *Plecoptera* [*Chloroperla* (Figure 23), *Leuctra* (Figure 49), *Protonemura* (Figure 104), *Amphinemura* (Figure 105)] and *Trichoptera* (*Hydropsyche*, Figure 13), but these could have resulted from bits of the moss mixed in with their typical food. *Hydropsyche* is a filter feeder, spinning its own nets to trap food, but bits of drifting moss may get trapped in the net. Nevertheless, Jones did not find any *Fontinalis* in guts of either *Coleoptera* (beetles) or *Ephemeroptera* (mayflies) in these same collections.

### Nutritional and Antifeedant Properties

Few protein values are published for aquatic mosses, so we cannot judge if any relationship to protein content is typical. However, it has been a common view among biologists that mosses are avoided as food because of their low food value, among other reasons. Nevertheless, Winterbourn and co-workers (1986), using  $C^{13}$  ratios, found bryophytes to be important sources of carbon for the benthic fauna in two British rivers.



Suren and Winterbourn (1991a) examined the gut contents of 23 invertebrate taxa that dwell among bryophytes in two New Zealand alpine streams. Fourteen of these taxa had bryophytes in the guts, but the researchers found that only the tipulid larvae of *Limonia hudsoni* (Figure 81) and caddisfly larvae *Zelandopsycha ingens* (Figure 82) and *Oeconesus similis* (Figure 83) regularly consumed the bryophytes. They found that the bryophytes contained more refractory and indigestible compounds than other riparian plants and were thus less nutritious for the animals. They suggested that the bryophytes might also contain **antifeedant** compounds (compounds that discourage herbivory). Such compounds do exist in aquatic bryophytes, including *Fontinalis* (Liao 1993; LaCroix 1996). But we must keep in mind that modifications of digestive systems and their pH and enzymes make these "indigestible" foods digestible to some specialists (see discussion in Chapter 10-3 on *Asellus*).



Figure 81. *Limonia* larva; some species are regular consumers of bryophytes. Photo courtesy of State Hygienic Laboratory, University of Iowa, with permission.



Figure 82. *Zelandopsycha* larva & case; some species include bryophytes in their regular diet. Photo by Stephen Moore, Landcare Research, NZ, with permission.

But sometimes the consumed mosses carry with them associated periphyton that might be the real food source, as in *Micrasema* (Figure 69) of the Pyrénées (Decamps & Lafont 1974). Dudley (1988) likewise considered that the real food might be the associated periphyton. Suren (1988) similarly concluded that the mosses were not an important food source, citing the similarity of faunal communities on

artificial mosses that became colonized with periphyton. But separating assimilation of moss tissue vs periphyton is a challenging endeavor.

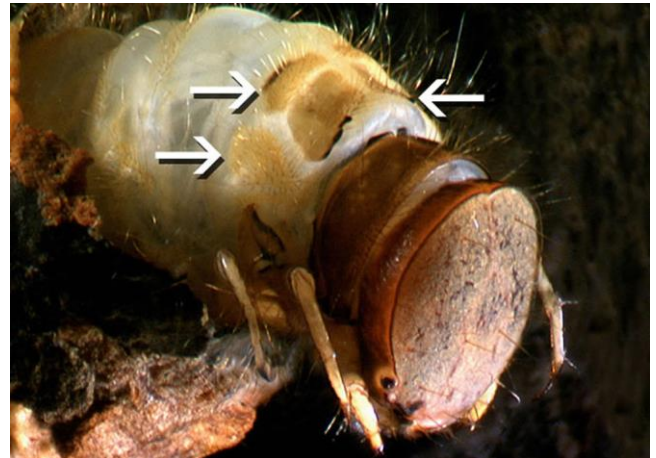


Figure 83. *Oeconesus* larva head; *O. similis* frequently eats bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Modern methods have made it somewhat easier to determine the diets of aquatic insects. Using  $\Delta^{13}\text{C}$ , Winterbourn *et al.* (1986) demonstrated the importance of bryophytes as important food sources. It is surprising that so many invertebrates eat aquatic mosses. Pritchard and Berté (1987) found that the aquatic moss *Leptodictyum* (Figure 84) had the lowest protein content of the five foods tested (wheat flakes, alder, burreed, willow leaves, *Leptodictyum*). Wheat flakes and alder had the most, burreed and willow leaves were next. Nevertheless, Pritchard and Berté (1987) found that despite the low nutritional value in *Leptodictyum*, the caddisfly *Limnephilus externus* (Figure 85) chose mosses second out of the five choices, and the caddisfly *Nemotaulius hostilis* (Figure 86) chose mosses third among these choices. As the larvae grew, they increased their intake of moss, preferring it over alder or willow. Their preference for burreed over moss varied and was sometimes equal. Nevertheless, *N. hostilis* grew more slowly on mosses than on alder or burreed.



Figure 84. *Leptodictyum riparium*, an aquatic moss with lower protein content than several tracheophytes, but still eaten by the caddisfly *Limnephilus externus*. Photo by David T. Holyoak, with permission.





Figure 85. *Limnephilus externus* larvae, consumers of the moss *Leptodictyum*. Photo by Bob Newell, with permission.



Figure 87. *Calliergon cordifolium*, a moss in which acetylenic fatty acids comprise 6.6% of the triacylglycerols. Photo by Michael Lüth, with permission.



Figure 86. *Nemotaulius hostilis* larva in case. This species chooses mosses third compared to tracheophyte choices. Photo by Donald S. Chandler, with permission.



Figure 88. *Riccia fluitans*, a thallose aquatic liverwort that contains 80.2% acetylenic fatty acids in its triacylglycerols. Photo by Jan-Peter Frahm, with permission.

### Tracing Bryophytes in the Food Chain

If identification of assimilated bryophytes is a challenge, the identification of the role of bryophytes in the food chain is an even greater challenge. To what degree is the assimilated carbon from bryophytes passed upward to predators and top carnivores? Or is it simply stored in the insect tissues and unavailable to them? Or is it mostly lost through **egestion** (process of ridding the body of undigested or waste material; defecation; not to be confused with elimination of nitrogenous waste such as that in urination)?

Identification of unique acetylenic fatty acids in bryophytes, including *Fontinalis antipyretica* (Figure 18) (Anderson & Gellermann 1975; Dembitsky & Rezanka 1995; Sushchik *et al.* 2007), has enabled us to use these fatty acids as markers. These unique acetylenic fatty acid markers are absent in tracheophytes, algae (*e.g.* Sushchik *et al.* 2007), and bacteria, providing us with a tool to trace bryophytes in their consumers (Dembitsky & Rezanka 1995). When testing five aquatic bryophytes, Dembitsky and Rezanka determined that acetylenic fatty acids occurring in the triacylglycerols of bryophytes comprised from 6.6% of the fatty acids in the moss *Calliergon cordifolium* (Figure 87) to 80.2% in the thallose liverwort *Riccia fluitans* (Figure 88). Identification of these unique acetylenic fatty acids opened the possibility of determining if the bryophytes were actually assimilated into tissues of their consumers (Kalachova *et al.* 2011).

Torres-Ruiz *et al.* (2007) used fatty acid content to identify the food groups eaten by several aquatic invertebrates. They found the aquatic primary producers had a higher EFA content for 18:2 $\omega$ 6 and 18:3 $\omega$ 3 in green algae, 20:5 $\omega$ 3 in diatoms, and 20:4 $\omega$ 6 in bryophytes. Furthermore, they identified specific markers for diatoms (20:5 $\omega$ 3 [eicosapentaenoic acid], 16:1 $\omega$ 7, 16:1 $\omega$ 4s, 16C-polyunsaturated FAa [PUFAa]), green algae (18:3 $\omega$ 3 [ $\alpha$ -linolenic acid], 18:2 $\omega$ 6 [linoleic acid], 16C-PUFAB), and bryophytes (20:4 $\omega$ 6, 20:3 $\omega$ 3), permitting them to identify aquatic primary producers as the primary food source for the moss-dwelling mayfly *Ephemerella* (*s.l.*) (Figure 3, Figure 8) and caddisfly *Hydropsyche* (Figure 13). Gladyshev *et al.* (2012) used stable isotope composition of fatty acids to trace a food web from periphyton and mosses, to consumers, including **Trichoptera**, and finally to the secondary consumer fish, the grayling, in the Yenisei River in Siberia.

Kalacheva *et al.* (2009) and Kalachova *et al.* (2011) used similar logic to determine the use of *Fontinalis antipyretica* (Figure 18) as a food source in the Yenisei River. In addition to the differences among fatty acids listed above by Torres-Ruiz *et al.* (2007), green algae and Cyanobacteria synthesize high amounts of  $\alpha$ -linolenic acid



(18:3 $\omega$ 3); bacteria synthesize odd-numbered, branched fatty acids (Kalacheva *et al.* 2009; Kalachova *et al.* 2011). Bryophytes differ from these and from tracheophytes not only by having highly specific acetylenic fatty acids, but also the levels in the bryophytes maintain a high level of these fatty acids throughout the year (Kalacheva *et al.* 2009).

Kalacheva *et al.* (2009) used fatty acid and stable isotope analyses in a 4-year study on the food sources of macroinvertebrates in the Yenisei River. Using the highly specific biomarkers of acetylenic acids in *Fontinalis antipyretica* (Figure 18), they determined that the lipids of gammarids, **Ephemeroptera**, **Trichoptera**, and **Chironomidae** (Figure 9) all demonstrated the presence of these acetylenic acids in their fatty acids. In some cases, these were seasonal. For example, the amphipod *Eulimnogammarus viridis* exhibited maximum levels of the *F. antipyretica* biomarker in winter and minimum levels in summer. In particular, *Serratella ignita* (Figure 25) and *S. setigera* had the highest level of acetylenic acids A18 and A20 when analyzed. On the other hand, the **Chironomidae** *Prodiamesa olivacea* (Figure 89) and *Pseudodiamesa branickii* (Figure 90) and **Trichoptera** *Apatania crymophila* (Figure 91) had the lowest. The researchers concluded that for most of the aquatic insects the *Fontinalis antipyretica* in the Yenisei River played only a minor role in assimilation. On the other hand, the aquatic insects seemed to have a more depleted  $^{13}\text{C}$  content than the biofilms, an indication that the consumption of *F. antipyretica*, which likewise has a lower  $\delta^{13}\text{C}$  value than biofilms, contributed to their assimilation. Although the moss was consumed as a minor supplement year-round, consumption in general increased in winter when food sources such as epilithic biofilms were greatly reduced.



Figure 89. *Prodiamesa* sp. larva. *Prodiamesa olivacea* had low levels of bryophyte-derived acetylenic fatty acids, indicating little or no consumption of bryophytes. Photo by Peter Cranston, with permission.

Kalachova and coworkers (2011) raised the question of whether the moss was consumed directly or transferred up the food pyramid by consumption of invertebrates that had eaten it. They concluded that it was direct consumption because of lack of the marker fatty acids in the invertebrates lower in the food pyramid. Perhaps the most important conclusion is that these mosses were assimilated

into the tissues of the mayfly *Serratella* (Figure 25) species and others, a conclusion that cannot be supported by gut analysis alone. This line of research is worth pursuing further in other systems to determine the importance of bryophytes in the food web.



Figure 90. *Pseudodiamesa branickii*, a species that had low levels of bryophyte-derived acetylenic fatty acids, indicating little or no consumption of bryophytes. Photo from <Benthos.narod.ru>, with online permission.



Figure 91. *Apatania crymophila* larva, a caddisfly with low levels of acetylenic acid. Photo from Omnilexicon, through Creative Commons.

Macroinvertebrates can be flexible in their choices of food. In four acid streams of northeastern France, only 24-36% of the biomass consumed by shredders was comprised of leaf fragments; 44% of their diet was benthic algae and bryophytes (Dangles 2002). Some taxa such as the stonefly *Brachyptera seticornis* (Figure 92) and caddisfly *Chaetopterygopsis maclachlani* (Figure 93), specialized on benthic algae and bryophytes. Even though the caddisfly *Pycnopsyche guttifera* (Figure 77) is a classical shredder, it eats algae and is known to eat even terrestrial mosses (Williams & Williams 1982).



Figure 92. *Brachyptera seticornis* naiad, stonefly that specializes in eating algae and bryophytes. Photo from <<http://www.nebudbaiduzhym.com>>.

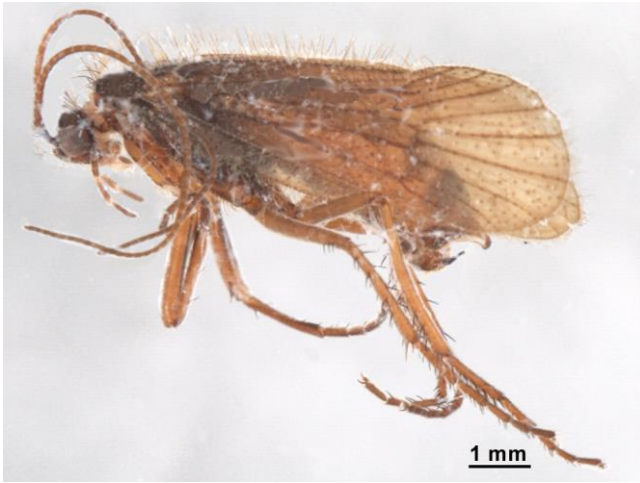


Figure 93. *Chaetopterygopsis maclachlani* adult. The larvae specialize on bryophytes as food. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Few preference experiments have been done with aquatic mosses as a choice. Leberfinger and Bohman (2010) gave detritivores *Limnephilus bipunctatus* (caddisfly, Figure 94) and *Nemoura* sp. (stonefly; Figure 40) the choice of shrubby cinquefoil, birch, Swedish whitebeam, dead and fresh grass, aquatic moss, and algae. Both insects preferred leaves of shrubby cinquefoil; *Nemoura* sp. also ate algae. The dead grass was the least preferred food. The shrubby cinquefoil had the highest nutritional value among the detritus choices. Leberfinger and Bohman considered the high carbon to nitrogen content of the fresh foods to be a contributing factor in their choice.



Figure 94. *Limnephilus bipunctatus* larva in case, a species that preferred aquatic mosses over grass, but less than shrubby cinquefoil. James K. Lindsey, with permission.

The **Tipulidae** (craneflies) are known from both terrestrial and aquatic habitats. In the terrestrial realm they typically live in wet habitats such as cedar swamps. *Tipula oropezoides* (Figure 95) is one such species. And it feeds on both mosses and liverworts. Wyatt and Stoneburner (1989) observed the larvae feeding on the moss *Rhizomnium punctatum* (Figure 96). It would strip the one-cell-thick lamina from the thick costa and leaf borders.



Figure 95. *Tipula* larva, a genus that is common among bryophytes and leaf litter and is known to feed on both mosses and liverworts. Photo by J. C. Jones, through Creative Commons.



Figure 96. *Rhizomnium punctatum*, food for *Tipula oropezoides*. Photo by Jan-Peter Frahm, with permission.

### Food when Food Is Scarce

Bryophytes are often considered to be emergency foods for aquatic insects (Dangles 2002; McWilliam-Hughes *et al.* 2009; Kalachova *et al.* 2011). They can be particularly important as a winter food source when other foods become scarce (Kalachova *et al.* 2011). Even within the growing season, the abundance of insects changes and this changes their impact on the bryophytes they consume (Figure 97) (Dangles 2002).

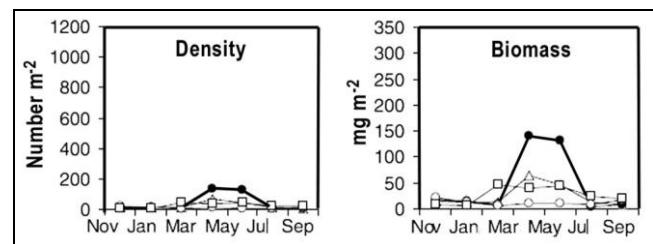


Figure 97. Density and biomass of insect shredders feeding on bryophytes in four streams in four replicate study streams (shown by 4 different symbols and lines) in Vosges Mountains (northeastern France). Modified from Dangles 2002.



Bryophytes can also serve as food in areas of a stream where other food sources are scarce (McWilliam-Hughes *et al.* 2009). Based on  $\delta^{13}\text{C}$  values, McWilliam-Hughes and coworkers determined that scrapers in low-order streams were more dependent on *Fontinalis* sp. (Figure 23) than scrapers in high-order streams depended on the *Drepanocladus* sp. (Figure 72) that was dominant there. In fact, 98% of the scraper  $\delta^{13}\text{C}$  values were enriched relative to bryophyte  $\delta^{13}\text{C}$  values and those two measures correlated well ( $r=0.53$ ). When the values from pool habitats were removed, the correlation increased to  $r=0.76$ . McWilliam-Hughes and coworkers suggested that in low-productivity rivers, primary consumers might switch to alternative marginal food sources such as *Fontinalis* sp.

### Epiphytes and Meiofauna of Bryophytes

In aquatic habitats, bryophytes are typically covered with periphyton. This periphyton coating can serve as food for many kinds of insects. The most common of these are diatoms (Ward 1994; pers. obs.). Amos (1999) found diatoms, desmids, and filamentous algae associated with *Fontinalis* (Figure 62). In New Zealand, Suren (1988) found that as day length increased the mosses were covered with flocculent masses of the diatom *Diatoma* sp. (Figure 98) and the filamentous green alga *Ulothrix* sp. (Figure 99) **Cyanobacteria** included *Placoma* (Figure 100), *Tolypothrix* (Figure 101), and *Chamaesiphon* (Figure 102). Suren (1992b) found that the bryophytes provided an abundant and persistent food source for invertebrates, one that was more stable than that on plain tiles. The bryophytes grew a high biomass of the filamentous diatom *Diatoma hiemale* (Figure 98) in the unshaded site and the crustose diatom *Epithemia sorex* (Figure 103) at the shaded site. The masses of filamentous diatoms were of short duration because they were easily washed away.

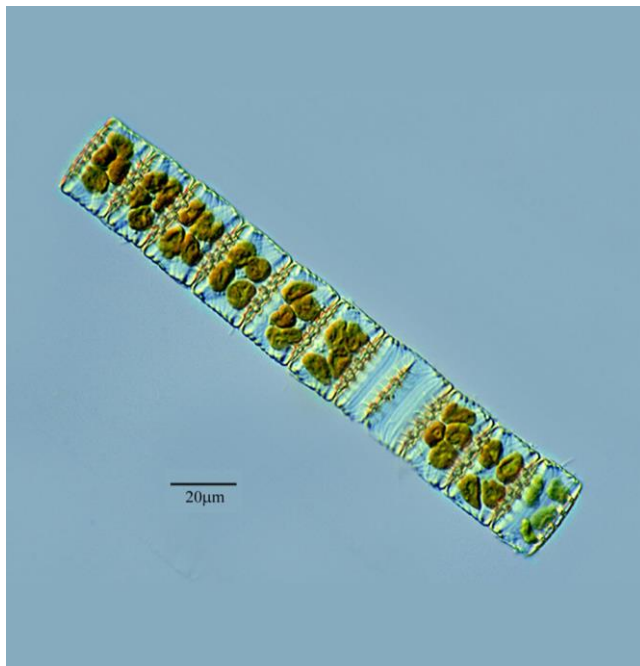


Figure 98. *Diatoma hiemale*, a common diatom on bryophytes at unshaded sites in New Zealand. Photo from Proyecto Agua, with permission.

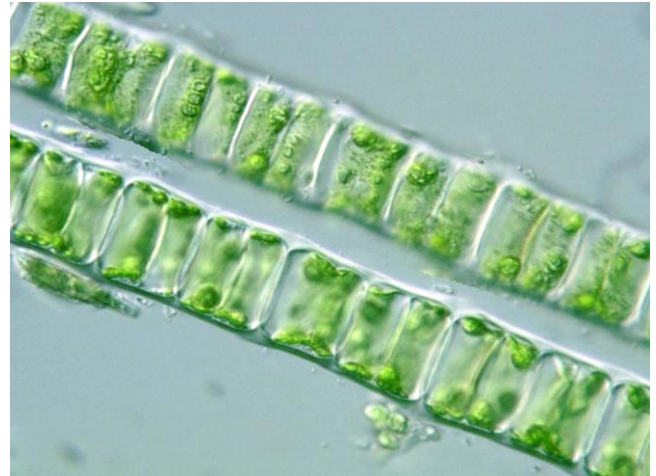


Figure 99. *Ulothrix*, a filamentous green alga that covers stream mosses as days grow longer in spring. Photo by Yuuji Tsukii, with permission.

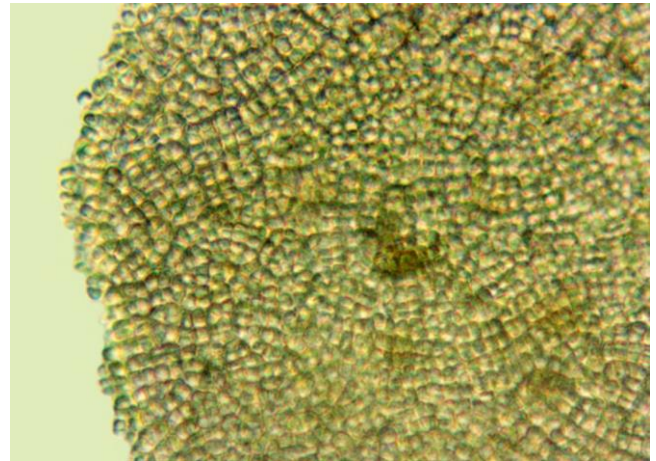


Figure 100. *Placoma* sp., a member of **Cyanobacteria** that covers stream mosses as days grow longer in spring. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 101. *Tolypothrix tenuis*, a member of **Cyanobacteria** that covers stream mosses as days grow longer in spring. Photo by Yuuji Tsukii, with permission.





Figure 102. *Chamaesiphon* sp., member of **Cyanobacteria** that covers stream mosses as days grow longer in spring. Photo by Stephen Moore, Landcare Research, NZ, with permission.

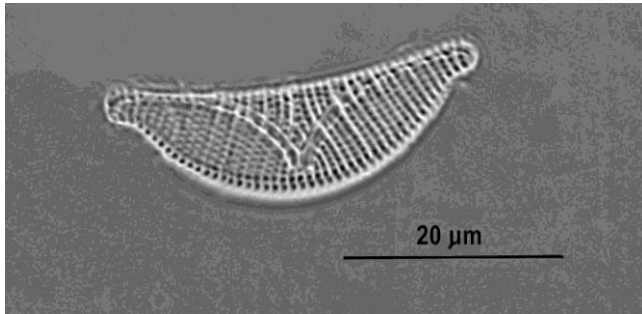


Figure 103. *Epithemia sorex*, a common inhabitant on bryophytes in shaded streams of New Zealand. Note the **puncta** (holes) in the cell wall. Photo by Ralf Wagner, with permission.

Diatoms (**Bacillariophyta**) at first appear to be indigestible boxes with glass shells of  $\text{SiO}_2$ . However, Ogilvie and Clifford (1986) reported that insects can digest the cytoplasm of diatoms through the tiny holes (**puncta**; Figure 103) in the cell wall. Diatoms and detritus are important foods for the tiny insect inhabitants of bryophytes. But meiofauna, intolerant of high water velocity (Winner 1975), can also reside there, seeking refuge from the high velocity of water on rocks and other substrata in the area.

As already noted, Chantha *et al.* (2000) found that as the moss biomass increased in a Quebec, Canada, stream, the invertebrates became more abundant but smaller. Clumps of moss with greater depth provided more spaces for invertebrates, but the algae did not increase proportionally, presumably due to diminishing light deeper into the mat. Both the algal biomass (5-fold) and invertebrate density (10-fold) was much greater on mosses compared to the nearby rocks, but the overall invertebrate biomass was similar on these two substrates because of the much greater area of bare rock.

### Trapping Detritus

The ability of bryophytes to trap detritus (Butcher 1933; Cowie & Winterbourn 1979; Gurtz & Wallace 1984; Suren & Winterbourn 1992a, b) as well as other food resources (Devantery 1987) undoubtedly plays an important role in feeding many kinds of inhabitants. Bryophytes trap **CPOM** (coarse particulate organic matter), **FPOM** (fine particulate matter), and **UFPOM** (ultra fine particulate organic matter) (Habdija *et al.* 2004). The fine particulate matter may be particularly important for the

meiofauna, including such small insects as the **Chironomidae** (Figure 9) (Aguila-S. 1998). Trapping is possible due to the reduced flow within the bryophyte mat, and this same slower flow provides a refuge from flow for stream insects (Madaliński 1961; Elliott 1967a, b; Gurtz & Wallace 1984; Suren 1992a, b; Glime 1994).

Hury and Wallace (1987) found that in mountain stream areas where bedrock outcrops are covered with mosses, collector-gatherers consume the FPOM (fine particulate organic matter) collected by the moss colony. Some probably also eat the dung that accumulates there from the many inhabitants (Fisher & Gray 1983).

Cherchesova *et al.* (2012) suggested that small and medium stoneflies living among mosses and other locations where **detritus** (Figure 5) is common probably eat detritus. These include *Protonemura aculeata* (see Figure 104), *Amphinemura trialetica* (Figure 105), *Taeniopteryx nebulosa* (Figure 106), *Taeniopteryx caucasica*, *Brachyptera transcaucasica* (see Figure 107), *Chloroperla* sp. (Figure 23), *Nemoura cinerea* (Figure 108), *Capnia nigra* (Figure 109), *Leuctra fusca* (Figure 110), and *Leuctra hippopus* (Figure 111), all in genera that commonly live among mosses.



Figure 104. *Protonemura meyeri* naiad, seen here amid a bed of detritus. Photo by James K. Lindsey, with permission.



Figure 105. *Amphinemura* naiad, a stonefly that blends well with detritus. Photo by Bob Henricks, with permission.





Figure 106. *Taeniopteryx nebulosa* naiad, a detritus dweller. Photo by Niels Sloth, through Creative Commons.



Figure 107. *Brachyptera risi* naiad. Photo by Guillaume Doucet <[www.guillaume.doucet.free.fr](http://www.guillaume.doucet.free.fr)>, with permission.



Figure 108. *Nemoura cinerea* naiad, a moss and detritus dweller. Photo by James K. Lindsey, with permission.



Figure 109. *Capnia* sp. naiad, a detritus dweller. Photo by Jason Neuswanger, with permission.



Figure 110. *Leuctra fusca*, a probably detritus feeder. Photo by Louis Boumans, through Creative Commons.



Figure 111. *Leuctra hippopus* naiad, a probably detritus feeder. Photo by Niels Sloth, with permission.

Suren (1992b) found that bryophytes increase the periphyton and detritus through increased habitat stability, acting much like debris jams in forested North American streams, but on a micro scale. The variation of periphyton among the bryophytes was much lower than that of plain tiles, suggesting that this food source is more stable than that on rocks. Thus the bryophyte periphyton and detritus provide persistent food sources for the bryophyte inhabitants.

Linhardt *et al.* (2002a, b) found that **Chironomidae** (Figure 9) and rotifers responded negatively to flow velocity, but correlated positively with the fine detrital matter trapped within the moss clump. Within *Fontinalis antipyretica* (Figure 18), the amount of trapped fine matter was dependent on the local flow velocity. Egglishaw (1969) found that detritus was the most important factor determining the structure of the community.

The moving waters provide a continuous renewal of organic particles that serve as food items. This permits the filter feeders among the Trichoptera and the Simuliidae to form large populations there (Galdean *et al.* 2001).

Macan and Worthington (1951) found that the fauna on different bryophyte growth forms differed. The not-so-thick moss housed the mayflies *Baetis* (Figure 43) and *Ephemerella* (*s.l.*) (Figure 8), stoneflies, and the scud *Gammarus* (Figure 52). Thick mosses supported great numbers of **Chironomidae** (Figure 9) (75% of the individuals). These mosses support some of the greatest productivity of the fish food organisms.

In Appalachian headwater streams, Wallace *et al.* (1988) found that thick mats of moss on the bedrock were important in retaining large amounts of organic matter. This seemed to account for the 48% collector-gatherers (insects) in the stream with dense mosses compared to 31% in the one with mostly cobbles and pebbles that were free of mosses. Haddija *et al.* (2000) found a positive correlation between flow velocity and the deposition rate of CPOM in moss mats, the location where most of the CPOM was deposited in an alkaline stream. Miliša *et al.* (2006) found similar relationships in the Plitvice Lakes of Croatia.

It is interesting that some folks in the UK have proposed that the increase of aquatic bryophytes downstream of sheep-dip (insecticide & fungicide mix) or heavy metal mines may be evidence that invertebrates are a major factor controlling aquatic bryophyte abundance (Richard Lansdown, Bryonet 13 January 2008). I wonder if the metals, at least, reduce the growth of periphyton, reducing competition and permitting higher productivity among the bryophytes. On the other hand, it is possible that sheep feces provide a food source, as suggested by Fisher and Gray (1983) in regard to macroinvertebrates living in a moss matrix in a desert stream.

Seasonal fluctuations in water level can present a challenge to stream macroinvertebrates. Wood *et al.* (2016) examined the role of trapped organic matter among the inundated clumps of the leafy liverwort *Porella pinnata* in the Middle Oconee River, GA, USA. This liverwort is generally above the water level, but during periods of high flow it becomes inundated. They found a significant increase in macroinvertebrate biomass, insect density, and organic matter among the *P. pinnata* than on adjoining

bare rock. Thus, the presence of bryophytes explained the additional organic matter, insect biomass, and density. Among these opportunistic insects were the **Diptera** and **Plecoptera** as the most abundant. I would suggest that additionally, the liverworts may have provided "landing sites" for insect that were caught up in the high-water flow.

## Detrimental Effects?

But the encroachment of bryophytes is not good for all members of the stream community. Bryophytes displace epilithic algae that would otherwise occupy the rocks. These diatoms and other algae serve as food for the scrapers, some of whom cannot carry out the same feeding strategy on the bryophytes. The soft structure and irregular surface of bryophytes sometimes requires a different scraping apparatus from that used on a rock. Slavik *et al.* (2004) found that added phosphorus in an Alaskan stream increased epilithic algae initially, but that after eight years of fertilization the bryophytes replaced the diatoms as primary producers. This increased moss growth altered ammonia uptake rates, benthic gross primary productivity, habitat structure, insect abundance, and faunal species composition.

The detrimental effects of bryophyte encroachment was apparent in a South African stream when managers chose to transplant *Fontinalis* (Figure 18) into the stream to increase habitat for insects and ultimately increase fish production (Richards 1947). While the idea sounded good, the mosses took over the rock surfaces that had been inhabited by scrapers and insects adapted to clinging to smooth rock surfaces and displaced the native fauna. Unfortunately, I don't know the long-term outcome, which may indeed have increased the number of insects once the bryophyte-adapted species were able to colonize.

## Bryophytes vs Tracheophytes

It is clear that bryophytes house numerous aquatic insects. And we know that aquatic insects serve as fish food. But do the insects that live among the bryophytes achieve that role? Bowden *et al.* (1999) found that such a role was unclear. As will soon be seen, bryophytes serve as safe sites for the insects. On the other hand, tracheophytes usually provide a more open habitat than the small chambers of bryophytes. And the tracheophytes can house larger individuals, sheltering fish that seek food there.

Macroinvertebrate biomass, insect density, and organic-matter content were significantly greater in patches of *P. pinnata* than on adjacent bare rock. Bryophyte biomass explained additional variation in organic matter, insect biomass, and density. The most abundant insects in *P. pinnata* patches were Dipterans and Plecopterans.

A legitimate comparison between the bryophyte fauna and that of tracheophytes is difficult because these two plant groups tend to occupy different habitats. In lakes the bryophytes are able to extend into deeper water where there is less light than that needed to support the more rapidly growing tracheophytes. The greater depth furthermore coincides with lower temperatures and less temperature fluctuation. Nutrients and dissolved O<sub>2</sub> also differ. And the meshlike nature of the bryophyte more easily traps detritus that can serve as a food source.



In streams, most tracheophytes are unable to tolerate the rapid flow regime that bryophytes can withstand. Since bryophytes occupy greater flow, their surface interface can have a higher oxygen concentration. And since the bryophytes tend to occupy upstream reaches that are steeper and more rocky, they coincide with a different group of insects adapted to faster water, sometimes lower temperatures, some drying in summer, and different species of predators, especially fish. With such limitations on the comparisons, it should be no surprise that studies designed to compare the inhabitants between bryophytes and tracheophytes are rare.

Harrod (1964) found that in a UK chalk stream four aquatic tracheophytes [*Ranunculus fluitans* (Figure 112), *Callitriche platycarpa* (Figure 113), *Veronica beccabunga* (Figure 114), and *Carex* sp. (Figure 115)] had some inhabitants, present on all four species, that are also known bryophyte inhabitants: *Baetis rhodani* (mayflies; Figure 2) (Frost 1942), *Rhyacophila dorsalis* (free-living caddisflies; Figure 116) (Slack 1936), and *Chironomidae* (midges; Figure 9) (Hynes 1961). *Hydropsyche* sp. (net-spinning caddisflies; Figure 13) and *Ephemerella* (s.l.) spp. (mayflies; Figure 3, Figure 8, Figure 25) preferred *C. platycarpa*. *Simulium ornatum* (blackflies; Figure 117) dominated both *Carex* sp. and *R. fluitans* (Harrod 1964).



Figure 112. *Ranunculus fluitans* with flower, a species where *Simulium ornatum* is dominant. Photo by Rasbak, through Creative Commons.



Figure 113. *Callitriche platycarpa*, a preferred substrate for *Hydropsyche* and *Ephemerella*. Photo by J. C. Schou, with permission.



Figure 114. *Veronica beccabunga* with flowers. Photo by Jacopo Werther, through Creative Commons.



Figure 115. *Carex hystricina* with flowers, a species where *Simulium ornatum* is dominant. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 116. *Rhyacophila dorsalis* larva, a bryophyte inhabitant that also occurs on aquatic tracheophytes. Photo by Walter Pfliegler, with permission.

Krecker's (1939) model contends that invertebrate abundance varies with macrophyte biomass, but also with plant species. Those plants with finely dissected leaves have more inhabitants than do plants with broad leaves. Cyr and Downing (1988) tested this assumption with macrophytes and found that the dissected *Myriophyllum* spp. (Figure 118) harbored significantly ( $p < 0.01$ ) more epiphytic invertebrates than did the broad-leaved taxa of *Potamogeton amplifolius* (Figure 119), *P. robbinsii* (Figure 120), or *Vallisneria americana* (Figure 121). But they also



found more invertebrates on the large *P. amplifolius* than on the other two broad-leaved species. The numbers of **Trichoptera** (caddisflies; Figure 91) and **Chironomidae** (midges; Figure 90) varied based on plant species. Interestingly, they found that plants with dissected leaves (*Ceratophyllum demersum* (Figure 122) and *Myriophyllum* spp.) did not usually support more invertebrates than did species with large leaves, attesting to the importance of surface area.



Figure 117. *Simulium ornatum* / *intermedium* / *trifasciatum* adult, a blackfly species complex whose larvae are common on both *Ranunculus fluitans* and *Carex*. Photo by Malcolm Storey, through Discover Life online permission.



Figure 118. *Myriophyllum* sp., a tracheophyte with intermediate densities of insects, inferior to that of mosses. Photo by Alison Fox through USDA, with permission.



Figure 119. *Potamogeton amplifolius*, a broad-leaved aquatic plant that harbors fewer insects than those found among dissected leaves. Photo by Jean Pawek, with online permission.



Figure 120. *Potamogeton robbinsii*, a broad-leaved aquatic plant that harbors fewer insects than those found among dissected leaves. Photo by Barre Hellquist, through Creative Commons.

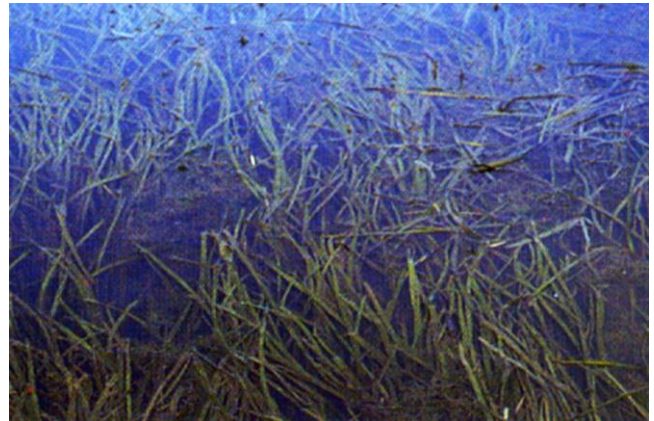


Figure 121. *Vallisneria americana* showing its dense habit of growth. Photo by William & Wilma Follette, through Creative Commons.



Figure 122. *Ceratophyllum demersum*, an aquatic plant with dissected leaves that does not support as many invertebrates as macrophytes with large leaves. Photo from DoralBio5 website, through Creative Commons.



Epele *et al.* (2012) conducted a similar study on **Chironomidae** (midge) assemblages in Patagonia. They recorded 35 taxa of **Chironomidae**. The most abundant subfamilies were **Orthoclaadiinae** (20), **Chironominae** (7), and **Podonominae** (4). The five most abundant species represented five genera: *Parametriocnemus* (Figure 123), *Parapsectrocladius*, *Paratrichocladius* (Figure 124), *Pseudochironomus*, and *Rheotanytarsus* (Figure 125) most abundant taxa. *Myriophyllum quitense* (Figure 126) is structurally complex and was inhabited by 11 taxa. *Isoetes savatieri*, a structurally simple plant, hosted only 5 taxa. Among the bryophytes in areas of rapid flow they found **Podonominae**, *Eukiefferiella* spp., *Parapsectrocladius* sp. They found that stability of the substrate was important, with boulders, cobbles, and rooted plants supporting more **Chironomidae** abundance, richness, and diversity than did sand/gravel. They concluded that more complex substrates supported greater diversity.

generally had the highest density of **Chironomidae** (larvae per sq cm on wood or per gram dry weight on all others). On 11 June the density among mosses was more than double that among filamentous algae, with the others having only 1/6 or less density than that among the mosses. But on 21 June, *Hippuris* had 457 midge larvae compared to 268 on mosses; the algae had none, and the other plants had much lower densities than the mosses. By 11 July, the density among the mosses was nearly double that on *Hippuris* with all others trailing behind. Similar results persisted on 31 July, but on 20 August no insects were reported for the mosses! On 1 October the moss inhabitants reached their highest density (1817 per gram), nearly twice that on *Hippuris*. Differences in surface area are likely to account for the generally higher habitation among mosses (Table 1). Could the low numbers on 20 August have been movement of larvae from mosses to a better food source during low flow?



Figure 123. *Parametriocnemus* sp., a common genus on aquatic plants in Patagonia. Photo by Gillian Martin, Biodiversity Institute of Ontario, through Creative Commons.



Figure 124. *Paratrichocladius skirwithensis* pupa, a genus that is common on macrophytes in Patagonia. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Boerger *et al.* (1982) compared the **Chironomidae** (midge larvae; Figure 9) fauna on several aquatic plants and the moss *Drepanocladus revolvens* (Figure 127) in the North Fork of the Bigoray River, Alberta, Canada, on several sampling dates. When compared to *Sparganium* (Figure 128), *Potamogeton* (Figure 129), *Hippuris* (Figure 130), sponge, filamentous algae, and wood, the moss



Figure 125. *Rheotanytarsus*, a genus that is common on macrophytes in Patagonia. Photo by Jason Neuswanger <Troutnut.com>, with permission.



Figure 126. *Myriophyllum quitense*, home to 11 taxa of **Chironomidae** in Patagonia. Photo from Jardín Botánico Nacional, through Creative Commons.





Figure 127. *Drepanocladus revolvens*, a moss with higher density of *Chironomidae* when compared with nearby aquatic tracheophytes. Photo by Kristian Peters, with permission.



Figure 128. *Sparganium angustifolium* with flowers, a tracheophyte with fewer *Chironomidae* than that on mosses. Photo by Barbara Studer, through Creative Commons.



Figure 129. *Potamogeton perfoliatus*, a plant with fewer fauna than found on nearby mosses. Photo by Donald Cameron, through public domain.

Table 1. Comparison of surface area and volume per weight of three tracheophytes, *Drepanocladus revolvens* (Figure 127), filamentous algae, and willow leaves. From Boerger *et al.* 1982.

Plant type	n	area/wt cm <sup>2</sup> g <sup>-1</sup>	vol/wt cm <sup>3</sup> g <sup>-1</sup>	area/vol cm <sup>2</sup> g <sup>-1</sup>
<i>Sparganium</i>	8	707±13	19.7±1.2	37.6±2.4
<i>Potamogeton</i>	10	1028±116	14.0±0.9	73.6±7.2
<i>Drepanocladus revolvens</i>	10	1526±136	15.2±1.5	103±9.4
<i>Hippurus</i>	9	2549±638	20.9±2.2	122±9.6
Filamentous algae	5	—	23.5±5.6	—
Willow leaves	9	250±9		

In UK lakes and rivers, Macan and Worthington (1951) found that thick mosses on stones and boulders had a mean of 431,941 animals per square meter, whereas *Potamogeton perfoliatus* (pondweed; Figure 129) had only 243,972 and bare rocks had only 4600. Both rooted plants and mosses increased the food used by fish. Percival and Whitehead (1929) likewise found that bryophytes in UK streams had greater insect densities, with intermediate densities on the alga *Cladophora* (Figure 131) and loose mosses, but with the highest densities on thick moss and river weed (Podostemaceae?).



Figure 130. *Hippuris vulgaris*, a tracheophyte with only half the insect density found on mosses. Photo through Creative Commons.





Figure 131. *Cladophora crispata*, member of a genus that is home to aquatic insects. Photo by Yuuji Tsukii, Protist Information Server, with permission.

In Doe Run, Kentucky, USA, Minckley (1963) found intermediate densities on the vascular plants *Nasturtium* (Figure 132), *Myriophyllum* (Figure 118), and *Myosotis* (Figure 133), with the highest densities on mosses. Gregg (1981) found that when the insects were counted on available surface area (3-d, not stream bed), the bare substrate had significantly more insects than did the tracheophytes *Ranunculus* (Figure 134) or *Rorippa* (Figure 135). It seems that the most important role of these tracheophytes was to increase available substrate. It is likely that bryophytes have that role as well.



Figure 132. *Nasturtium officinale* with flowers, an emergent plant with lower insect densities than that found on mosses. Photo by Matt Lavin, through Creative Commons.



Figure 133. *Myosotis scorpioides*, an emergent tracheophyte that had fewer insect inhabitants than mosses. Photo by Les Mehrhoff, through DiscoverLife <<http://www.discoverlife.org>>.



Figure 134. *Ranunculus aquatilis*, a tracheophyte genus that had even fewer insects than bare substrate in a Kentucky, USA, stream. Photo by Teun Spaans, through Wikimedia Commons.



Figure 135. *Rorippa palustris*, an emergent tracheophyte genus that has fewer insects than the bare substrate in a Kentucky, USA, stream. Photo by Mel Harte, through DiscoverLife <[www.discoverlife.org](http://www.discoverlife.org)>.

Unlike the bryophytes that trap large quantities of detritus, the tracheophytes tend to be somewhat cleaner because they have fewer pockets in which to trap things. Soszka (1975) used both laboratory and field experiments to examine how insects in a Polish lake used the tracheophytes. He found that only the larvae of Lepidoptera depended on the tracheophytes for food. Rather, most of the insects ate the epiphytic algae and detritus.

Nearly 60% of the invertebrate taxa associated with macrophytes studied by Krull (1970) occurred on only three or fewer species of macrophytes and 33 invertebrate taxa were associated with only one species. **Odonata** (Figure 136) are relatively common among macrophytes (Corbet 1962) but nearly totally absent among bryophytes (see Chapter 11-4 of this volume). The reasons remain to be explored, but the **Odonata** are large and tend to occur in quiet water where they can lie in wait for prey, whereas bryophytes are more common in rapid water.





Figure 136. A head-on view of the dragonfly *Tanypteryx hageni* naiad lying in wait for its prey. Photo by Greg Courtney, with permission.

The morphology of the plant appears to be of a major importance. Kreckler (1939) found that the lowest number of insects occurred on *Vallisneria* (Figure 121), a plant with smooth, linear leaves. On the other hand, *Myriophyllum* (Figure 118) species (Figure 118) are divided and provide a large surface area. *Potamogeton crispus* (Figure 137) has very wavy leaves and had high faunal densities. Harrod (1964) considered the colonization of aquatic macrophytes to depend on four factors: morphology, position in stream, epiphytes present, and chemical nature. Habitat permanence may be important in lakes (Hargeby 1990). (Hutchinson 1975) suggested that chemical defenses were not well developed in aquatic macrophytes compared to terrestrial plants. Presumably they are also less well developed than in bryophytes.



Figure 137. *Potamogeton crispus* showing dense growth. Photo by J. C. Schou, with permission.

Despite the open nature of most macrophytes, Tarzwell (1936) found more organisms on the tracheophytes than on the mosses in Michigan, USA, streams. Using a relative scale in which 1.0 represented the numbers on sand, he reported individuals on the tracheophytes *Ranunculus* (Figure 134) (194), *Rorippa* (Figure 135) (301), and *Elodea* (Figure 138) (452) to be greater than those on mosses on gravel (111) or mosses on gravel and rubble (140). Similarly, Percival and Whitehead (1929) found that fauna

on a square decimeter of the tracheophyte *Potamogeton* (Figure 129) (2405) exceeded that of both loose moss (709) and thick moss (2140).



Figure 138. *Elodea canadensis* flowering. Note detrital accumulation on substrate but little at leaf bases. Photo by Christian Fischer, through Creative Commons.

The ability to colonize tracheophytes vs bryophytes often depends on the suitability of the morphology. Although bryophytes have a large surface area, most of it is below the interface with flowing water, hence creating surfaces that may be lacking in sufficient oxygen as well as being unsuitable for filter feeders that depend on the flow. This appears to be the case for blackflies. Niesiolowski (1980) found a greater number of blackflies on *Potamogeton* (Figure 137) than on *Fontinalis* (Figure 62). He attributed this to the differences in leaf size and setting. *Potamogeton* leaves are all exposed to the current whereas only tips of bryophyte branches that interface with the water flow are available for these filter-feeding larvae.

Clearly the relationships between aquatic insects and bryophytes are complex and may be indirect. They serve as refuges and food sources, but these roles may change as the seasons change. Their importance in increased diversity is certain, but their role in overall productivity of the habitat is still elusive.

## Summary

Bryophytes provide a stable habitat with lots of surface area, a variety of internal spaces with oxygen and flow gradients, a place to hide from predators or escape from flow (enemy-free space/refuges/safe sites), a trap for algae and detritus to serve as food, and a place to hunt for smaller organisms while hiding from larger predators. Bryophytes can also serve as a moist refuge and a place to find food during times of low water. Hence, a rich bryophyte fauna exists to take advantage of these benefits, increasing the functional diversity. The bryophytes provide habitats for insects in streams, rivers, lake margins, deep waters of lakes, ponds, bogs, and fens.

Two strong determinants of the bryophyte faunal composition are velocity and pH. Nutrients can change the dynamic, in some cases increasing moss cover and fauna, but in others increasing algal dominance and reducing bryophyte cover due to competition for light and CO<sub>2</sub>.



Some insects specialize on parts of the mosses, with some in leaf axils, some in liverworts, some on the leaf lamina. Morphology of the bryophyte may help to define the faunal community. Other insects specialize on the food types that grow on the mosses – diatoms, Cyanobacteria, filamentous green algae. Some preferences for bryophyte species may relate to the preference of the bryophyte for a particular pH range, flow, or other conditions. Bryophytes can also serve as a trap for drifting insects while helping others to avoid the drift altogether. The bryophytes seem to keep at least some species from joining the drift at emergence by providing a substrate where they can climb out of the water.

Artificial string mosses are colonized by the same dominant insects as are mosses, but Visqueen strips have a smaller, more selective fauna.

New methods using fatty acids have supported the gut analyses that reveal bryophytes in the diets of a number of insects. These fatty acids have been used as tracers to implicate the movement of bryophyte carbon upward in the food pyramid. Antiherbivore compounds may keep some insects from eating the bryophytes; in other cases they keep predators from attacking the insects because they prefer eating among plants that lack these compounds. But it appears that trapped detritus and adhering periphyton may play the most important role in determining bryophyte insect inhabitants.

Although macroinvertebrate density and richness increase with moss weight, lower reaches within the mat may be unacceptable habitats for many, so that area covered is more important. And in some cases, encroachment by bryophytes can eliminate insects adapted to smooth rocks.

Bryophytes offer different advantages compared to those of tracheophytes. They occur in rapid water of streams where tracheophytes are unable to survive, they provide enclosed, protective spaces, they trap more detritus, and they persist year-round. But large-leaved tracheophytes provide better habitats for such taxa as **Simuliidae** because more of their surface area is in direct flow where these blackflies can filter out their food.

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# CHAPTER 11-3

## AQUATIC INSECTS: BRYOPHYTE HABITATS AND FAUNA

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# CHAPTER 11-3

## AQUATIC INSECTS: BRYOPHYTE HABITATS AND FAUNA



Figure 1. *Sphagnum* blanket bog. Photo through Creative Commons.

### Aquatic Bryophyte Habitat and Fauna

Insect distribution and abundance depend on freedom from predation, interspecific competition, and physical disturbance (McAuliffe 1983). Bryophytes offer a refuge from all three of these dangers. Aquatic insect biodiversity depends on gradients in habitat size and acidity (Harrison & Agnew 1962; Heino 2009). Bryophytes can contribute to the acidity, particularly in *Sphagnum* (Figure 1) habitats, and add to both habitat size diversity and complexity. Thus, bryophytes can increase the diversity of insects in streams, lakes, bogs, and springs by creating more niches for occupation.

Moon (1939) summarized his study of aquatic insects as evidence that the substrate provides mechanical support for the fauna and is the surface on which food grows or is

deposited. Bryophytes can contribute greatly to the available substrate, growing periphyton, and trapping detritus. For carnivorous insects, the bryophytes also harbor animal food organisms. Others have reported similar advantages of the moss substrate: increased substrate area (Glime & Clemons 1972), increased algal cell counts (Gurtz & Wallace 1984), replacing scour or sediment-buried algal cover (Hains 1981), protection from scour (Gurtz & Wallace 1984), filtering and trapping detritus (Gurtz & Wallace 1984), providing high prey density (Gurtz & Wallace 1984). The mosses also permit the insects to gain a hold in areas of high velocity where the insects may be able to reduce ventilation needed to gain oxygen, thus saving energy (Johnson 1978; Gurtz & Wallace 1984).



Gurtz and Wallace (1984) found that after a clearcut in the southern Appalachians, USA, the insect fauna increased in density more on the moss-covered (mostly *Hygroamblystegium tenax* – Figure 2) rock faces than on other stream substrates. It was primarily the collector-gatherers and scrapers that increased, whereas shredders declined. They considered that the mosses contributed to the biological stability of their substrates. They were most important in areas of rapid, shallow, turbulent flow. These habitats not only replenished the CO<sub>2</sub> and nutrient supply for the mosses, but provided the flow needed for the net-spinning caddisfly *Parapsyche* (Figure 3).



Figure 2. *Hygroamblystegium tenax*, where insect fauna increased after a forest clearcut in the southern Appalachians, USA. Photo by Barry Stewart, with permission.



Figure 3. *Parapsyche apicalis* larva, a net-spinning caddisfly that lives on mosses. Photo by Donald S. Chandler, with permission.

By experimenting on colonization of *Fontinalis neomexicana* (Figure 4), Maurer and Brusven (1983) found that collector-gatherers were the most numerous (74% of the density), with shredders, collector-filterers, engulfers, and scrapers making up the remainder. Arrival of *Brachycentrus* sp. (Figure 5), a collector-filterer, and *Hydroptila* sp. (Figure 6), a scraper, both caddisflies, changed these percentages after three weeks. Maurer and Brusven believed that fine particulate matter and epiphytic algae may have facilitated the rapid recolonization.



Figure 4. *Fontinalis neomexicana*, home to many collector-gatherers. Photo by Belinda Lo, through Creative Commons.



Figure 5. *Brachycentrus appalachia* (larger), a common bryophyte dweller that colonized after three weeks. Photo by Bob Henricks, with permission.



Figure 6. *Hydroptila* in case, one of the smallest caddisflies, and a colonizer on *Fontinalis neomexicana* (Figure 4). Photo by Bob Henricks, with permission.

In a Nepalese river system, altitude was an important determinant of the bryophytes and associated fauna (Ormerod *et al.* 1994). Not only did the substrate change, with bryophytes being more common at higher altitudes, but attached diatoms were more common among higher altitude streams. The high altitude springs supported dense



cover of bryophytes, but bryophytes were not well supported by the cold streams of ice and glacial melt.

Ward (1986) studied altitudinal relationships in the Rocky Mountains, USA. As in the Nepalese system, aquatic tracheophytes were absent in the high mountain sites. Rather, bryophytes dominated in the headwaters. The **zoobenthos** (animals that live on the bottom) density experienced a 3-fold to 6-fold increase from the tundra to the plains at lower elevations. Vinson and Hawkins (2003) likewise found that diversity of genera decreased as elevation increased, with only **Plecoptera** (stoneflies; Figure 25) being an exception.

Like altitude, latitude affects stream insect richness. Vinson and Hawkins (2003) examined data on **Ephemeroptera** (mayflies; Figure 8-Figure 9), **Plecoptera** (stoneflies; Figure 25), and **Trichoptera** (caddisflies; Figure 6) from 495 published studies on richness. **Ephemeroptera** showed three richness peaks (~30°S, 10°N, 40°N) with the highest near 5-10°N and 40°N latitude. **Plecoptera** richness was distinctly highest at ~40°N latitude and similarly at 40°S latitude. **Trichoptera** richness showed less latitudinal variation than the other two orders, although it was slightly higher near the equator and at 40°N and S latitude than at other latitudes.

In a study of mosses growing on filter beds, Hussey (1982) found that growth of mosses [*Leptodictyum riparium* (Figure 7) was most common] changed the macroinvertebrate community. Even the thickness of the moss will cause differences among communities (Macan & Worthington 1951). The mayflies *Baetis* (Figure 8) and *Ephemerella* (Figure 9), **Plecoptera** (Figure 25), and the scud *Gammarus* prefer not-so-thick moss, whereas thick moss harbors abundant **Chironomidae** (Figure 15). Macan and Worthington found that of the 431,941 animals per sq m of thick moss, 75% were **Chironomidae**. Despite the small size of the moss inhabitants, they found that rooted plants and attached mosses provide the greatest productivity of fish food organisms. That probably refers to the kinds of organisms that fish eat, not to organisms among the mosses that are actually eaten as these may be unavailable unless they enter the drift. (See Chapter 11-2, Bryophyte Roles as Insect Habitats – Food.)



Figure 7. *Leptodictyum riparium*, a moss whose growth changed the macroinvertebrate community. Photo by Jan-Peter Frahm, with permission.



Figure 8. *Baetis rhodani*, a common bryophyte inhabitant. Photo by J. C. Schou, with permission.



Figure 9. *Ephemerella dorothea* on moss (*Platyhypnidium riparioides* or *Hygrohypnum* sp.). Photo by Donna Bennett, with permission.

## Streams

Streams can be rich habitats for aquatic fauna. In the Åland Islands of Finland, Autio and Salmela (2010) collected 104 **Diptera** species from 19 sites, using Malaise traps. These sites included open mires, wooded mires, rich fens, Baltic shore meadows, ditches, and a grove. These **Diptera** included the semiaquatic families **Limoniidae**, **Tipulidae**, **Pediciidae**, **Cylindrotomidae**, **Ptychopteridae**, **Psychodidae**, and **Dixidae**. But the species richness was less than that in other parts of Finland, a phenomenon that Autio and Salmela attributed to the absence of brooks and springs.

In a Victorian Australia upland stream the habitats included mossy stones and the tracheophyte *Ranunculus fluitans*, with number of species reaching 19 among mosses compared to 5 in stony riffles (McKenzie-Smith 1987). The densities among the bryophytes were greater than that McKenzie-Smith could explain on the basis of greater surface area, so he concluded that they offered more than just space.

In Appalachian Mountain streams, I found that the insect communities on the leafy liverwort *Scapania undulata* were most similar to those on *Fontinalis dalecarlica* (Figure 16) (Glime 1968). These seem like strange similarities because these two bryophyte species



were the most different from each other structurally. However, they did tend to occur in the same streams, suggesting that conditions of flow, nutrients, and temperature may have been more important for the insects. *Scapania undulata* provided a unique habitat where insects were able to hide within the folded leaves. The large, streaming moss *Fontinalis dalecarlica* may have offered a similar advantage by having a leaf that was somewhat rolled, making it tubular and providing good shelter for the very small.

In many northern streams the bryophytes remain throughout the year, providing a habitat for insects when the tracheophytes disappear. But in English rivers, *Fontinalis antipyretica* (Figure 10), *Fissidens crassipes* (Figure 11), and *Leptodictyum riparium* (Figure 7) decline considerably during winter (Wehr & Whitton 1983; Kelly & Whitton 1987).



Figure 10. *Fontinalis antipyretica*, a species that declines in English winters. Photo by Bernd Haynold, through Wikimedia Commons.



Figure 11. *Fissidens crassipes*, a moss that diminishes in English rivers in the winter. Photo by Michael Lüth, with permission.

As noted earlier, bryophytes in streams increase the heterogeneity of the habitat, increasing the available niches for insects (Allan 1975; Williams 1980). And size matters – sometimes (Bourassa & Morin 1995). Although the taxonomic composition differs among streams, the size distribution is quite similar. But substrate composition in nine Canadian streams did affect overall abundance – more

than it did their size. Eutrophic sites favored higher abundance, but only for organisms larger than 1 mm (approximately 1  $\mu\text{g}$  dry mass). These small organisms contribute to less than 3% of the respiration of the stream ecosystem, contrasting with the results of Smith-Cuffney (1987 – see above). Does this mean that bryophytes, with their fauna of the smallest organisms, contribute little to the stream ecosystem? I think not, because it is these small organisms that become big ones, and without the shelter of bryophytes they are more likely to be food for predators.

In a Tennessee, USA, springbrook, Stern and Stern (1969) found that the highest number of insects on bryophytes and algae occurred in winter. In February they found 768 individuals per 0.1 m<sup>2</sup>, whereas in July they found only 43 per 0.1 m<sup>2</sup> (Figure 12). **Diptera** comprised 84.4% of the fauna, Trichoptera 9.6%, **Plecoptera** 3.1%, and **Ephemeroptera** 2.8%. **Coleoptera** comprised only 0.1%.

Following logging in a southern Appalachian, USA, stream, Gurtz and Wallace (1984) found that the stonefly *Amphinemura wui* (Figure 13) increased in numbers, a response they attributed to the particulate accumulation by bryophytes. Baetid mayflies and the spiny crawler mayfly *Ephemerella* (s.l.) (Figure 9) increased most among mosses, correlating with a similarly high increase in diatoms among mosses. And as one might expect, the **Orthocladinae** (**Chironomidae** – midges, Figure 15) increased in response to the increased sediment among the mosses.

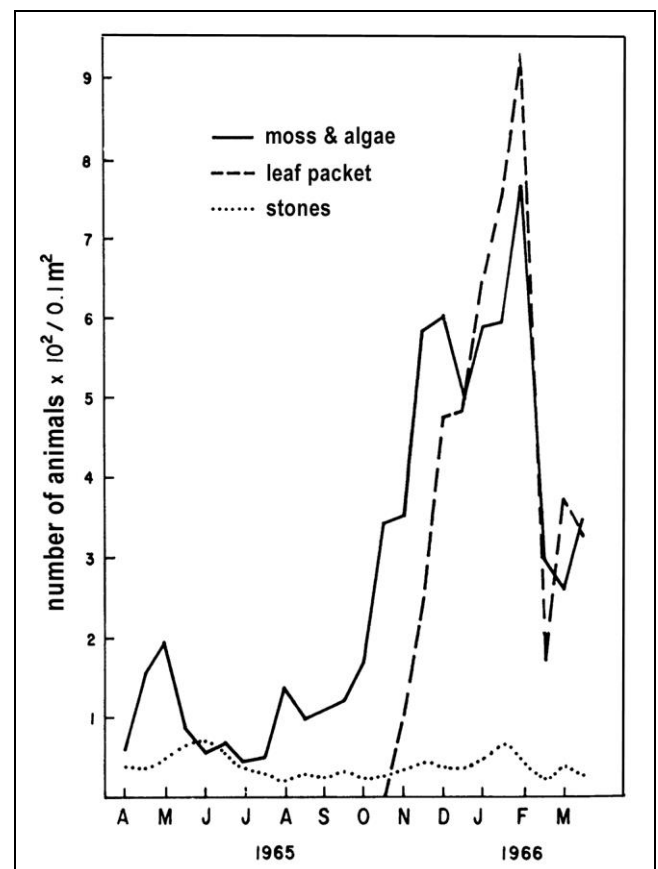


Figure 12. Seasonal distribution of invertebrates on three substrate types in a springbrook in Tennessee, USA. Redrawn from Stern & Stern 1969.



Figure 13. *Amphinemura wui* adult, a species that lives among mosses in its naiad state and feeds on detritus. Photo by Donald S. Chandler, with permission.

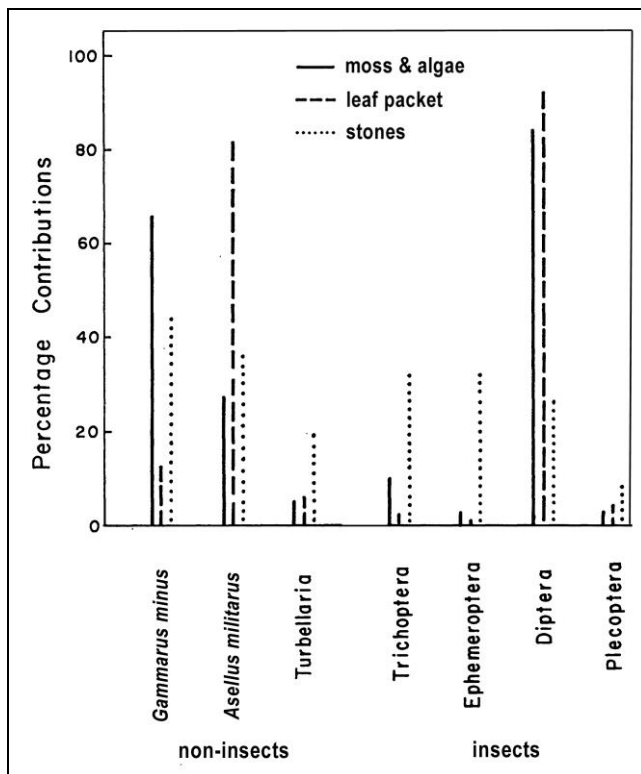


Figure 14. Comparison of insects and other invertebrates among mosses and algae, leaf packets, and stones in a Tennessee springbrook. Redrawn from Stern & Stern 1969.

One of the uses of bryophytes in stream studies could be to serve as **surrogates** – indicators of the habitat and the organisms one might expect to find there. But it seems that bryophytes do not make very reliable surrogates (Paavola 2003; Paavola *et al.* 2003, 2006). Paavola and coworkers, using 101 boreal stream sites, found that within stream areas, the insect communities correlate primarily with stream size, pH, and water color. Bryophytes, on the other hand, correlate with nutrient levels and habitat heterogeneity, whereas fish correlate with oxygen levels, depth, and substrate size. But the surrogate role is not as dismal as it may seem. At the level of ecoregions, all three respond to acidity and depth as well as spatial coordinates

and the community concordance is much smaller than it is on the level of a single stream or stretch of stream. Nevertheless, these three taxonomic groups had low predictive value. When Virtanen *et al.* (2009) examined bryophyte correlations in 138 boreal springs, temperature was a major driver of communities. The **EPTC** insects [**Ephemeroptera** (Figure 8-Figure 9), **Plecoptera** (Figure 25), **Trichoptera** (Figure 6), and **Coleoptera** (Figure 41-Figure 43), *i.e.* major orders on bryophytes and in fast streams] were not good surrogates for the bryophytes, nor were the **Chironomidae** (Figure 15). Concordance between bryophytes and **Chironomidae** was a little better than with the EPTC group.



Figure 15. **Chironomidae** larva, a common bryophyte inhabitant that is not a good surrogate for bryophytes. Photo by Jason Neuswanger, with permission.

In their study of *Fontinalis dalecarlica* (Figure 16) communities, Cattaneo *et al.* (2004) found that depth was an important contributor to differences in invertebrate biomass. Shallow mosses supported lower invertebrate biomass than did the deeper ones, possibly due to frequent exposure of the shallow mosses.



Figure 16. *Fontinalis dalecarlica*, a moss able to occupy a wide range of depths that affect the composition of the insect communities. Photo by Kristoffer Hylander, with permission.



## Streamside

The streamside habitat is one of changing water levels, providing a moisture gradient and a place to leave behind the naiad or pupal stage and crawl to the terrestrial environment for adulthood. Lindegaard *et al.* (1975) examined four zones related to the fauna on the moss *Cratoneuron* (Figure 17). Underlying the moss they found a detritus zone, with numerous flies and earthworms. Above it was a zone of water-covered mosses. The **madicolous** zone occurred just above the water surface and the moss remained constantly wet by splash and capillary water. This madicolous zone and the water zone were suitable for caddisflies, flies, and molluscs. Above that the moss was dry, occupied by springtails, beetles, spiders, and predaceous mites.



Figure 17. *Cratoneuron filicinum*, member of a genus that creates faunal zones. Photo by Barry Stewart, with permission.

## Artificial Bryophytes

Artificial substrata provide important information on the role of the moss in the association with invertebrates (Cox 1988). Suren (1988) used mosses constructed from nylon twine woven into squares. These artificial mosses were colonized by the stoneflies *Zelandoperla* (Figure 18) and *Zelandobius* (Figure 19), midges, nematodes, mites, copepods, and ostracods.



Figure 18. *Zelandoperla pennulata* adult from the Takitimu Mountains, N Z. Photo by Brian Patrick, with permission.



Figure 19. *Zelandobius illiesi*, a stonefly that colonized artificial mosses in New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.

Glime and Clemons (1972) found that aquatic insects may only colonize mosses as a place to live. In their experiments, insects on artificial string mosses (Figure 20) formed similar communities to those on *Fontinalis* (Figure 16), but the number of species on mosses made of polyethylene strips was more limited.



Figure 20. Artificial string moss used in study by Glime & Clemons (1972). Photo by Janice Glime.

Suren (1987, 1988) found that artificial mosses in high alpine streams of New Zealand provided habitat similar to that of mosses, but some taxa, for example **Collembola**, were not restored due to lack of suitable food. Others can be absent due to lack of suitable materials for building their "houses." Suren did find that these surrogate mosses did develop abundant periphyton in one stream, but in another they collected primarily detritus and silt. For substitute mosses, the right kind of artificial structure must be found to also house the needed food. This most likely would require longer for the dependent organisms to colonize.

Suren (1991b) also found that colonization of artificial bryophytes was rapid, reaching a peak in abundance after only 4 weeks. After two months, the density and richness resembled that of the natural bryophytes. Nevertheless, some taxa did not reach normal levels, with larvae of **Empididae** (Diptera; Figure 21) and the crane fly *Limonia hudsoni* (see Figure 22) having lower numbers. Taxa that were characteristic of riffles, *e.g.*, the mayflies *Deleatidium* sp. (Figure 23) and *Nesameletus* sp. (Figure 24), or stoneflies *Stenoperla prasina* (Figure 25) and *Zelandobius* sp. (Figure 19), did not colonize the "stems" of artificial



bryophytes very well but did colonize the bases of these and the bedrock beneath. TWINSPAN identified a strong similarity between the artificial mosses and the real mosses, but the fauna of the artificial substrates were different from that of the riffles.

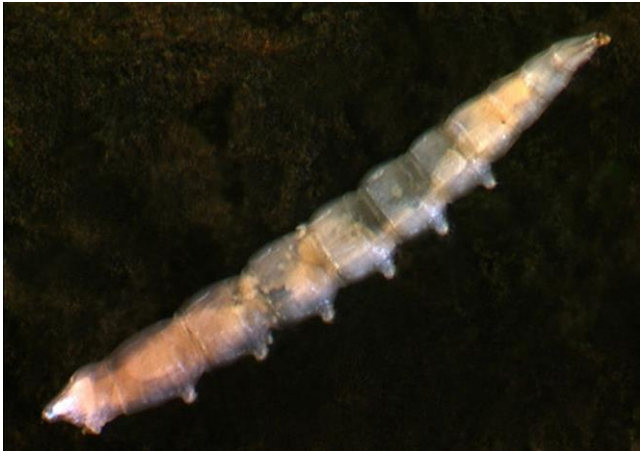


Figure 21. **Empididae** larva, a dipteran group that did not reach normal numbers on artificial mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 22. **Limonia** larva, a genus with lower numbers on artificial mosses than on the real ones. Photo from State Hygienic Laboratory, University of Iowa, with permission.



Figure 23. **Deleatidium** sp., a riffle stonefly that colonized the bases, but not the stems, of artificial mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 24. **Nesameletus** naiad, a riffle mayfly that colonized the bases, but not the stems, of artificial mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 25. **Stenoperla prasina** naiad, a stonefly that colonized the bases, but not the stems, of artificial mosses in New Zealand. Photo by Kanji Saito, with permission.

Suren and Winterbourn (1992) experimented with artificial bryophytes in shaded and unshaded New Zealand portions of an alpine stream. The artificial mosses consisted of pieces of nylon twine woven into 4 mm pores of nylon mesh cut into 0.01 m<sup>2</sup> squares. They found that at the unshaded site seven taxa preferred substrata with high detrital and periphytic biomass. Of the 22 taxa there, 8 were influenced by periphyton biomass, three by detrital biomass, and two by exposure time. At the shaded site, only two taxa had a relationship with these food groups. Exposure time was the most important variable for four of these taxa.

### Preference Experiment

Corona (2010) experimented with substrate choice of wood, cobble, sand, and moss to help explain the distributions of **Ephemeroptera** (Figure 8-Figure 9), **Plecoptera** (Figure 25), and **Trichoptera** (Figure 6) in streams in the San Bernardino National Forest (SBNF) in Southern California. She placed three of these preference samplers (615 cm<sup>2</sup> Plexiglass trays) in each of the three streams to determine where the insects chose to live. The actual stream had the leafy liverwort **Porella** sp. (Figure 26), but moss with a similar 3-d structure was chosen



because it was available commercially. Of the possible combinations of substrata, only two pairs were significantly different: large gravel vs sand and sand vs moss. The majority of species had greater species abundance in the liverwort and experimental moss compared to other microhabitats. Species diversity was greater in the experimental moss habitat compared to the sand habitat (Table 1). Corona suggested this could be a response to the greater food source that accumulated in the more complex structure of the mosses. In the stream, *Drunella grandis* (Figure 27) characterized the *Porella* habitat. Other species seemed to be influenced by habitat availability, with *Plecoptera* sp. 1 characterizing sand in the natural habitat, but characterizing the moss in the experimental preference habitat.



Figure 26. *Porella pinnata*. This genus provides a suitable habitat for *Drunella grandis* in California, USA, streams. Photo by Jan-Peter Frahm, with permission.



Figure 27. *Drunella grandis*, a stonefly naiad that inhabits *Porella pinnata*. Photo by Bob Newell, with permission.

### Torrents and Waterfalls

The precipice nears and the clump of mosses soon finds itself in a freefall, wet, and being carried by the pounding water and convection currents. Soon it will rejoin the stream below, bumping along until it gets pinned behind a log or rock.

In that same freefall are insects, dwellers of the water, giving in to the strong movement of the water, then drifting with the stream. Like the moss, they await a place where they can lodge. But for them, that lodging place might be the moss itself, a haven out of the torrent that takes them to

unknown destinations. A haven where they can lay their eggs and find algae, bacteria, fungi, or smaller insects to eat. A haven where they can rest safe from larger hungry predators. A place to be until that day when they must climb to the water's surface and take their maiden flight, free from the rushing torrent that made their life so tenuous.

Table 1. Field Tray Results for species contributors with a cut-off at 90% contribution characterizing microhabitats across all depths.

	Moss	Large Gravel	Sand	Wood
Lower Barton Creek				
<i>Baetis tricaudatus</i>	8.24	59.89	100	24.85
<i>Diphetero hageni</i>	28.15	34.76		45.08
<i>Micrasema</i>	8.01			
Nemouridae immature	9.30			
Plecoptera sp. 1	8.01			
<i>Zapada cinctipes</i>	9.61			
Santa Ana				
<i>Baetis tricaudatus</i>	51.87	18.45	74.47	31.99
<i>Ephemerella dorothea</i>	6.51	27.95	12.77	12.52
<i>Lepidostoma errigenum</i>	23.92	25.69	12.77	15.99
<i>Paraleptophlebia</i>	12.12	27.91		35.49
Upper Barton Creek				
<i>Baetis tricaudatus</i>				57.14
<i>Psychoglypha</i>	100			42.86

Thomas (1980) successfully reared the torrential dweller *Porricondyla ramadei* (Diptera: Cecidomyiidae), taken from submerged bryophytes in the turbulent water of a mountain stream in the Pyrénées. There were also hundreds of other strictly torrential invertebrates in the sample. Wallace and Ross (1971) described a new species of caddisfly, *Pseudogoera singularis* (Odontoceridae) from mosses in waterfalls of the Southern Appalachians, USA.

### Springs

Virtanen *et al.* (2009) investigated bryophyte inhabitants in 138 boreal springs. They found that water chemistry and temperature determined bryophyte assemblages. By contrast, Ilmonen (2009) found that the macroinvertebrate assemblages correlated with physical habitat but not with changes in chemistry.

Chironomids likewise responded to temperature, but water chemistry had little effect on them in 138 springs in Finland; physical habitat was somewhat important in their distribution (Virtanen *et al.* 2009). The **Chironomidae** (Figure 15) had a closer correspondence with **Ephemeroptera** (Figure 27), **Plecoptera** (Figure 25), **Trichoptera** (Figure 6), and **Coleoptera** (Figure 41-Figure 43) than with the bryophytes. Hence, as in stream habitats, spring bryophytes and insects are relatively poor surrogates for each other. Even when the insect assemblages were similar, the environmental characters differed. As in streams, better concordance occurred when larger geographic areas were included.

Hurny *et al.* (2005) found that springs in the Arctic separated from other stream types based on nutrient concentrations and likelihood of freezing. Glacier and



mountain streams separated from both springs and tundra streams on substrate instability and likelihood of freezing.

Lindegaard *et al.* (1998) concluded that the high variability of substrate within a spring accounted for the low variation among Danish streams. This same variability also made it impossible for Lindegaard and coworkers to correlate environmental variables with fauna. They classified the macroinvertebrates associated with springs and springbrooks into seven groups: (1) **cryobiotic** species restricted to the spring area, (2) **crenophilous** species with maximum abundances in springs, (3) **lotic** species also living in the spring area, (4) **lentic** species found in **limnocrenes**, (5) **ubiquitous** species, (6) **madicolous** species, and (7) **terrestrial** species.

Thorup (1963) described insects from Danish springs. Although I don't know how they correlated with the bryophytes, the genera and some of the species mentioned are known from bryophytes: *Baetis rhodani* (Figure 8), *Brachyptera risi* (Figure 28), *Nemurella picteti* (Figure 29), *Leuctra hippopus* (Figure 30), *Leuctra fusca* (Figure 31), *Agapetus fuscipes* (Figure 32), *Crunoecia irrorata* (Figure 33), *Pericoma* cf. *blandula* (Figure 34), and *Simulium ornatum* (Figure 35).



Figure 28. *Brachyptera risi* naiad, a bryophyte inhabitant in Danish springs. Photo by Guillaume Doucet <[www.guillaume.doucet.free.fr](http://www.guillaume.doucet.free.fr)>, with permission.



Figure 29. *Nemurella picteti* adult, a stonefly whose naiads live in Danish springs. Photo by Pete Hillman, with online permission.



Figure 30. *Leuctra hippopus* naiad, a stonefly that lives in Danish springs. Photo by Niels Sloth, with permission.



Figure 31. *Leuctra fusca* naiad, a stonefly that lives in Danish springs. Photo by James K. Lindsey, with permission.



Figure 32. *Agapetus fuscipes* larva in its case, an insect that inhabits Danish springs. Photo by J. C. Schou, with permission.



Figure 33. *Crunoecia irrorata* larva in its case, an insect inhabiting Danish springs. Photo by Niels Sloth, with permission.





Figure 34. *Pericoma blandula* adult, a species whose larvae live in Danish springs. Photo Copyright by Nick Upton <www.naturepl.com>, with permission.



Figure 35. *Simulium ornatum / intermedium / trifasciatum* complex adult, a species group that lives in Danish springs as larvae. Photo by Malcolm Storey, through Discover Life online permission.

Unlike other studies on surrogates, Ilmonen (2009) found that a rare spring-dwelling caddisfly (*Crunoecia irrorata*) was a good surrogate for springs that had a high conservation value. These springs had high overall species diversity, including other rare (red-listed) species. But as in other studies cited herein, these relationships held on a regional, but not within-spring system basis. Ilmonen and Paasivirta (2005) found that while there were differences in relative abundances among types of springs, the most common taxa were the same in all of them. The insects were somewhat more abundant in moss carpets and less abundant in sites that were pools. The strongest separators related to water flow and minerogenic substrate, a relationship supported by studies in Spain (Barquin & Death 2009).

Depth is an important factor for some insects. At the Puppu Springs, NZ, the invertebrates on the moss *Cratoneuropsis relaxa* (Figure 36) were 20 times more abundant at 0.6 m depth than at 4.3 m depth (Michaelis 1977). Such depth differences can relate to temperature, oxygen availability, and photosynthetic organisms (algae)

for food. Boulders with bryophytes had more invertebrates than those at similar depths with no bryophytes.



Figure 36. *Cratoneuropsis relaxa*, a moss where depth matters to the insects. Photo by Tom Thekathiyil, with permission.

Bottazzi *et al.* (2011) found that springs with mosses served as home for predominately **Chironomidae** (Figure 15) and **Plecoptera** (Figure 29-Figure 31), as well as the crenophilic microcrustaceans in **Harpacticoida** and **Ostracoda**. Only pH and temperature explained the diversity pattern, factors demonstrated as important by (Virtanen *et al.* 2009). Nevertheless, the presence of mosses increased the species diversity of the springs.

Seepage areas differ from other springs by having small flow rates in which the source water has filtered into permeable earth. These are often suitable habitats for bryophytes. In England, these seepage areas provide habitat for the crane fly *Tipula cheethami* (Figure 37) larvae living among the moss *Platyhypnidium riparioides* (Figure 38) and the snipefly *Spania nigra* (Figure 39) larvae on the liverwort *Pellia neesiana* (Figure 40) (Boyce 2002). On cliff seepages, one might find the tiny beetle *Sphaerius acaroides* (Figure 41-Figure 42) among the mosses. *Ochthebius poweri* (Figure 43) (**Coleoptera: Hydraenidae**) live in these seeps, eating the algae there. Some caddisflies occur there as well.



Figure 37. *Tipula abdominalis* larva, member of a genus that is found among *Platyhypnidium riparioides* in seepage areas of England. Photo by Tom Murray, through Creative Commons.





Figure 38. *Platyhypnidium riparioides*, a moss home for insects in seepage areas in England. Photo by David T. Holyoak, with permission.



Figure 39. *Spania nigra* adult, a snipefly whose larvae are known from the liverwort *Pellia neesiana* in seepages. Photo by Marko Mutagen, through Creative Commons.



Figure 40. *Pellia neesiana*, home for the snipefly *Spania nigra* in seepages. Photo by Jan-Peter Frahm, with permission.



Figure 41. *Sphaerius acaroides* adult, an inhabitant of mosses on cliff seepages. Photo by David Maddison, through Creative Commons.



Figure 42. *Sphaerius acaroides* larva, an inhabitant of mosses on cliff seepages. Photo by David Maddison through Creative Commons.



Figure 43. *Ochthebius exaratus* adult, an inhabitant of mosses in seepage cliffs, where it eats algae. Photo by Udo Schmidt through Creative Commons.



Ward and Dufford (1979) found that mosses and water cress (tracheophyte) had similar macroinvertebrate biomass in a Colorado springbrook-pond system. The tiny caddisfly *Hydroptila* (Figure 6) developed its largest populations on the moss. The crane fly *Limonia* (Figure 22) was present in large numbers and was restricted to mosses; *Euparyphus* (Stratomyiidae; Figure 44), another dipteran, was the second most abundant organism. Surprisingly, the *Coleoptera* (Figure 41) were the most diverse on mosses.



Figure 44. *Euparyphus* sp. larva, a genus that was restricted to mosses in a Colorado springbrook-pond system. Photo from EPA, through public domain.

Bryophytes in springs provide a continuous gradient from land to water, both vertically and horizontally (Lindegaard *et al.* 1975; Thorup & Lindegaard 1977; Bottazzi *et al.* 2011). Thus they provide a wide range of niches that promote a high invertebrate diversity. This transition furthermore makes an easy transition area for insects emerging from their aquatic stage into adults.

### Bogs and Fens

Bogs and fens are dominated by bryophytes at the ground level, creating unique and generally favorable habitats for invertebrates. Bogs have a wide temperature range within a single day (Gerson 1969). At the surface, the temperature can have a 30°C span in a single day while the stem layer experiences only a 5°C temperature span. Similarly, the surface humidity can range 40-100% while the stem layer remains at 100%. The pH ranges widely from acid bogs to rich fens, having a strong influence on some members of the insect assemblages.

Bogs have been widely studied for their unusual plant assemblages, but invertebrates have received much less attention, an omission known for a long time (Jewell & Brown 1929). Muttkowski (1912) summarized the insects in trout bogs in Yellowstone National Park, USA. These included *Ephemeroptera* (rare), *Odonata* (rare), *Hemiptera* (few), *Trichoptera* (rare), *Chironomidae* (Figure 15) (common), *Psychodidae* (common), and *Tipulidae* (frequent).

Many insects live in peatlands because of the diversity of habitats present there. For example, Bordoni (1972) found 179 species of beetles (Coleoptera) in a Tuscan fen, but only a few were actually bryophilous. Members of the *Staphylinidae* are known to feed on mosses (Mani 1962) and were well represented in that Tuscan fen. The *Sphaeriidae* (minute bog beetles) live among mosses (Arnett 1971).

A member of the insect order *Grylloblattodea* (crickets and grasshoppers) lays its eggs among mosses (Gerson 1969; Richards & Davies 1977). Crickets and grasshoppers in peatlands even feed on *Sphagnum* (Figure

1) (Vickery 1969). Uvarov (1977) suggested that these insects may eat the mosses to obtain water. Paasivirta *et al.* (1988) found that aquatic sites had greater insect emergence than semi-terrestrial sites in a boreal raised bog of central Finland.

As the hummocks and hollows build, the *Sphagnum* species change. *Sphagnum* (Figure 1) bogs undergo succession and their fauna changes as the *Sphagnum* species change (Murphy 1955). This succession of species is true for oribatid mites (Tarras-Wahlberg 1952-53) and pselaphid beetles (Reichle 1966). The fauna often occupy a specific position relative to the water table, presumably due to a preferred moisture level. Murphy (1955) found that the springtail *Sminthurides malmgreni* (Figure 45) became associated with the most humid hollow and pool species, *Sphagnum cuspidatum* (Figure 46) and *S. subsecundum* (Figure 47). When the mosses *S. papillosum* (Figure 48) and *S. magellanicum* (Figure 49), typical hummock mosses, become available, the springtails *Folsomia brevicauda* (see Figure 50) and *Isotoma sensibilis* (see Figure 51) are likely. Still others are present in the dry *Calluna* (Figure 52) and *Cladonia* (probably *Cladina*) habitat.



Figure 45. *Sminthurides malmgreni*, a bog dweller in hollows and pools. Photo by Jan van Duinen, with permission.



Figure 46. *Sphagnum cuspidatum*, a hollow and pool species where one can find *Sminthurides malmgreni*. Photo by Jonathan Sleath, with permission.





Figure 47. *Sphagnum subsecundum*, a bog hollow and pool species where one can find *Sminthurides malmgreni*. Photo by Michael Lüth, with permission.



Figure 48. *Sphagnum papillosum*, a hummock species that is home to *Folsomia brevicauda* and *Isotoma sensibilis*, with sundew. Photo by Michael Lüth, with permission.



Figure 49. *Sphagnum magellanicum*, a hummock species that is home to the springtails *Folsomia brevicauda* and *Isotoma sensibilis*. Photo by Michael Lüth, with permission.



Figure 50. *Folsomia fimetaria*, a springtail that lives in hummocks of bogs. Photo by Andy Murray, through Creative Commons.



Figure 51. *Isotoma* sp., a genus found in hummocks of *Sphagnum papillosum* and *S. magellanicum*. Photo by Anki Engström at <[www.krypinaturen.se](http://www.krypinaturen.se)>, with permission.



Figure 52. *Calluna vulgaris* heath on drier hummocks in the Outer Hebrides. Photo by Alan Silverside, with permission.

Bryophytes play a major role in the fauna of bogs. That fauna is often shared with fauna of surrounding habitats, but some unique organisms prefer that habitat, and others use it seasonally.

### Collembola - Springtails

Whereas **Collembola** are not common among submerged bryophytes, a number of species occur among bryophytes, especially *Sphagnum* (Figure 1, Figure 46-Figure 49), in bogs. Ussinger (1974) suggests collecting these bog taxa by submersing the moss in water until the **Collembola** float.

Bright (2002) reported 15 springtail species in Michigan bogs. These included *Bourletiella arvalis*



(Figure 53), *Folsomia prima* (Figure 54), *Heteraphorura subtenuis*, *Hydroisotoma schaefferi* (Figure 55), *Hypogastrura nivicola* (Figure 56), *Isotoma viridis* (Figure 57), *Neelus minutus* (see Figure 58), *Orchesella albosa* (Figure 59), *Sminthurides aquatica* (Figure 60-Figure 61), *Sminthurides malmgreni* (Figure 62), *Sminthurides occultus*, *Sminthurides penicillifer* (Figure 63), *Sminthurinus aureus* (Figure 64), *Sminthurinus bimaculatus* (Figure 65), and *Tomocerus flavescens* (Figure 66).



Figure 53. *Bourletiella arvalis*, a tiny bog-dwelling springtail. Photo by Jan van Duinen, with permission.



Figure 54. *Folsomia* sp.; *F. prima* is a bog dweller. Photo by Jan van Duinen, with permission.



Figure 55. *Hydroisotoma schaefferi* male, a species that can be found with *Sphagnum* (Figure 1, Figure 46-Figure 49) in bogs. Photo by Tom Murray, through Creative Commons.



Figure 56. *Hypogastrura nivicola*, a bog inhabitant. Photo by Scott Justis, with permission.



Figure 57. *Isotoma viridis*, a species that occurs in bogs. Photo by Jan van Duinen, with permission.



Figure 58. *Neelus murinus* with eggs – a bog inhabitant. Photo by Frans Janssens, with permission.





Figure 59. *Orchesella cincta*, member of a genus with bog inhabitants. Photo by Malcolm Storey, through Creative Commons.



Figure 60. *Sminthurides aquatica*, a bog-dweller. Photo by Andy Murray, through Creative Commons.



Figure 61. *Sminthurides aquatica* on frog's eye, demonstrating its small size. Photo by Kim Fleming, through Creative Commons.



Figure 62. *Sminthurides malmgreni*, a bog dweller. Photo by Jan van Duinen, with permission.



Figure 63. *Sminthurides* cf. *penicillifer* female. Photo by Andy Murray, through Creative Commons.



Figure 64. *Sminthurinus aureus*. Photo by Andy Murray, through Creative Commons.



Figure 65. *Sminthurinus bimaculatus*. Photo by Andy Murray, through Creative Commons.





Figure 66. *Tomocerus flavescens*, a bog dweller. Photo by Royce Bitzer, with permission.

### Coleoptera - Beetles

*Crenitis punctatostrata* (Hydrophilidae; Figure 67) is a true **bryobiont** (animal exclusively associated with bryophytes) that lives its entire life among *Sphagnum* (Figure 1) and is known from the Jura Mountains (Matthey 1977). This species lays its eggs among the mosses and the larvae remain there. The pupa lives in a cell formed from the bryophytes.

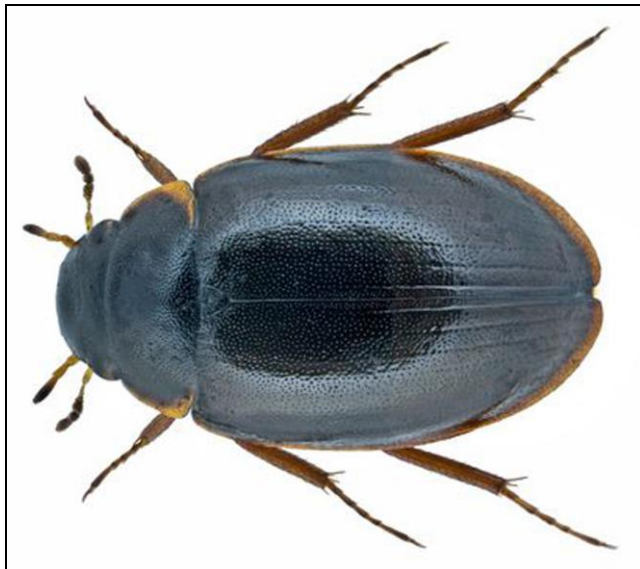


Figure 67. *Crenitis punctatostrata* adult, a species that lays its eggs among mosses and the larva develop there. Photo by Udo Schmidt, through Creative Commons.

For some *Sphagnum* (Figure 1)-associated insects, this moss provides a safe haven during unfavorable seasons. One of the more unusual of these is the tiny water beetle *Hydroporus morio* (quick silver diver; Figure 68) (Jackson 1956 in Gerson 1982). This beetle lives in *Sphagnum* pools in Europe and is sensitive to heat. When these pools dry out in summer, the exposure to heat on a sunny *Sphagnum* mat can be dangerous for *H. morio*. To survive, the beetle bores small round holes into the damp *Sphagnum* in the "dried" pool and **aestivates** (summer equivalent of hibernates) in that protected (and insulated)

location until the rains return. In the southern parts of its range, it is disappearing, apparently due to climate warming (Anderson 2015).



Figure 68. *Hydroporus morio* adult, an insect that lives in *Sphagnum* pools, then bores holes into the mat to aestivate when the pools dry. Photo by Niels Sloth, with permission.

Others find bryophytes a suitable place to survive the winter (Reichle 1966). More than 20 species of beetles in the **Pselaphidae** live in *Sphagnum* (Figure 1) bogs, where they can find a microclimate similar to that of their early postglacial ancestors. Among these are beetles that overwinter as adults in the interstitial spaces of frozen moss mats.

Larson and House (1990) found that small pools were dominated by oligochaetes, beetles, and mosquitoes. Hebauer (1994) listed **Coleoptera** (Figure 68) species he considered to be **tyrphophils**, *i.e.*, living among *Sphagnum* (Figure 1), in middle Europe. These included *Ilybius erichsoni* (Figure 69), *Agabus congener* (Figure 70), *I. wasastjernai* (Figure 71), *Bidessus grossepunctatus* (Figure 72), *Hygrotus novemlineatus* (Figure 73), *Colymbetes paykulli* (Figure 74), *C. striatus*, *Enochrus affinis*, *E. coarctatus*, *E. ochropterus* (Figure 75), *Hydrochus brevis* (Figure 76), *H. megaphallus*, *Hydroporus brevis* (Figure 77), *H. melanarius* (Figure 78), *H. memnonius* (Figure 79), *H. scalesianus* (Figure 80), *H. tristis* (Figure 81). Underground springs with *Sphagnum* housed *Hydroporus ferrugineus* (Figure 82), *H. obsoletus*, and *H. longicornis* (Figure 83). Leng (1913) reported **Parnidae** and **Elmidae** (Figure 84) in *Sphagnum* (Figure 1) bogs.



Figure 69. *Ilybius erichsoni* adult, a tyrphophil, on *Sphagnum*. Photo by Niels Sloth, with permission.



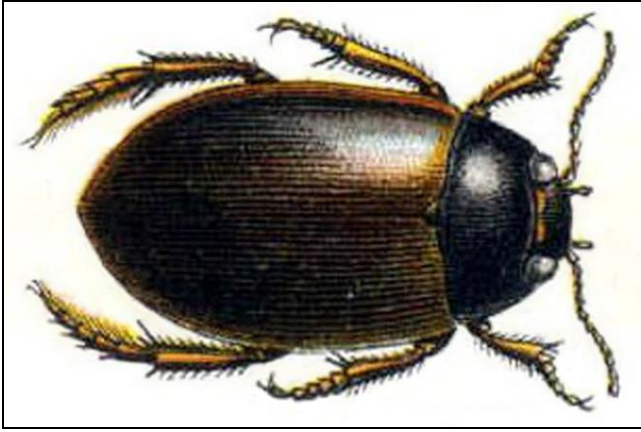


Figure 70. *Agabus congener* adult, a *Sphagnum* dweller. Image through Creative Commons.

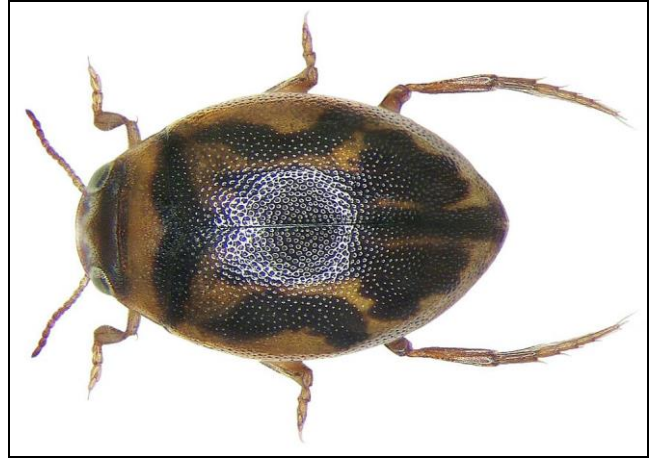


Figure 73. *Hygrotus inaequalis* adult, a *Sphagnum* dweller. Photo by Udo Schmidt, with permission.



Figure 71. *Ilybius wasastjernai* adult, a *Sphagnum* dweller. Photo by Niels Sloth, with permission.



Figure 74. *Colymbetes paykulli* adult, a *Sphagnum* dweller. Photo by Niels Sloth, with permission.



Figure 72. *Bidessus unistriatus* adult, a *Sphagnum* dweller. Photo by Udo Schmidt, through Creative Commons.



Figure 75. *Enochrus ochropterus* adult, a *Sphagnum* inhabitant. Photo by Niels Sloth, with permission.





Figure 76. *Hydrochus brevis* adult, a *Sphagnum* inhabitant. Photo by Christoph Benisch <kerbtier.de>, with permission.



Figure 77. *Hydroporus brevis* adult, a *Sphagnum* inhabitant. Photo by Niels Sloth, with permission.



Figure 78. *Hydroporus melanarius*, a bog dweller, on moss. Photo by Niels Sloth, with permission.



Figure 79. *Hydroporus memnonius* adult, a bog dweller, on moss. Photo by Niels Sloth, with permission.



Figure 80. *Hydroporus scalesianus* adult on leaf litter. Photo by Niels Sloth, with permission.



Figure 81. *Hydroporus tristis* adult on moss. Photo by Wolfram Sondermann, through Creative Commons.



Figure 82. *Hydroporus ferrugineus*, an inhabitant of underground springs with *Sphagnum*. Photo by Roger S. Key, with permission.



Figure 83. *Hydroporus longicornis* adult on moss, an inhabitant of underground springs with *Sphagnum*. Photo by Niels Sloth, with permission.





Figure 84. *Elmidae* larva, a *Sphagnum* bog dweller. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Reichle (1967) considered temperature and humidity to be the most important variables influencing the pselaphid beetles in bogs. These beetles respond to saturated humidities of 95-100%, and these match the conditions found among the interstices created by the mosses. The temperature stratification created by the mosses could explain the differences in species at different **seral stages** (stages in succession).

For the five species of pselaphids Reichle (1967) studied, these preferences were *Bythinopsis tychoides*, mean  $21.5 \pm 0.81$ , range  $25.9-15.3^{\circ}\text{C}$ ; *Decarthron defectum*,  $28.5 \pm 0.55$ ,  $31.4-24.0$ ; *Pselaphus bellax* (Figure 85),  $19.5 \pm 0.86$ ,  $24.7-13.0$ ; *Reichenbachia borealis* (Figure 86),  $21. \pm 0.99$ ,  $26.2-14.4$ ; and *Rybaxis clavata* (Figure 87),  $28.3 \pm 0.41$ ,  $29.9-25.1$ . These preferences correlated well with the natural conditions of the microhabitats where they resided in the New York bog.

To these species, a report from the New York Entomological Society (Anonymous 1925) added the pselaphid *Pselaphus erichsoni* and the staphylinid *Boreaphilus henningianus*, cohabiting in a New York, USA, bog with *Bythinopsis tychoides*. Mr. Nicholay, at that same meeting, recommended using sifting to locate the **Coleoptera** in such habitats.



Figure 85. *Pselaphus bellax* adult, a *Sphagnum* bog dweller. Photo by Yann Gobeil, through Creative Commons.



Figure 86. *Reichenbachia borealis* adult, a *Sphagnum* bog dweller. Photo by Tom Murray, through Creative Commons.



Figure 87. *Rybaxis* female adult, a *Sphagnum* bog dweller. Photo by Tom Murray, through Creative Commons.

### Odonata – Dragonflies and Damselflies

The **Odonata** are commonly seen flying about bogs. These strong fliers can easily migrate there. Boudot and Jacquemin (2002) identified 20 species of **Odonata** as tyrphobionts in France. Larson and House (1990) found that **Odonata** dominated, along with **Chironomidae** (**Diptera**; Figure 15), in the large, stable, vegetated pools. With two or more years in their naiad stage, the **Odonata** are important consumers in this habitat and may be a major factor in the insects that survive there. These dragonflies included *Aeshna subarctica* (Figure 88), *Somatochlora arctica* (Figure 89), *Leucorrhinia dubia* (Figure 90), and *Somatochlora alpestris* (Figure 91). The bog habitat influences these dragonflies by its strong pH fluctuations, low secondary productivity, few vertical plant structures (needed for emergence), and the isolation of bogs from each other (Dreyer 1988). Goffart and Fichet (2003) observed female *Aeshna subarctica* laying eggs (Figure 88) by inserting them into *Sphagnum* (Figure 1) at the water surface. Sahlén *et al.* (2004) found that *Aeshna subarctica elisabethae* from central and eastern Europe was "strictly" related to *Sphagnum* habitats.





Figure 88. *Aeshna subarctica* laying eggs in *Sphagnum*. Photo by Guillaume Doucet <[www.guillaume.doucet.free.fr](http://www.guillaume.doucet.free.fr)>, with permission.



Figure 89. *Somatochlora arctica* adult male; females lay eggs in *Sphagnum*. Photo by Piet Spaans, through Creative Commons.



Figure 90. *Leucorrhinia dubia*, a prominent predator in bogs. Photo by L. B. Tettenborn through Creative Commons.

Michiels and Dhondt (1990) observed dragonflies (*Sympetrum danae* – Figure 92) during their egg-laying activities in bogs. This species typically oviposits in flight while still paired in copulation. This behavior seems to make them subject to frog predation – those that were post-

tandem were attacked less frequently by the frogs. The females seemed to prefer *Sphagnum* (Figure 1) as a substrate for their eggs. They avoided warmer sites and often chose sites that already had ovipositing females on them. Michiels and Dhondt reported several threatened and potentially threatened *Odonata* species living in these diminishing habitats. These included *Nehalennia speciosa* (Figure 94), *Coenagrion johanssoni* (see Figure 93), *Aeshna caerulea* (Figure 95), *A. crenata*, *A. subarctica elisabethae* (Figure 88), *Somatochlora arctica* (Figure 89), and *S. alpestris* (Figure 91). In northern Europe where the habitat is common, these species, except *N. speciosa* and *A. crenata*, are likewise common.



Figure 91. *Somatochlora alpestris* adult, a prominent predator in bogs. Photo by Gilles San Martin, through Creative Commons.



Figure 92. *Sympetrum danae* female adult, a species that lays her eggs in bogs. Photo by L. B. Tettenborn, through Creative Commons.



Figure 93. *Coenagrion hastulatum* adult. Photo by L. B. Tettenborn, through Creative Commons.





Figure 94. *Nehalennia speciosa* mating damselfly adults. These bog dwellers lay their eggs in bogs. Photo by Guillaume Doucet <<http://guillaume.doucet.free.fr/>>, with permission.



Figure 95. *Aeshna caerulea* adult emerging. Photo by Guillaume Doucet <[guillaume.doucet.free.fr](http://guillaume.doucet.free.fr/)>, with permission.

The ground cricket *Pteronemobius* sp. (Figure 96) not only eats bryophytes, but also punctures *Sphagnum* leaves with its ovipositor to place its eggs in the resulting cavity (Vickery 1969).



Figure 96. *Pteronemobius heydenii*, a genus of cricket that eats bryophytes and punctures *Sphagnum* leaves to lay its eggs. Photo through Flickr Creative Commons.

### Diptera – Flies

If you have ever walked through a forest surrounding a bog on a humid summer evening, you probably have not forgotten the experience of blood-giving. Mosquitoes are not typical bryophyte fauna, but in bogs *Aedes excrucians* (Figure 97) occurs in bog pools and occasionally among the *Sphagnum* (Figure 1) mosses there (Elgmork & Sæther 1970).



Figure 97. *Aedes excrucians* larvae, bog pool dwellers. Photo by Donald S. Chandler, with permission.

The **Tipulidae** (Figure 98) often deposit eggs and live as larvae and pupae among the peat mosses. *Tipula* (Coulson 1962; Freeman 1968) and *Dolichopeza* (Byers 1961) also feed on the mosses. The moss-mimicking tipulid *Phalacrocer* *replicata* feeds on *Sphagnum* spp. (Clymo & Hayward 1982). Other tipulid species burrow into *Sphagnum* (Figure 1) spp.

But bogs often attract human traffic for berry picking and other interests. This traffic can be detrimental to these developing **Diptera**. *Molophilus ater* (Figure 99) (**Limoniidae**) numbers are lower among the peat along a path than in adjacent areas (Duffey 1979). These limoniid crane fly adults seem to spend more time where there is vegetation than on bare ground, although they seem to prefer the bare ground for laying eggs. This same preference for egg laying is not true for large bare areas. Unfortunately, larvae are often crushed along the paths, especially those near the surface.





Figure 98. **Tipulidae** adult, a common family in bogs. Photo by Bob Armstrong, with permission.



Figure 99. **Molophilus ater** adult, a species negatively affected by bog traffic. Photo by James K. Lindsey, with permission.

As in most aquatic moss habitats, **Chironomidae** (Figure 15) are important contributors to the fauna (Muttkowski 1912; Larson & House 1990). Smirnov (1961) did not find any abundant species in *Sphagnum* (Figure 1) bogs to specialize on a food group, but one chironomid, *Psectrocladius psilopterus*, was the only species to eat submerged *Sphagnum*; even so, it ate primarily algae.

### Other Insects

The moisture available within a *Sphagnum* habitat, perhaps made safer by the antibiotic properties of the moss, provides a suitable habitat for nests of *Myrmica ruginodis* (Figure 100-Figure 101) and *Formica picea* (Figure 102) (Matthey 1971). These ants also feed on the mosses (Plitt 1907) and become major predators when the bog dries up (Grdović & Sabovljević 2008).



Figure 100. **Myrmica ruginodis** pupa among mosses. Photo by James K. Lindsey, with permission.



Figure 101. **Myrmica ruginodis** adult amid mosses. This species makes its nest of *Sphagnum* fragments. Photo by James K. Lindsey, with permission.



Figure 102. **Formica picea** adult, a species that makes nests of *Sphagnum*. Photo by April Nobile <[www.antweb.org](http://www.antweb.org)>.

On one fortunate adventure into a Michigan, USA, fen I had the privilege of watching ants on one of their nests on a windy day (Figure 103). The light-weight *Sphagnum* pieces were flying off the nest faster than they could grab new ones and repair the nest. This of course created great activity among the ants (Figure 104).





Figure 103. Ant nest in *Sphagnum* in a Michigan fen. Photo by Janice Glime.



Figure 104. Close view of ants repairing nest of *Sphagnum* in a Michigan fen as its bits of *Sphagnum* are being scattered by wind. Photo by Janice Glime.

A number of terrestrial insect types can be found in bogs and fens as well, including crickets and grasshoppers (Vickery 1969), caterpillars of moths (Chapman 1894), and aphids in the genera *Myzodium* (Figure 105) and *Muscaphis* (Figure 106) (Gerson 1969). But aquatic and semi-aquatic types occur there as well, including the biting midge *Forcipomyia* (Figure 107) (Oldroyd 1964) and mayfly naiads (Richardson 1981).



Figure 105. *Myzodium mimulicola*, aphids that live in bogs. Photo by Andrew Jensen, through Creative Commons.



Figure 106. *Muscaphis utahensis*, a bog-dwelling aphid. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Figure 107. *Forcipomyia* sp. larvae, a biting midge that lives among mosses in bogs. Photo by Tom Murray, through Creative Commons.

Although some of the insects eat *Sphagnum*, Danks and Rosenberg (1987) report that most species in Canadian bogs are generalists. Flannagan and Macdonald (1987) likewise found the **Ephemeroptera** and **Trichoptera** of Canadian peatlands to be generalists. They suggested that the ability for some insects to survive in temporary pools provided adaptations that also permitted them to live in other wet habitats such as peatlands. Mayfly naiads even use *Sphagnum* species for "nests" (Richardson 1981).

## Lakes and Ponds

Floating bryophytes can be abundant in small lakes and ponds. The thallose liverwort *Riccia fluitans* (Figure 108) can form dense 3-d mats that provide a protective network. The spaces formed house numerous invertebrates in these floating habitats (Armstrong 2014).

Needham (1901) found layers of shed exuviae of the dragonfly *Gomphus exilis* (Figure 109), with *G. spicatus* mixed in, among mosses on logs at the edge of Little Clear Pond, suggesting the mosses created a preferred site for emergence.





Figure 108. *Riccia fluitans*, home for numerous insects in the floating mats. Photo by Jan-Peter Frahm, with permission.



Figure 109. *Gomphus exilis* female, a species that uses mosses for emergence. Photo by Sheryl Pollock, with permission.

One of the unusual habitats at the edge of lakes is the **moss ball**. Moss balls generally begin on a small pebble that gets moved back and forth across the shoreline as the water gets blown onto the shore and recedes. These are able to develop a special fauna of *Asellus aquaticus* oligochaetes, and leeches on balls formed by *Fontinalis antipyretica* (Figure 10) and *Drepanocladus sendtneri* (Figure 110), but insects were not mentioned (Luther 1979 in Gerson 1982).



Figure 110. *Drepanocladus sendtneri*, a moss-ball former that is inhabited by invertebrates. Photo by Michael Lüth, with permission.

Floating plants provide a habitat that is constantly wet, yet does not require breathing under water. Plants such as those in the flowering plant family Lemnaceae (duckweeds) have their own fauna of insects. And in some lakes and ponds, the floating thallose liverwort *Ricciocarpus natans* (Figure 111) may occur with the duckweeds. In these habitats one might find the springtail *Sminthurides aquaticus* (Figure 112) that eats from the surface, the beetle *Tanysphyrus lemnae* (Figure 113) that completes its entire life cycle in only two weeks on *Lemna* (Figure 113), but it is not yet known from *Ricciocarpus*, and *Mesovelis mulsanti* (Figure 114), a bug known as the water treader, crawling on the surface and in depressions on the surface of this floating habitat (Scotland 1934). The liverwort *Ricciocarpus natans* is also capable of rearing the dipteran *Phytoliriomyza mesnili* (Agromyzidae) (Spencer 1990), but it can pupate on more occasionally inundated species such as *Riccia beyrichiana* (Figure 115) and feed on this and other terrestrial bryophytes (Hering 1966).



Figure 111. *Ricciocarpus natans*, home for springtails and other surface dwellers. Photo by Jan-Peter Frahm, with permission.



Figure 112. *Sminthurides aquaticus*, a springtail that lives on *Ricciocarpus natans*. Photo by Andy Murray, through Creative Commons.





Figure 113. *Tanysphyrus lemnae* on *Lemna*. Note the holes chewed in the leaves by these weevils. Photo by Aydin Örstan through, Creative Commons.



Figure 114. *Mesovelis mulsanti*, a surface dweller. Photo by Matt Bertone, through Creative Commons.



Figure 115. *Riccia beyrichiana*, site for pupation of *Phytoliriomyza mesnili* when the thallus is inundated. Photo by Jan-Peter Frahm, with permission.

## Arctic and Alpine

In investigating alpine streams of New Zealand, Suren (1993) found that streambed stability strongly influenced the bryophyte distribution. These communities are dominated by **Nematoda**, **Oligochaeta**, **Copepoda**, and **Chironomidae** (Figure 15). These differed in fauna from bryophytes outside New Zealand, particularly certain families of **Ephemeroptera**, **Plecoptera**, and **Trichoptera** (EPT) that are also present elsewhere in New Zealand. Nevertheless, the invertebrate densities within the bryophytes are higher above treeline than below. The invertebrate densities are higher among bryophytes that have a high periphyton component compared to those with a higher detrital component.

In the alpine area of the South Island of New Zealand, Suren (1988) found that the dominant bryophyte dwellers are the stoneflies *Zelandoperla* (Figure 18) and *Zelandobius* (Figure 19) and the midges (**Chironomidae**, Figure 15). The mosses had 5-15 times as many invertebrates as the rocky areas, but these moss-dwelling invertebrates also include nematodes, mites, copepods, ostracods, and other non-insect invertebrates. The most common mayflies are restricted to rocky areas.

In the Southern Alps of New Zealand, Cowie and Winterbourn (1979) found 44 species of invertebrates among the mosses. These are mainly immature stages of insects, with the fauna varying by moss; the moss species reflects differences in habitat. *Fissidens rigidulus* (Figure 116) grows in the torrential middle channel of the stream and supports *Zelandoperla fenestrata* (**Plecoptera**; see Figure 18), *Zelolessica cheira* (**Trichoptera**; see Figure 117-Figure 118), *Empididae* (**Diptera**; Figure 21) and the ever-present **Chironomidae** (Figure 15). Among the clumps of *Pterygophyllum quadrifarium* (Figure 119) in the saturated inner spray zone Cowie and Winterbourn found *Austroperla cyrene* (**Plecoptera**), and **Helodidae** (**Coleoptera**) as the most abundant species, along with the flatworm *Neppia montana*. *Cratoneuropsis relaxa* (Figure 36), in the outer spray zone, was not a good insect habitat, housing primarily the isopod *Styloniscus otakensis*. Water Saturation, flow rates, and available detritus as a food source seem to have the greatest influence on the locations of these insects.



Figure 116. *Fissidens rigidulus*, a moss that grows in the torrential mid-channel where **Plecoptera** and **Diptera** are common. Photo by Bill & Nancy Malcolm, with permission.





Figure 117. *Zelolessica* sp., prevalent among *Fissidens rigidulus* midstream in Southern Alps of New Zealand. Photo by Stephen Moore, Landcare Research NZ, with permission.



Figure 118. *Zelolessica* sp., prevalent among *Fissidens rigidulus* midstream in the Southern Alps of New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 119. *Pterygophyllum quadrifarium*, a moss that houses insects in the spray zone of torrential channels in New Zealand. Photo by Bill and Nancy Malcolm, with permission.

Robinson *et al.* (2001) studied the glacial streams of the Swiss Alps. These streams experience strong seasonal changes in water chemistry resulting from the seasonal changes in glacial melt, especially in water turbidity, particulate phosphorus, and conductivity. The macroinvertebrates likewise vary seasonally, with winter macroinvertebrate taxon richness being 2-3 times as high as that in summer. These same differences are also reflected in higher numbers and biomass in winter. Although taxa are not delimited by substrate in this study, many of the dominant taxa are species known as common bryophyte inhabitants.

**Diptera**, common among temperate streams, are even more common in Alaskan streams (Oswood 1989). **Plecoptera** and **Ephemeroptera** are next in abundance, but **Trichoptera** are somewhat rare. The **Hemiptera**, **Odonata**, **Megaloptera**, **Coleoptera**, net-spinning caddisflies, burrowing mayflies, and the stoneflies **Pteronarcyidae**, **Peltoperlidae**, and **Perlidae** are rare or absent. On the other hand, the ever present **Chironomidae** (**Diptera**; Figure 15) and **Nemouridae** (**Plecoptera**) actually increase from south to north in the northern hemisphere.

A similar predominance of **Chironomidae** (Figure 15) is seen in the European Central Alps – comprising 90-95% of the emergence (Füreder *et al.* 2005). As in Oswood's (1989) Alaskan study, **Ephemeroptera**, **Plecoptera**, and **Trichoptera** comprised much fewer numbers. Füreder *et al.* (2001) considered seasonal shifts from harsh summers to less severe autumn and winter conditions in the Tyrolean Alps, Austria, to affect the insect life history patterns and maintain a relatively high insect diversity and productivity in glacier-fed streams. As in glacial streams, the individual alpine streams of the French Pyrénées seem to differ greatly in diversity, displaying distinct benthic macroinvertebrate communities. Within a stream, the 15 most abundant taxa were consistently more stable and persistent from one year to the next than was the entire stream community (Brown *et al.* 2006).

Miller and Stout (1989), working in Alaska, suggested that to be so successful the dipterans that compose the most numerous and variable taxa in the Arctic must have variable **diapause** (period of suspended development; state of physiological dormancy), ability to grow in cold waters, and good dispersal powers.

## Disturbance

Disturbance greatly reduces the number of invertebrates, and in some cases the bryophytes, on stones in streams (Englund 1991; Parker & Huryn 2006). Small stones rarely have bryophytes (Slack & Glime), except when they are embedded in the substrate (Englund 1991). Rock size likewise affects the diversity of stream insects (Hart 1978). In Englund's study, following disturbance, several invertebrate taxa increased their density on moss-covered undersides of over-turned stones. The undisturbed moss-covered rocks acquired increased density of invertebrates as a result of the disturbance. On the other hand, on disturbed rocks recovery of lost mosses [*Fontinalis dalecarlica* (Figure 16), *Hygrohypnum* (Figure 120-Figure 121)], and hence invertebrate inhabitants, was poor even 14 months after the stones were overturned.



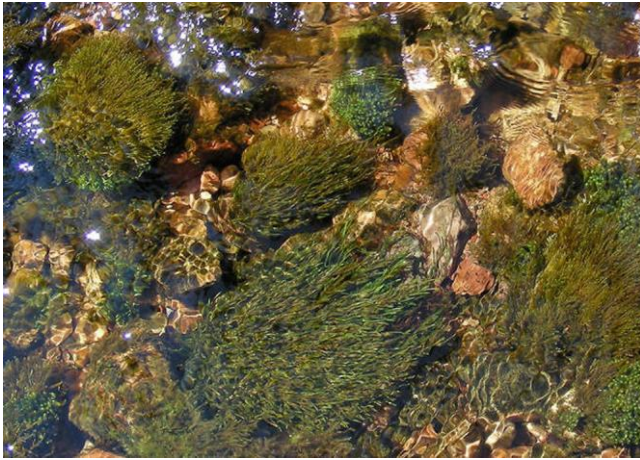


Figure 120. *Hygrohypnum ochraceum* habitat, a genus that can have poor recovery after disturbance, resulting in loss of insects. Photo by Dick Haaksma, with permission.



Figure 121. *Hygrohypnum ochraceum*, home to many insects. Photo by Michael Lüth, with permission.

In an Alaskan stream, Parker and Huryn (2006) attributed the high macroinvertebrate density in a spring stream to the density of bryophytes there. That biomass was more than 1000 times the density of the mountain stream where disturbance among the loose rocks was great during spring melt.

Disturbance can take the opposite form as well. During the dry season, aquatic insects must find a place of refuge that provides sufficient moisture, or go dormant. In a first-order stream in the Atlantic Forest, Brazil, Rosa *et al.* (2011) found that Chironomidae dominate in both the rainy and dry seasons, but that in the rainy season the Ceratopogonidae are second, whereas in the dry season it is the annelid family Naididae that is second. Rosa and coworkers concluded that the bryophyte habitat provides refuge during spates, minimizing downstream movement of the invertebrate fauna. The density of the fauna is much greater during the rainy season, but the diversity is similar.

## Retention

Restoration is not always friendly to mosses. In a headwater stream, the moss cover declined dramatically following restoration (Muotka & Laasonen 2002). This resulted in increases of insects only among the algae-eating scrapers. The mosses were an important retentive feature

for macroinvertebrates, but the restoration techniques knocked them loose from numerous locations, favoring the growth of algae.

## Colonization

The rapidity of invertebrate recolonization of mosses can be amazing. Maurer and Brusven (1983) found that insects colonized insect-free *Fontinalis neomexicana* (Figure 4) to capacity within one week. The moss substrate had 5-30 times the densities of insects compared to the mineral substrate. As in many streams, larvae of midges (Chironomidae, Figure 15) were most abundant. Thienemann (1936), in his enumeration of alpine Chironomidae, commented on the importance of mosses as a habitat.

Korsu (2004) found that the restoration procedure in one Finnish stream destroyed almost half of the bryophytes and invertebrate densities plummeted. But recolonization was rapid. The disturbed area was recolonized within two weeks and peak numbers were reached within one month. Korsu found that recovery was especially fast in winter, with bryophytes playing a major role. It is interesting that the density of insects on bryophytes was higher after the restoration than before. The mayfly *Baetis* (Figure 8) had a negative correlation with the bryophytes before restoration, but afterwards (within 1 day!) it had a positive correlation. A similar response occurred for *Hydropsyche siltalai* (Figure 122). Korsu concluded that bryophytes provided refugia during the disturbance and remained a shelter long afterwards.



Figure 122. *Hydropsyche siltalai* larva, a species that increased in numbers after restoration of a stream in Finland. Photo by Urmas Kruus, with permission.

Experimental studies on colonization of mosses are relatively rare. Some of these have been discussed earlier under Artificial Mosses (Chapter 11-1). Maurer and Brusven (1983), however, designed a study using live *Fontinalis neomexicana* (Figure 4) in an Idaho, USA, river. After removing all the insects, they trimmed the moss clumps into 40 X 15 cm plots and arranged them in a natural streambed in five staggered rows with three clumps per row, as well as two comparative samplings. After three weeks of colonization, moss clumps were collected in nylon organdy net (250 µm mesh) to keep insects intact. Insects were removed by washing and hand picking. It



took only one week for insects to reach carrying capacity of the mosses (compared to controls)! The caddisfly *Micrasema* sp. (Figure 123) and mayfly *Dipheter hageni* (= *Baetis parvus*; Figure 124) were especially prevalent among moss clumps during the study. At the same time, the moss cover did not change the insect densities in the underlying hyporheic zone.



Figure 123. *Micrasema charonis* larva with a case made from moss parts. Photo by Bob Henricks, with permission.



Figure 124. *Dipheter hageni* naiad, common among *Fontinalis neomexicana* in Idaho. Photo by Donald S. Chandler, with permission.

Maurer and Brusven (1983) found that the **Ephemeroptera** were the most abundant in both test and control clumps, with **Diptera**, **Trichoptera**, **Coleoptera**, and **Plecoptera** following in that order. The **Chironomidae** (Figure 15) made up ~94% of the **Diptera**. The riffle beetle *Cleptelmis ornata* (Figure 125) was a slow colonizer, reaching carrying capacity only after 4-6 weeks.

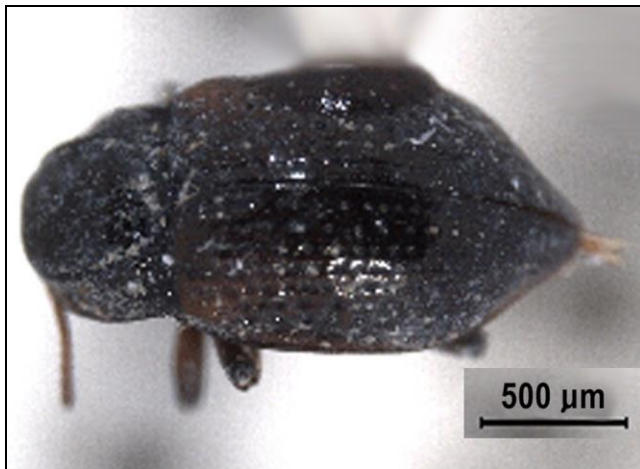


Figure 125. *Cleptelmis ornata* adult, a slow colonizer of bryophytes. Image modified from Biodiversity Institute of Ontario, through Creative Commons.

Mackay and Waters (1986) found that mosses provided suitable sites for the **Hydropsychidae** (net-spinning caddisflies; Figure 3) downstream of impoundments. They suggested that the mosses and algae provided suitable sites for attachment of their nets and the location benefitted from the settling effect of the impoundment on abrasive sand.

Streams suffer natural disturbance. In two North Swedish woodland streams nearly 17% of the moss-covered stones were overturned in just a few years (Englund 1991). In experiments, overturning rocks with mosses resulted in a reduction of both ash-free dry weight and diversity. On the other hand, three out of 16 taxa actually increased density on the underside of the overturned stones, living among the buried mosses. All the other taxa decreased in density. Even after 14 months the mosses and invertebrate populations had not recovered.

As already noted, Gurtz and Wallace (1984) found that presence of mosses increased the density of taxa following clear cutting surrounding a southern Appalachian Mountain stream. But disturbance resulting from the insecticide fenitrothion on bogs did not have as favorable a result (Fairchild & Eidt 1993). The poison caused a reduction in insect emergence for the next 6-12 weeks, with the **Chironomidae** (Figure 15) and **Ceratopogonidae** (Figure 126) experiencing more than 50% reduction for at least 1 month after the treatment. Since bog pool insects carry the nutrients to land, this nutrient transfer diminished and more nutrients accumulated in the bog pools.



Figure 126. *Bezzia* larva, in a family (**Ceratopogonidae**) that is quickly reduced by fenitrothion in bogs. Photo from <www.dfg.ca.gov>, through public domain.

It is interesting that in a study of Swedish streams, Malmqvist and Hoffsten (2000) found a negative correlation between macroinvertebrate richness and moss (*Fontinalis* – Figure 10) coverage. In a glacial river in Iceland, Gislason *et al.* (2001) found that distance from glacier, altitude, bryophyte biomass, and Pfankuch Index of channel stability explaining 31% of the variability in the macroinvertebrate data. The **Chironomidae** (Figure 15) predominated, but **Simuliidae** (Figure 35), **Plecoptera** (Figure 28-Figure 31), and **Trichoptera** (Figure 123) were present in low numbers.

In New Zealand alpine streams, bryophytes were confined to stable substrates (Suren 1991a). Suren (1988) found a negative effect on **Collembola** (Figure 45) when real mosses were replaced by artificial mosses in the high

alpine streams of the South Island of New Zealand. Among those moss-inhabited substrates, *Limonia hudsoni* (see Figure 22) and *Zelandoperla* sp. (Figure 18) were typically associated with bryophytes (Suren 1991a).

Not all bryophyte growths bring a positive recovery of the insect fauna. In the Kuparuk River, Alaska, USA, fertilization by phosphorus encouraged the growth of mosses after eight years of increased phosphorus. Persistence of the mosses had both positive and negative effects on the insect populations. It prevented the recovery of *Ephemerella* (Figure 9) (Slavik *et al.* 2004) and midge (Chironomidae, Figure 15) taxa, including the tube-building *Orthocladus rivulorum* (Figure 127-Figure 128) that had been affected by the shifts in primary producers. This shift included the loss of epilithic algae due to human activity, but they subsequently returned within 2-3 years. Once the bryophytes became established, they persisted, changing the morphology of the stream bottom.



Figure 127. *Orthocladus rivicola* larva, an insect that did not recover from phosphorus fertilization that caused an increase in moss growth in an Alaskan river. Photo from Stroud Water Research Center, through Creative Commons.



Figure 128. Orthoclad in silt tube. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Disturbances that remove mosses can greatly affect the invertebrate fauna. Gurtz and Wallace (1984) found that moss (*Hygroamblystegium tenax* – Figure 2) density and leaf detritus were the most important characters determining abundance of aquatic insects following a disturbance. Following clearcutting, the greatest increase in taxon density in the stream that drained the clear-cut watershed occurred in the moss-covered rock face compared to any other substrate. Moss habitats experienced increases of the shredder stonefly *Amphinemura wui* (Figure 13), a response that Gurtz and Wallace attributed to the accumulation of particulate matter

by the moss. The **Baetidae** mayflies likewise increased, experiencing their greatest increase among mosses where there was also the greatest increase in number of diatoms. But the chironomid *Eukiefferiella* spp. (Figure 129) showed the sharpest increase among the insects, occupying mosses on the rock face.



Figure 129. *Eukiefferiella* (arrow) on *Nesameletus ebop-ohaupapa*. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Forestry practices for logging and drainage often have considerable impact on the bryophytes and their inhabitants. In a small headwater stream where *Fontinalis dalecarlica* (Figure 16) formed the dominant habitat in riffles, forestry disturbances by ditch construction changed these mossy habitats to sand riffles (Vuori & Joensuu 1996). Transplanted mosses in the disturbed sites accumulated considerably more inorganic matter than did undisturbed controls. Subsequently, the invertebrate richness was significantly lower as well. The mosses at the control site supported a dominance of shredder stoneflies whereas the disturbed site was dominated by blackflies (*Simuliidae*; Figure 35).

## Pollution Effects

In addition to physical disturbances of flooding and human activities, pollution affects both the bryophytes and their fauna. Winterbourn *et al.* (2000) looked for effects on the food chain in New Zealand streams where mosses were a significant component. Despite the lowering of pH and increases in aluminium and iron in the water, there was not a biomagnification effect in the food web. The metal concentrations in the invertebrates was considerably lower than that in the mosses. It is possible that the bryophytes were able to sequester the metals, thus protecting the invertebrates from those that might have increased in their algal and detrital food.

## Geographic Differences

If one were to examine bryophytes in New Zealand streams, the fauna would be significantly different from that of bryophytes in the North Temperature Zone. In New Zealand, instead of the typical mayflies, stoneflies, and caddisflies, the fauna is dominated by nematodes, oligochaetes, and copepods, with the only abundant insect being **Chironomidae** (Figure 15) (Suren 1993). In fact, other types of insects comprise less than 2% of the



invertebrate fauna. This is not due to a difference in bryophytes, but rather the absence of families that typically inhabit the North Temperate bryophyte habitat.

By contrast, Egglisshaw (1969) found that mayflies occupied up to 16% of the invertebrate fauna of Scottish streams. Suren (1993 – updated in Table 2) reviewed studies from other parts of the world and found that the most important bryophyte insects were **Plecoptera** (**Nemouridae**, **Perlodidae**, **Leuctridae**, **Chloroperlidae**),

**Ephemeroptera** (**Baetidae**, **Heptageniidae**, **Ephemerellidae**), and **Trichoptera** (**Brachycentridae**, **Glossosomatidae**, **Lepidostomatidae**, **Limnephilidae**, and **Sericostomatidae**). These families mesh well with my own studies in bryophytes of Appalachian Mountain streams, eastern USA, except for **Perlodidae**, **Heptageniidae**, and **Sericostomatidae**. Others (**Baetidae**, **Lepidostomatidae**, **Limnephilidae**) were uncommon in the Appalachian streams.

Table 2. Percentages of the contributions by invertebrate taxa > 0.1% of the total invertebrate density in ten studies on invertebrate fauna of stream bryophytes: 1) Percival & Whitehead 1929 from a) thin moss & b) thick moss; 2) Percival & Whitehead 1930; 3) Frost 1942; 4) Egglisshaw 1969; 5) Stern & Stern 1969; 6) Glime & Clemons 1972; 7) Lindegaard *et al.* 1975; 8) Cowie & Winterbourn 1979; 9) McKenzie-Smith 1987; 10) Smith-Cuffney 1987 from a) unshaded and b) shaded streams; 11) Suren 1991a from a) unshaded and b) shaded streams; 12) Vlčková *et al.* 2002; - = not reported with abundances > 0.1% total density. (from Suren 1993). The last two columns indicate the number of studies presented here in which the taxon was represented by >0.1% and the average percent of the community the taxon represented.

	1a	1b	2	3	4	5	6	References			10a	10b	11a	11b	No. Studies	Av % Comp	
Turbellaria	-	-	-	0.4	-	0.3	-	-	-	-	1.6	-	-	-	0.26	3	0.2
Nematoda	-	-	-	-	-	-	-	-	-	-	1.8	2.8	22.1	12.5	14.65	4	2.8
Oligochaeta	3.6	3.3	24.1	0.4	-	-	-	10.3	-	2.9	6.0	1.4	-	-	0.57	8	5.8
Tardigrada	-	-	-	-	-	-	-	-	-	-	-	-	2.4	-	0.59	1	0.2
Amphipoda	1.2	1.1	0.1	-	-	4.8	-	6.9	-	42.5	-	-	-	-	-	6	4.0
Copepoda	-	-	57.8	2.5	-	-	-	-	-	-	-	4.0	9.0	1.5	0.47	5	5.3
Ostracoda	-	-	-	-	-	-	-	-	-	-	-	-	-2.8	0.7	0.13	2	0.3
Isopoda	-	-	-	-	-	1.9	-	-	-	-	-	-	-	-	-	1	0.2
Hydracarina	3.3	3.0	3.6	1.0	-	0.1	-	6.3	-	-	2.7	7.0	1.1	5.9	0.73	10	2.4
Collembola	-	-	-	-	-	-	-	4.2	-	-	1.2	-	-	-	-	2	0.9
Ephemeroptera	15.9	6.5	-	4.0	4.2	2.6	2.0	-	-	5.46	15.2	1.8	-	-	0.88	9	4.1
Plecoptera	-	-	-	-	44.6	2.9	5.7	16.7	22.5	5.4	3.1	8.2	2.1	2.5	0.01	10	11.4
Diptera	1.3	1.5	0.1	2.3	2.3	-	12.6	-	21.2	-	1.1	6.1	1.5	7.7	1.96	11	5.2
Chironomidae	54.3	40.9	9.2	83.0	34.1	77.9	71.7	33.2	33.7	21.6	54.0	53.0	57.7	63.4	33.81	14	49.1
Coleoptera	6.2	4.2	3.6	2.0	-	0.1	2.9	0.7	-	2.3	-	-	-	-	0.15	8	1.5
Trichoptera	4.0	0.3	0.1	3.7	1.4	9.1	3.4	-	23.6	13.4	6.2	7.9	-	-	0.29	11	5.2

## Summary

Bryophytes increase the number of niches for occupancy by aquatic insects. They increase surface area, culture algae, collect detritus, provide high prey density, and provide a refugium against the current. At the same time they permit the insects to live in the greater oxygen provided by the rapid flow, saving them ventilation energy. Feeding groups of these insects include collector-gatherers, scrapers, shredders, collector-filterers, and engulfer, with collector-gatherers typically being most abundant.

Altitude and latitude are important determinants of both the bryophytes and the associated fauna. Thickness of the moss mat also is important in determining the fauna, with thicker mats creating more niches.

The most common orders of moss dwellers in streams are **Ephemeroptera** (mayflies), **Plecoptera** (stoneflies), **Trichoptera** (caddisflies), and **Diptera** (flies). Streams in the Arctic and alpine habitats lack most of the **Trichoptera** (caddisflies), but otherwise have similar order representation among stream bryophytes, with even more **Chironomidae**. The associations of insects with the species of bryophytes may be a consequence of both needing similar conditions, as exemplified by the similarities of insect

communities on the moss *Fontinalis dalecarlica* and the liverwort *Scapania undulata*, two species that often occur side-by-side. Nevertheless, bryophytes do not make good surrogates for the stream inhabitants, correlating primarily with nutrient levels and habitat heterogeneity, whereas insects correlate more with stream size, pH, and water color. In fact, clumps of string and other artificial mosses seem to attract communities similar to those on real mosses. On the other hand, the presence of bryophytes will usually indicate a high density of insects.

The bryophytes may serve as a refuge for insects in winter when non-bryophyte plants are absent and the bryophytes are common in fast water where freezing is less common. The bryophytes furthermore serve as a location of collected detritus and a site for winter diatoms.

Within the clump of bryophytes of a stream one can find a detritus zone with little or no flow, a water zone within the moss clump, and a **madicolous** zone just above the water surface but where the bryophytes are still wet. And at the surface of the moss, but submerged, the highest water velocity and therefore the most oxygen exist.

Waterfalls may have specialists that live among the wet mosses, avoiding the torrent itself. Springs often have dense bryophyte cover. **Chironomidae** here

respond to temperature; many insects also respond to nutrient concentrations or pH. Depth of streams, pools, and springs can influence insect community composition, in part because of temperature and oxygen gradients. Bogs and fens have both pool and dry hummock conditions, contributing a wide range of niches that differ in moisture, temperature, and light. Consequently, there is a wide variety of insects, and even flying adults make use of the mosses for egg deposition, mating, and resting. More **Collembola** (springtails) are found in bogs and fens than in most aquatic habitats. **Coleoptera** (beetles) and **Odonata** (dragonflies and damselflies) likewise are common in these habitats. **Hymenoptera** (ants, bees) are absent from streams and lakes, but in bogs and fens ants build nests from the *Sphagnum*. Little seems to be published about insects associated with lake bryophytes. Some of the beetles are associated with floating *Riccia fluitans* and *Ricciocarpos natans* in shallow lakes. In one case, the latter is inhabited by the leaf miner *Phytoliriomyza mesnili*.

Disturbance immediately reduces the number of invertebrates, but if mosses remain or are replaced, they are quickly recolonized by remaining drifting organisms or from egg-laying. Attempts at restoration can cause the bryophytes to break loose and reduce the insect fauna.

If one compares the bryophyte fauna around the world, differences in relative abundance of the orders are apparent. These differences are often the result of evolutionary and distributional differences. For example, the families of the insects are different in Australia and New Zealand from those in North America.

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# CHAPTER 11-4

## AQUATIC INSECTS: HEMIMETABOLA – COLLEMBOLA AND EPHEMEROPTERA

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# CHAPTER 11-4

## AQUATIC INSECTS: HEMIMETABOLA – COLLEMBOLA AND EPHEMEROPTERA



Figure 1. *Serratella ignita*, a common moss dweller. Photo by J. C. Schou, with permission.

### COLLEMBOLA – Springtails

This group was traditionally considered to be one of the insect orders, but more recently they have been classified in the class **Entognatha**. **Collembola** are quite small and lack wings. They have three pairs of legs, like insects, but have only six abdominal segments (Thorp & Covich 1991). The young (**nymphs**) resemble the adults, changing to adults by breaking their outer covering (**exoskeleton**) and discarding it, then expanding while the new exoskeleton is still soft.. They are unique in having a **furcula** (Figure 3-Figure 5) that forms the spring and a **collophore** (cylindrical ventral tube; Figure 3, Figure 6). When at rest, the furcula bends forward under the abdomen and is held in place by the **tenaculum** (Figure 3), a midventral structure that clasps the furcula. The springtail accomplishes rapid distance movement by releasing the furcula, which springs backward, propelling the springtail forward several centimeters. This can be used even on the

water surface. Some can be seen bouncing around on the snow in winter.



Figure 2. *Podura aquatica* molting; note split in outer skeleton. Photo by Jan van Duinen, with permission.



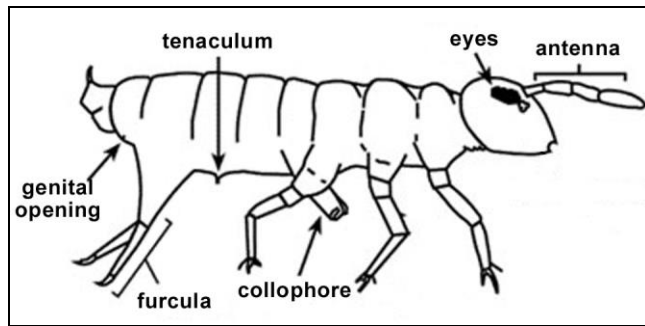


Figure 3. *Collembola* external anatomy. Modified from Cooperative Extension illustration, University of Missouri.

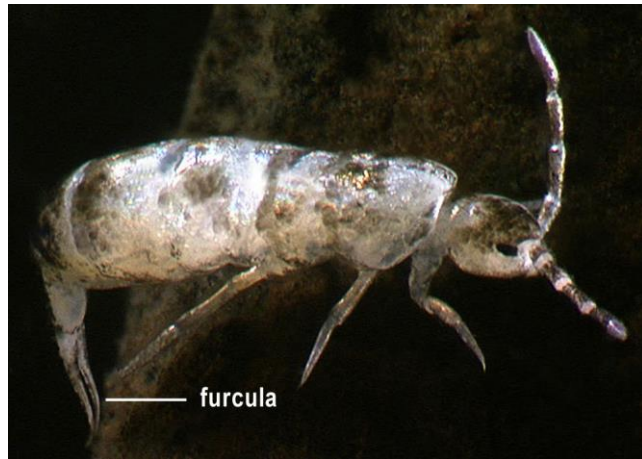


Figure 4. *Arthropleona oruarangi* showing furcula. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 5. *Dicyrtomina ornata* ventral side showing furcula. Photo by Jan van Duinen, with permission.

*Collembola* can be sexual or parthenogenetic. Sexual males deposit **spermatophores** in clusters or individually. Females stimulate this deposition by producing pheromones (Waldorf 1974). But among many of the soil *Collembola*, presumably including bryophyte dwellers, females lay eggs (Figure 7-Figure 8) that have not been fertilized, *i.e.*, are produced **parthenogenetically**. Since few reproductive studies exist, I cannot generalize of aquatic bryophyte dwellers. What makes this reproduction so interesting is the role of symbiotic bacteria in the genus *Wolbachia* (Werren *et al.* 1995). These bacteria live in and reproduce in the female reproductive organs and eggs of

the springtail. It is these bacteria that control the parthenogenesis in the colonized species. That is, they feminize the springtails.



Figure 6. *Isotoma* (springtail) showing collophore (arrow). Photo by U. Burkhardt, through Creative Commons.



Figure 7. *Collembola* eggs. Photo by Jan van Duinen, with permission.



Figure 8. *Sminthurides* eggs in duckweed. Photo by Jan van Duinen, with permission.



The **Collembola** are predominately moist terrestrial organisms, but some can hop on the water surface (Figure 9) or live among wet mosses. Waltz and McCafferty (1979) considered only 10 species as semiaquatic and five as **riparian** (relating to bank of river or other moving water). The waxy cuticle (Chang 1966), coupled with small size, permits them to float on water. The **collophore** (ventral tube) serves a double function: absorption of water and respiration.

The **Collembola** seem to be particularly responsive to drawdown and drainage (Silvan *et al.* 2000). On older drained sites their numbers were up to 100 times as high compared to pre-drawdown. Other invertebrates were typically about ten times as high. The **Collembola** occurred mostly in the top 4 cm of the drained land.

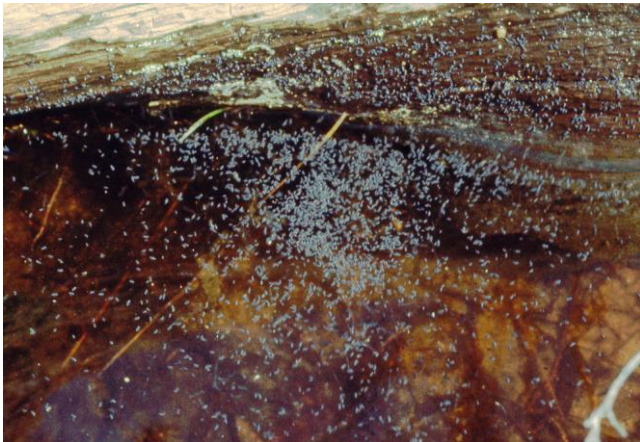


Figure 9. **Collembola** (springtails) on water where they can jump about on the surface tension. Photo by Janice Glime.

In my search for information on the bryophyte-dwelling springtails, I was surprised to find so little that related to aquatic habitats. In my own studies in the Appalachian Mountain, USA, streams, I found representatives of eight families, albeit not frequently. The species in these collections were *Odontella lamellifera* (Figure 10) (**Brachystomellidae**), *Entomobrya griseoolivata* (Figure 11) and *Orchesella quinquefasciata* (Figure 12) (**Entomobryidae**), *Hypogastrura armatus* (see Figure 13), and *Schotella glasgowi* (**Hypogastruridae**), *Hydroisotoma schaefferi* (Figure 14), *Isotoma violacea*, *Isotoma viridis* (Figure 15), and *Isotomurus palustris* (Figure 16) (**Isotomidae**), *Pseudachorutes lunatus* (**Neanuridae**; see Figure 17), *Onychiurus subtenius* (**Onychiuridae**), *Sminthurides aquaticus* (Figure 18) (**Sminthuridae**), and *Tomocerus flavescens* (Figure 19) (**Tomoceridae**). Of these taxa, only *Isotomurus palustris* was present in more than two collections. Nevertheless, I recorded *Orchesella quinquefasciata* in North America for the first time (Toliver Run, Garrett County, MD) (Richard Snider, pers. comm.). The *Hydroisotoma schaefferi* was an atypical blind form from Little Bennett Creek, Montgomery Co., MD. Snider also found this species (not blind) in ponds surrounded with mosses in Michigan, USA (Snider 1967). It is likely that some of these springtails were living at the surface of emergent mosses. But the tiny size of these insects suggests they may have been missed in

collections using insect nets. Others may have "sprung" away from surface locations as the collector approached.



Figure 10. *Odontella* cf. *incerta*; *O. lamellifera* is a springtail that occasionally occurs among stream bryophytes in the Appalachian Mountains, USA. Photo by Andy Murray, through Creative Commons.



Figure 11. *Entomobrya griseoolivata*, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Domingo Zungri, through Creative Commons.



Figure 12. *Orchesella quinquefasciata*, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Malcolm Storey, through DiscoverLife Creative Commons.





Figure 13. *Hypogastrura nivicola*; *H. armatus* is a springtail that sometimes occurs among Appalachian Mountain stream bryophytes in eastern USA. Photo by Scott Justis, with permission.



Figure 16. *Isotomurus palustris*, an aquatic springtail that keeps its offspring together for two days after birth. Photo by Scott Justis, with permission.



Figure 14. *Hydroisotoma schaefferi*, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Tom Murray, through Creative Commons.



Figure 17. *Pseudachorutes* sp.; *Pseudachorutes lunatus* lives among mosses in mountain streams. Photo by Jan van Duinen, with permission.



Figure 15. *Isotoma viridis*, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Kyron Basu, through Creative Commons.



Figure 18. *Sminthurides aquaticus*, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Andy Murray, through Creative Commons.



Figure 19. *Tomocerus flavescens*, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Royce Bitzer, through Creative Commons.

### Isotomidae

The family **Isotomidae** was most frequently (almost exclusively among springtails) represented in the publications I found regarding bryophyte fauna. Among these, *Isotomurus palustris* (Figure 16) is most typically considered to be aquatic, although a few other species, including *Sminthurus aquaticus* (Figure 18), have names that suggest they are aquatic.

*Isotomurus palustris* (Figure 16) is able to float on the water because of their non-wetting waxy epicuticle composed of a lipid monolayer that is extremely impermeable to water (Beament 1960). But Noble-Nesbitt (1963) provided evidence that the presence of wax gives it **hydrofuge** (shedding water) properties. A cementing substance contributes to this hydrofuge ability. The cuticle, combined with surface hairs, provides this springtail with a protective air layer that both makes these springtails **unwettable** (repelling water) and makes them float. Springtails also are very sensitive to desiccation, so the protection by the cuticle is important.

The **collophore** is **wettable** (doesn't repel water) and doubles as both a respiratory and water-taking organ (Noble-Nesbitt 1963). The air layer on the surface also behaves as a **plastron** (breast plate breathing apparatus). These springtails also take water by mouth and this may additionally supply dissolved oxygen. I wonder if they ever get hiccups! This tubule, combined with their small size, would permit them to drink water from the leaves of emergent mosses.

But it appears that the cuticle may also play an important role in their locomotion on the water surface (Noble-Nesbitt 1963). In the water, the furcula is used as a spring, much as it is on land. On the water surface the insect actually walks, using only its limbs.

*Isotomurus palustris* (Figure 16) is **viviparous**, producing one egg at a time (Chang 1966). These eggs are carried internally and hatched inside the female with the nymph emerging from the genital pore. The female arches its body to permit the emerging nymph to reach the water surface. In observations on newborns of *Isotomurus palustris* (Figure 16) and *Folsomia fimetaria* (Figure 20), Chang found that the newborns stayed close to the mothers for the first two days. The young are able to float, walking on the surface tension with their **non-wetting** (repelling water) claws, but if they are forced to submerge they will sink. The cuticle does not develop until they spend time above water.



Figure 20. *Folsomia fimetaria*, a springtail whose newborns stay close to the mother for two days. Photo by Andy Murray, through Creative Commons.

Antennae are important in assessing the environment in both *Isotomurus palustris* (Figure 16) and *Folsomia fimetaria* (Figure 20). They are the sensory organ, often in consort with the post-antennal organ, that recognizes light intensity, wind direction, and heat. When one or the other of these organs is removed or cauterized, the springtails move about aimlessly or not at all, whereas those with both organs intact wiggle their antennae and exhibit a directional movement in response to the stimulus.

Some **Collembola** like it cold – *Anurida frigida* (**Neanuridae**) occurs under mosses on stones and on stones by melt-water brooks in the high alpine of Swedish Lapland (Fjellberg 1973). The greatest numbers of these were located under mosses that were wet by ice-cold meltwater. In the Nordic countries, *Agrenia riparia* prefers wet mosses, especially on lowland stream banks (Fjellberg 2007b)

### Bog Springtails

These tiny creatures seem often to be overlooked, but a treatment of **Collembola** in Michigan, USA, indicates that many species can occur in bogs (Snider 1967):

*Hypogastrura nivicola* (**Onychiuridae**; Figure 21)

*Isotoma viridis* (**Isotomidae**; Figure 15)

*Lepidocyrtus cyaneus* (**Entomobryidae**; Figure 32)

*Lepidocyrtus lignorum* (**Entomobryidae**; Figure 22)

*Lepidocyrtus unifasciatus* (**Entomobryidae**)

*Lepidocyrtus violaceus* (**Entomobryidae**; Figure 23)

– in *Sphagnum*

*Neelus minutus* (**Neelidae**; see Figure 24)

*Orchesella ainsliei* (**Entomobryidae**)

*Orchesella albosa* (**Entomobryidae**)

*Pseudobourletiella spinata* (**Sminthuridae**; Figure 25)

*Sminthurides aquaticus* (**Sminthuridae**; Figure 18) – in *Sphagnum*

*Sminthurides lepus* (**Sminthuridae**)

*Sminthurides malmgreni* (**Sminthuridae**; Figure 26) – semi-aquatic habitats

*Sminthurides occultus* (**Sminthuridae**)

*Sminthurides penicillifer* (**Sminthuridae**; Figure 27)

*Sminthurinus aureus* (**Sminthuridae**; Figure 28)

*Sminthurinus bimaculatus* (**Sminthuridae**; Figure 29)

*Tomocerus flavescens* (**Tomoceridae**; Figure 19) – in *Sphagnum*





Figure 21. *Hypogastrura nivicola* on snow. Photo by Charley Eiseman, through Creative Commons.



Figure 22. *Lepidocyrtus lignorum*, a bog inhabitant. Photo by Jan van Duinen, with permission.



Figure 23. *Lepidocyrtus violaceus*, a bog *Sphagnum* dweller. Photo by Jan van Duinen, with permission.



Figure 24. *Neelus murinus* carrying eggs; *Neelus minutus* is a bog dweller. Photo by Frans Janssens, with permission.



Figure 25. *Pseudobourletiella spinata*, a bog inhabitant. Photo by Tom Murray, through Creative Commons.



Figure 26. *Sminthurides malmgreni*, a bog inhabitant. Photo by Andy Murray, through Creative Commons.



Figure 27. *Sminthurides* nr. *penicillifer* female, a bog inhabitant. Photo by Andy Murray, through Creative Commons.



Figure 28. *Sminthurinus aureus*, a bog dweller. Photo by Andy Murray, through Creative Commons.



Figure 29. *Sminthurinus bimaculatus*, a bog dweller. Photo by Andy Murray, through Creative Commons.

In his treatment of the **Collembola** of Fennoscandia and Denmark, Fjellberg (2007a) included *Maristoma canaliculata* as a species usually found in *Sphagnum* and *Maristoma tenuicornis* in *Sphagnum* bogs. The treatment for Nordic Collembola (Fjellberg 2007b) includes *Marisotoma canaliculata* in *Sphagnum* ponds; *Marisotoma tenuicornis* in boreal *Sphagnum* bogs; *Desoria olivacea* (Isotomidae; Figure 30) common in acidic forest bogs; *Desoria blufusata* (Figure 31) in bogs and wet meadows; *Lepidocyrtus cyaneus* (Entomobryidae; Figure 32) common in humid habitats including *Sphagnum*/*Salix* bogs; *Sminthurides schoetti* common in bogs and damp meadows; *Sminthurides*

*pseudassimilis* in boreal *Sphagnum* bogs and smaller lakes, boreal; *Sminthurides parvulus* uncommon in bogs, wet meadows, and shores of lakes; *Neelides minutus* uncommon in bogs; *Arrhopalites cochlearifer* and *Arrhopalites principalis* (common) in bogs; *Isotomurus unifasciatus* (Figure 33) in forest bogs; *Isotomurus balteatus* in boreal bogs and wetlands; *Dicyrtomina minuta* and *Dicyrtoma fusca* (Figure 34) common in bogs; *Heterosminthurus insignis* in wet meadows and bogs.



Figure 30. *Desoria olivacea*, a species of acidic forest bogs. Photo by Jan van Duinen, with permission.



Figure 31. *Desoria blufusata*, a common species in bogs and wet meadows. Photo by Arne Fjellberg, through Creative Commons.



Figure 32. *Lepidocyrtus cyaneus*, a species of *Sphagnum* bogs. Photo by Steve Hopkin, with permission.





Figure 33. *Isotomurus unifaciatus*, a species of boreal bogs and wetlands. Photo by Jan van Duinen, with permission.



Figure 34. *Dicyrtoma fusca*, a species common in bogs. Photo by Jan van Duinen, with permission.

Greenslade *et al.* (2006) suggests that *Mesaphorura macrochaeta* may have been introduced to the Southern Hemisphere by human importations of soil and moss peat.

## HEMIMETABOLA

The **hemimetabolous** insects are those with **incomplete metamorphosis**. Instead of a larva, they have a **nymph** or **naiad** stage that resembles the adult except for having reduced wings or only wing pads. They lack a pupa stage and pass directly from the nymph or naiad stage to the adult stage. Most of the aquatic Hemimetabola have a stage with gills and wing pads and are distinguished as **naiads**.

## EPHEMEROPTERA – Mayflies

As in most of the names of insect orders, *optera* refers to wings. In the **Ephemeroptera**, *ephemera* refers to short-lived. Hence, these are insects that are short-lived in the winged, or adult, stage.

The immature mayflies, known as **naiads**, are all aquatic (Thorpe & Covich 1991). They can be distinguished by their three (two in some) long caudal filaments that are also present in the adults. They are most similar to the stoneflies (**Plecoptera** – see subchapter on Plecoptera in this chapter), but differ in having abdominal gills (lacking in middle abdominal segments of stoneflies) and typically three tails (caudal filaments), which always number two in stoneflies. Most of the naiads are herbivores and some eat bryophytes.

The mayfly naiads are largely night-active and appear most often in the night-time drift (Elliott 1967). Adult mayflies emerge from the naiad first as a **sub-imago** (also known as a **dun**; Figure 35-Figure 40), a stage that often becomes a nuisance to motorists (Figure 36) in the area because of the large numbers that meet their demise (Figure 37) on the windshields. To complete emergence they must climb so they can pump fluids into their new wings (Figure 41). The adult does not eat – in fact lacking mouthparts – and typically lives for only a few days.



Figure 35. *Baetis* male subimago emerging to adult. Photo by Jason Neuswanger at <Troutnut.com>, with permission.



Figure 36. Adult mayflies on emergence day. Photo by Jeff Reutter, through Ohio Sea Grant public domain.

In my own studies in the Appalachian Mountain streams, USA (Glime 1968, 1994), the **Ephemerellidae** was by far the most abundant of the mayflies. Frost (1942) reported the importance of the mayflies *Ephemerella* (*s.l.*) (Figure 45) and *Baetis* (**Baetidae**; Figure 35-Figure 40) among aquatic mosses, where they feed mostly on algae, but occasionally on bryophytes (Hynes 1961; Chapman & Demory 1963). Frost (1942) found about 530 mayfly nymphs per 200 g of mosses in Ireland. In a cool mountain stream of central Japan, Tada and Satake (1994) found that *Baetis thermicus* (Figure 38) and *Ephemerella* (*s.l.*) sp.



were more abundant among the moss *Platyhypnidium riparioides* (Figure 39) than in bare rock areas.



Figure 37. Mayflies that met their end on a travelling car during an emergence in August in Michigan, USA. Photo by Eileen Dumire, with permission.



Figure 38. *Baetis thermicus* naiad, a common moss dweller of the moss *Platyhypnidium riparioides* in Japan. Photo from Shiiba Research Forest. Permission requested.



Figure 39. *Platyhypnidium riparioides* partially submersed at the edge of a waterfall. Photo by Michael Lüth, with permission.



Figure 40. *Baetis* sub-imago showing huge eyes. Photo by Jason Neuswanger at <Troutnut.com>, with permission.



Figure 41. Emerging **Ephemeroptera**. Mayflies live their immature lives as naiads in the water of streams and lakes. When they emerge as adults, they must climb, like these naiads, so they can pump up their wings once they have exited the naiad exuvia. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

With such a dwarfed lifespan, finding a mate quickly is paramount. This is accomplished by flying in giant swarms, facilitated by coordinated emergence time. At this time, they are a nuisance for motorists and a feast for birds (Figure 42). Those females that survive deposit their eggs, often among mosses.



Figure 42. Hermit thrush (*Catharus guttatus*) with mayfly subimago in its beak, enjoying the brief period of emergence. Photo by Bob Armstrong, with permission.



Increased biomass of bryophytes may increase some insects while having no effect on others. Lee and Hershey (2000) found that a dense growth of the moss *Hygrohypnum* (Figure 43-Figure 44) following stream fertilization in Alaska increased the density of the mayfly *Ephemerella aurivillii* (Figure 45) but not *Baetis* (Figure 46). In the fertilized zone, these mayflies both grew larger, a fact Lee and Hershey attributed to the greater growths of epiphytic diatoms. Furthermore, although the density of *Ephemerella* increased with increased moss density, the highest drift ratios were in the unfertilized zone with lower moss density. In enclosure experiments, they found that bare rock, mosses, and artificial mosses had no effect on any taxa except *Ephemerella*. They considered that the *Ephemerella* benefitted from the increased complexity of the moss habitat.



Figure 43. *Hygrohypnum ochraceum*, home for a variety of stream insects. Photo by Michael Lüth, with permission.



Figure 44. Close view of *Hygrohypnum ochraceum*, home for a variety of insects. Photo by Michael Lüth, with permission.



Figure 45. *Ephemerella aurivillii* naiad, a mayfly that increased with increased coverage of *Hygrohypnum* in Alaska. Photo by Tom Murray, through Creative Commons.



Figure 46. *Baetis* naiad, a bryophyte inhabitant in many streams. Photo by Bob Henricks, with permission.

Jones (1950) did extensive gut analysis of insects from the River Rheidol. Among the **Ephemeroptera**, none of the five species examined had fragments of the common moss *Fontinalis antipyretica* (Figure 47) in the gut. Detritus was the most common food. Gilpin and Brusven (1970) found six mayfly species with *Fontinalis* sp. in their guts, but these all amounted to less than 1% of the gut contents.



Figure 47. *Fontinalis antipyretica*, a moss found in the guts of some mayflies in the River Rheidol. Photo by Kristian Peters, with permission.



It is surprising to find such flattened, rock-adapted genera as *Heptagenia* (Figure 48) among mosses, but Muttkowski and Smith (1929) did find it several times among mosses in trout streams of Yellowstone National Park, USA.



Figure 48. *Heptagenia dalecarlica* naiad, a flattened species adapted for smooth rocks, but that occasionally visits mosses. Photo by Urmas Kruus, with permission.

## Suborder Furcatergalia

### Leptophlebiidae – Prong-gilled Mayflies

This is a family that lives in freshwater streams and lakes where the naiads eat detritus and algae (Leptophlebiidae 2013). Their length is up to 20 mm; they are **nocturnal** (active at night) and are poor swimmers, generally clinging to rocks. Only a few seem to live among bryophytes.

*Paraleptophlebia* (Figure 49) was a minor component of the bryophyte communities in my own Appalachian, USA, stream studies (Glime 1968). Maurer & Brusven (1983) found *Paraleptophlebia heteronea* (Figure 49) frequently in the clumps of *Fontinalis neomexicana* (Figure 79) in an Idaho stream. In their study of four Appalachian streams, Woodall and Wallace (1972) found this genus where there was moderate or slow current among decaying leaves, bark, and wood. Its food is predominately detritus (Chapman & Demory 1963).



Figure 49. *Paraleptophlebia* sp. naiad, a frequent dweller among *Fontinalis neomexicana*. Photo by Jason Neuswanger, with permission.

Macan (1957) found *Leptophlebia* (Figure 50) among mosses in Ford Wood Beck, UK. Berner (1959) described this genus as one that would live in submerged mossy banks and other quiet areas. The genus is negatively **phototactic** (movement of organism toward or away from source of light), explaining their presence in the secluded shade of streambank mosses. When it is time for the naiads to emerge into adults, they become positively phototactic and crawl upward onto sticks, logs, or other protruding structure, probably including emergent bryophytes.

Vuori *et al.* (1999) considered *Leptophlebia marginata* (Figure 50) to be among the dominant moss dwellers in the Tolvajärvi region of the Russian Karelia. Bengtsson (1981) found that *L. marginata* demonstrated a steady growth rate throughout winter, permitting it to thrive in such northern regions.



Figure 50. *Leptophlebia marginata* naiad on waterweed. Photo by Niels Sloth, with permission.

One advantage enjoyed by some members of this family is tolerance of somewhat low pH. Mayflies in general are indicators of fresh, unpolluted water. They do not generally tolerate extremes, low pH included (Raddum & Fjellheim 1988; Raddum *et al.* 1988; Braukmann 1992; Lingdell & Engblom 1995). Thus the streams that drain *Sphagnum* fens and bogs (Figure 51) are generally **depauperate** (lacking in numbers or kinds of species) of mayflies. However, this habitat is suitable for a few, including *Leptophlebia vespertina* (Figure 52) (Bauernfeind & Moog 2000). This intolerance of low pH may explain its relative rarity among bryophytes in the mid-Appalachian Mountain streams (Glime 1968).



Figure 51. *Sphagnum affine*, member of a genus that contributes H<sup>+</sup> ions, lowering the pH of bogs and their outflow waters. Photo by Michael Lüth, with permission.





Figure 52. *Leptophlebia vespertina* adult, a species whose naiads can inhabit the acid outflows of acid bog lakes. Photo by Niels Sloth, with permission.

In New Zealand *Austroclima sepia* (see Figure 53) frequently lives among mosses in small waterfalls (Winterbourn & Gregson 1981). Similarly, Towns (1987) reported this species along with *A. jollyae* and *Mauiulus luma* (Figure 54) as 72%, 13%, and 9%, respectively, of the fauna from mosses in rapid flow (where only 4 insect species lived!) on the Great Barrier Island, New Zealand.



Figure 53. *Austroclima* naiad, a genus with moss dwellers in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 54. *Mauiulus luma* naiad, a mayfly that lives among mosses in small waterfalls in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.

In his study of the River Rajciana, Krno (1990) found a genus I have not encountered elsewhere – *Habroleptoides*. *Habroleptoides modesta* (Figure 55) is a bryophyte dweller in the river, but like many of the mayfly genera, it is unable to live among the wet mosses above the water level.



Figure 55. *Habroleptoides modesta* naiad, a mayfly that sometimes lives among bryophytes in rivers. Photo by Alfeo Busilacchio, with permission.

### Caenidae - Small Squaregill Mayflies

The **Caenidae** are small sprawlers in quiet and sometimes stagnant water as well as streams (Caenidae 2014). They are adapted to the relatively low oxygen of silt.

*Caenis* (Figure 56) seems to prefer loose mosses (Percival & Whitehead 1929). Frost (1942) found that it was most likely to occur among mosses that had accumulated considerable silt. In the River Rajciana in Slovakia, *Caenis beskidensis* (Figure 56) lives among submerged bryophytes but is not found, like some mayflies, among the wet emergent bryophytes (Krno 1990). In the Appalachian Mountain, USA, streams naiads of *Caenis* were among the lesser of the moss inhabitants, appearing mostly among *Fontinalis dalecarlica* (Figure 69).



Figure 56. *Caenis lactea* naiad, a mayfly that prefers loose mosses. Photo by Niels Sloth, with permission.

### Neophemeridae

The rare genus *Neophemera* (Figure 57) sometimes lives deep within submerged moss mats in rapid water in eastern North America (Berner 1959), including

*Neophemera compressa* (Figure 57) among mosses on submersed parts of trees (Berner 1956). The naiad moves slowly, but when it bends its 3 tails over its abdomen, then suddenly lashes them back, this action propels it forward (see Figure 60).



Figure 57. *Neophemera compressa*, an inhabitant of mosses on submersed parts of trees. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

In Australia, *Neophemera* (Figure 57) naiads live in protected parts of streams with slow to moderate flow where they hide among debris, plant roots, and mosses (Edmunds *et al.* 1976). These naiads are difficult to dislodge from the mosses, partly because they grip the mosses. The membranous respiratory gills are fragile and they need the protection that is provided by the fused, sclerotized **opercula** (gill covers) (Notestine 1994). This genus relies heavily on these gills for respiration.

### Ephemerellidae – Spiny Crawlers

This family occurs throughout North America as well as the United Kingdom (Ephemerellidae 2014). These collector-gatherers occur where there is moving water, including lake shores subject to wave action, but seem to require reduced flow. They are able to live in fast water by accepting the protection of bryophytes.

When these mayfly naiads are threatened by a predator, they raise their three tails like a scorpion, arching them up and over their backs, making them appear larger (Ephemerellidae 2014). They will then project the tails forward to poke the enemy. Spines on the back of the abdomen (Figure 58) may contribute to their protection. One suggestion is that the spines help the mayflies hold their positions when attacked from behind by a predator.

This family takes advantage of the protection of the bryophyte habitat while modulating the oxygen and keeping its tuft of gills clean with its gill covers. When oxygen concentrations become too low, the **Ephemerellidae** move the gill covers (Figure 58) up and down to keep fresh water circulating across the gills (Figure 59) (Ephemerellidae 2014). Their bodies are somewhat flattened dorsiventrally and are adapted to crawling among the chambers of their mossy habitat. When they are in open water and need to move quickly, mayflies in this family flip their tails upward over their backs and down to act like a paddle (Figure 60), thrusting them forward.



Figure 58. *Ephemerella subvaria* naiad gill covers, closed over gills. Photo by Tom Murray, through Creative Commons.



Figure 59. *Drunella* sp. naiad with gill covers up to expose the tufts of gills. Photo by Bob Henricks, with permission.



Figure 60. *Ephemerella subvaria* naiad in a swimming position with its tails flipped upward. Photo by Bob Henricks, with permission.

Berner (1959) described some members of this family as living on the tops of rocks, deep within the moss. Arnold and Macan (1969) found that **Ephemerellidae** (Figure 58-Figure 64) were common among mosses in a



Shropshire Hill stream in the UK. In a study of the McKenzie River, Oregon, USA, Hawkins (1984) reported that 5 species [*Serratella teresa*, *C. hystrix* (Figure 61), *Caudatella cascadia* (now a synonym of *C. hystrix*), *C. edmundsi* (Figure 62), and *Drunella spinifera* (Figure 63)] out of 12 **Ephemerellidae** species were common among mosses, including *Fontinalis* sp. (Figure 79) and others. Gilpin and Brusven (1970) likewise found *C. edmundsi* among clumps of *Fontinalis*. Hawkins (1984) found those restricted to mosses were usually at upstream locations where the mosses were abundant. However, two moss dwellers [*Caudatella edmundsi* (100% moss usage - found only on *Fontinalis*), *Drunella spinifera* (54%)] were most abundant downstream, living among mats of the moss *Fontinalis* sp. For other species with more than 5% use of bryophyte habitats he found *Serratella teresa* (85%), *Caudatella cascadia* (46%), and *Caudatella hystrix* (22%).

Brittain and Saltveit (1989) found that river impoundments had "profound" effects on the **Ephemerellidae** (Figure 58-Figure 64) living there. Changes in temperature, discharge, flow patterns, food availability, and predator density all contribute to changes in living conditions for the mayflies. Increased growth of mosses and additional available substrata for periphyton below the dams often favor some of the **Ephemerellidae** while reducing suitable habitat for **Heptageniidae** (Figure 48). The mayflies living under these changeable regimes often have flexible life cycles or shorter periods of rapid growth with a long period of egg development that permit them to survive unsuitable periods.



Figure 61. *Caudatella hystrix* naiad, a common moss dweller in the McKenzie River, Oregon, USA. Photo by Bob Newell, with permission.



Figure 62. *Caudatella edmundsi* naiad, a common moss dweller. Photo by Bob Newell at <Troutnut.com>, with permission.

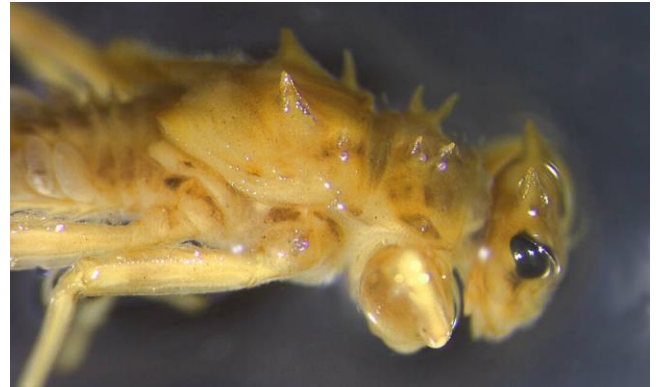


Figure 63. *Drunella spinifera* naiad. Photo by Bob Newell at <Troutnut.com>, with permission.

Percival and Whitehead (1929) considered mosses and algae to be the main food of the **Ephemerellidae** (Figure 58-Figure 64). Woodall and Wallace (1972) found *Eurylophella funeralis* (= *Ephemerella funeralis*, Figure 64) to be the most abundant *Ephemerella* species among mosses in the southern Appalachian Mountains, USA, and I found a similar relationship for *E. funeralis* and *E. temporalis* in the middle Appalachian Mountain streams (Glime 1968). The members of *Ephemerella* tended to avoid the heavily shaded hardwood stream where mosses and algae were scarce.



Figure 64. *Eurylophella funeralis*, a common mayfly among mosses in the southern Appalachian Mountain, USA, streams. Photo by Donald S. Chandler, with permission.

Brittain and Saltveit (1989) found that growth of mosses and associated periphyton below dams favored presence of **Ephemerellidae** (Figure 58-Figure 64). They reasoned that flexible life cycles permitted them to survive adverse conditions, including rapid nymphal growth and long period of egg development. Eggs typically form a ball (Figure 65).

Percival and Whitehead (1929) found *Eurylophella funeralis* (= *Ephemerella funeralis*) (Figure 64) to be the most abundant species of the *Ephemerella* genus group in their study of UK streams. The main foods of *Ephemerella* species are algae and mosses (Percival & Whitehead 1929; Jones 1949, 1950; Gerson 1969). This is convenient because this genus is common among mosses, but it also occurs on the pebbles on the bottom. Jones (1949, 1950) found that *Ephemerella* s.l. fed primarily on *Fontinalis* (Figure 47) and the alga *Ulothrix* (Figure 66) in **calcareous** (having dissolved chalk or limestone) streams of South



Wales. Among 14 specimens examined on 14 July the moss was the primary food, but they concluded that *Ephemerella* feeds on *Ulothrix* when it is abundant but switches to *Fontinalis antipyretica* (Figure 47) when the *Ulothrix* becomes scarce.

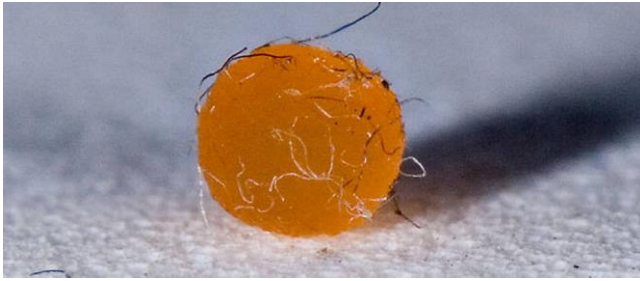


Figure 65. *Ephemerella* egg mass with debris stuck to it. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

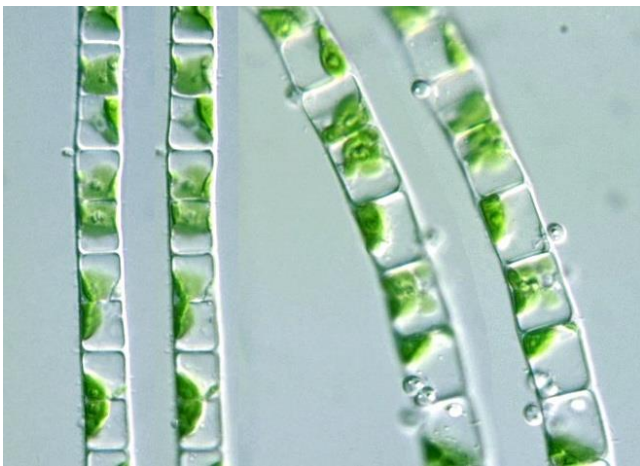


Figure 66. *Ulothrix*, food for *Eurylophella funeralis*. Photo by Yuuji Tsukii, with permission.

Reproduction in the mayflies involves swarming, a behavior that maximizes contact of males and females that typically live for only one day as adults. In *Serratella ignita* (Figure 67) this swarming occurs in the late afternoon and evening (Elliott & Humpesch 1980). The egg mass is a greenish ball. Once fertilized, eggs are laid in turbulent water, usually where there are mosses. The female flies upstream to deposit the eggs on the water surface. She then usually falls on the surface and is vulnerable to fish predation. The egg mass separates when it enters the water and each egg attaches to the substrate with its polar anchoring cap.



Figure 67. *Serratella ignita* naiad. Photo by J. C. Schou, through Creative Commons.

The family **Ephemerellidae** (Figure 58-Figure 64) seems to have bryological preferences, or preferences that match those of the bryophytes. They reach extremely high numbers among *Hygroamblystegium fluviatile* (Figure 68) in mid-Appalachian streams, but are nearly absent in *Fontinalis dalecarlica* (Figure 69) and *Scapania undulata* (Figure 70) in different streams (Glime 1968).



Figure 68. *Hygroamblystegium fluviatile*, home to large numbers of **Ephemerellidae**. Photo by Michael Lüth, with permission.



Figure 69. *Fontinalis dalecarlica*, a stream moss that houses some of the larger insects. Photo by Jan-Peter Frahm, with permission.



Figure 70. *Scapania undulata*, a leafy liverwort that has few of the typical moss-dwelling **Ephemerellidae**. Hermann Schachner, through Creative Commons.



D. N. Bennett (pers. comm. 19 April 2011) described her field experience with an aquatic entomologist, Bob Henricks. Henricks was attempting to distinguish between mosses and grasses, so she began looking at the inhabitants of the mosses. When the moss-covered rocks were removed from the stream, the insects began moving about and became more noticeable. There were often 40-50 **Ephemerellidae** naiads on a single moss-covered rock – determined to be *Hygroamblystegium*, probably *H. tenax* (Figure 71-Figure 72). The moss grew on and "under" the rock, and it was the submersed "under" portion that housed the many mayflies. She observed the naiads rolling up the algae from the moss leaf surface, starting at the leaf tip and moving to the stem.



Figure 71. *Hygroamblystegium tenax* in a dry stream bed. Photo by Janice Glime.



Figure 72. *Hygroamblystegium tenax*, home to many kinds of stream insects, including **Ephemerellidae**. Photo by Jan-Peter Frahm, with permission.

### Seasons

Seasonal differences in the life cycle stages spent in the water are often the key to success for these species. Timing differences in emergence times and hatching times can separate realized niches in closely related species. In the **Ephemerellidae** (Figure 58-Figure 64), the life cycle is typically one year with one brood per year (**univoltine**).

For example, *Serratella ignita* (Figure 1) has an annual cycle with the eggs spanning the winter in a dormant state, hatching in April and May in the River Endrick in Scotland (Maitland 1955). The naiads develop quickly, emerging in July and August, and adults typically lay eggs within 24 hours of emergence. These eggs are often laid among mosses in abundance (Percival & Whitehead 1928). The eggs are laid in evening light and are caught by *Platyhypnidium riparioides* (Figure 39) and *Fontinalis* species (Figure 47) where they adhere as a greenish gelatinous mass.

In a Shropshire Hill stream in the UK, Arnold and Macan (1969) found that the longest stage in *Serratella ignita* (Figure 1) was the egg, a stage that remained from late summer one year to late spring the next year, hence overwintering as an egg (Elliott 1967). Rosillon (1988) found that completion of naiad development on a diatom diet required about 950 **degree-days** above a temperature of 3.5°C (range 9.5-18°C). [Degree days for insect development can be calculated by adding the minimum and maximum temperature of the day and dividing by 2. The minimum required for development is subtracted from that number to determine how many degree-days have been added that day. (Townsend *et al.* 2010)]. Those reared on detritus rarely achieved adult stage. Rosillon suggested that poor food quality would reduce **fecundity** (reproductive rate) of females. Furthermore, it appears that under ideal conditions *Serratella ignita* could have a **bivoltine** (2 broods per year) life cycle.

Emergence patterns can be gleaned from the stages of the naiad development of mayflies in samples. Based on such sampling, Gurtz & Wallace (1984) estimated that in a stream in the southern Appalachian Mountains, USA, the moss inhabitants *Ephemerella catawba* (Figure 73) probably emerged from May to July, *E. hispida* from April to June, *E. excrucians* (Figure 81) in May and June, and *Drunella tuberculata* (Figure 74) from June to September. Both *Ephemerella catawba* and *Ephemerella invaria* occurred among mosses in the acidic mid Appalachian streams in my own studies (Glime 1968). *Ephemerella invaria* (Figure 75) increased in Big Hurricane Branch following a clearcut, but no specimens with fully developed wing pads were ever collected, suggesting that nymphs of this species might complete their development farther downstream in Shope Creek (Gurtz & Wallace 1984).



Figure 73. *Ephemerella catawba*, a moss inhabitant as a naiad that emerges May to July in the southern Appalachian Mountains, USA. Photo by Biodiversity Institute of Ontario, through Creative Commons.





Figure 74. *Drunella tuberculata*, a summer emerger. Photo by Bob Henricks, with permission.



Figure 75. *Ephemerella invaria* naiad. Photo by Bob Henricks, with permission.

*Ephemerella invaria* (Figure 75) occurred both above and below a hydroelectric plant on the Sturgeon River in northern Michigan, USA, with similar abundance and growth (Mundahl & Kraft 1988). *Ephemerella subvaria* (Figure 76) naiads were 4x as abundant below the plant (136 m<sup>-2</sup> below vs. 33 m<sup>-2</sup> above), but grew more slowly there. Nevertheless, the growth rate increased with distance downstream from the power plant for nearly 10 km. Extensive beds of *Fontinalis* (pers. obs.) may have

contributed to the improved growth rates, with the mosses serving as traps for **seston** (swimming or floating living organisms and non-living matter) being released from the reservoir. Both of these species occur among bryophytes in streams of the mid Appalachian Mountains, USA (Glime 1968).



Figure 76. *Ephemerella subvaria* naiad. Photo by Donald S. Chandler, through Creative Commons.

### Food

The **Ephemerellidae** (Figure 58-Figure 64) are the most commonly reported mayflies among the bryophyte consumers (Table 1). *Caudatella hystrix* (as *C. cascadia*; Figure 61) varies its diet depending on the site (Coffman *et al.* 1971; Hawkins 1985). Detritus is important in its diet, but the proportion decreases when that of moss increases (Hawkins 1985). The naiads of *Caudatella edmundsi* (Figure 62, Figure 101) feed primarily on diatoms, but also include detritus and mosses in their diet. Hawkins found that as size increased in the **Ephemerellidae**, especially in *Caudatella edmundsi* and *Ephemerella dorothea infrequens* (Figure 80), the consumption of both animal matter and mosses increased. Hawkins found that eight species demonstrated a correlation between moss consumption and size. López-Rodríguez *et al.* (2008) likewise found that the proportion of mosses in the diet increases in **Ephemerellidae** as naiads age. Several researchers (Hynes 1941; Chapman & Demory 1963; Gaevskaya 1969) found that mosses are eaten by members of this family more often than other aquatic macrophytes (not including algae). But it is not clear if the moss is eaten for its own food value or for the attached periphyton. Percival and Whitehead (1929) found that two species in this family ingested large amounts of moss, suggesting that the moss itself was an important food source. Among the members of **Ephemerellidae** studied by Hawkins (1985), *Caudatella edmundsi*, *C. heterocaudata*, *C. hystrix*, and *Serratella teresa* were moss shredders. Others living among the mosses and ingesting them were detritus shredders, including *Attenella margarita* (Figure 77), *Ephemerella dorothea infrequens*, *E. excrucians* (Figure 81), *E. velmae*, *Serratella tibialis* (Figure 84), and *Timpanoga hecuba* (Figure 78). *Drunella pelosa* is a diatom scraper, permitting it to eat the many diatoms adhering to the moss leaves.



Table 1. Correlations between size (mm) and percent composition of major food items in the gut. Values are correlation coefficients ( $r$ ). \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ . Percentages arcsine-transformed prior to analysis. From Hawkins 1985.

Species	n	diatoms	detritus	animal	moss	wood	fungus
<i>Caudatella cascadia</i> (= <i>C. hystrix</i> )	18	0.191	0.149	–	-0.369	0.027	-0.518*
<i>Caudatella hystrix</i>	23	-0.550**	0.166	0.203	0.398	-0.213	-0.117
<i>Caudatella edmundsi</i>	17	-0.115	-0.609**	0.313	0.573*	–	–
<i>Serratella teresa</i>	21	0.660**	-0.550**	-0.183	0.001	–	-0.412
<i>Serratella tibialis</i>	13	-0.095	-0.199	0.160	0.424	–	–
<i>Ephemerella dorothea</i> <i>infrequens</i>	60	-0.129	-0.177	0.109	0.295*	0	0.080
<i>Drunella spinifera</i>	33	0.037	0.050	-0.016	-0.057	-0.035	-0.128
<i>Drunella doddsi</i>	36	-0.067	-0.324	0.211	-0.255	–	-0.165
<i>Drunella coloradensis</i>	65	-0.313**	-0.138	0.433**	0.144	-0.168	-0.142
<i>Drunella pelosa</i>	29	-0.463*	0.256	0.179	0.330	–	–
<i>Drunella grandis</i>	5	-0.863	-0.371	0.394	0.245	–	0.158
All species	359	-0.115*	-0.099	0.257**	0.008	-0.034	-0.067



Figure 77. *Attenella margarita* naiad, a moss shredder. Photo by Donald S. Chandler, with permission.



Figure 78. *Timpanoga hecuba* naiad, a detritus shredder. Photo by Bob Newell, with permission.

### *Ephemerella*

*Ephemerella* and its segregates are usually the most common mayflies among mosses. Needham & Christenson (1927) reported *Ephemerella* s.l. from moss-covered boulders in streams of northern Utah, USA. In their study of colonization of *Fontinalis neomexicana* (Figure 79) in Idaho, USA, Maurer and Brusven (1983) found *E. dorothea infrequens* (Figure 80) to be common among these mosses. In the St. Maries River of Idaho, USA, Gilpin and Brusven (1970) occasionally found *E.*

*excrucians* (Figure 81) and *E. dorothea infrequens* clinging to *Fontinalis* and other vegetation, but mostly they were on submerged logs and rocks. Nevertheless, mosses comprised 8% of the diet of this variety (Hawkins 1985).



Figure 79. *Fontinalis neomexicana*, home to several species of *Ephemerella* naiads. Photo by Belinda Lo, through Creative Commons.



Figure 80. *Ephemerella dorothea infrequens* naiad. Photo by Bob Henricks, with permission.



Figure 81. *Ephemerella excrucians*, a common inhabitant of *Fontinalis neomexicana* in streams of Idaho, USA. Photo by Jason Neuswanger, with permission.

In Straffan, UK, *Ephemerella notata*, a species once considered close to *Serratella ignita*, lived among mosses (Frost 1942; Kimmins & Frost 1943), including *Fontinalis* (Figure 47) (Kimmins & Frost 1943). Although *Ephemerella* sometimes eats a considerable diet of bryophytes, Jones (1950) did not find moss tissue in the guts of any of the five species of mayflies, including *Ephemerella notata*, in the River Rheidol, UK.

Bob Henricks reported 40-50 spiny crawlers (*Ephemerella*) on a mossy rock in a stream. He noted that in this stream the mosses held tiny sand grains and minute rocks instead of fine silt. In the mountain streams the mosses held fine silt and organic matter with many fewer of these mayflies. They avoid the mosses that grow on the tops of rocks and that float on the surface where the moss reaches the air. Rather, they tend to be on the under-surface of the mosses that wrap around the rocks in the water (Figure 82).

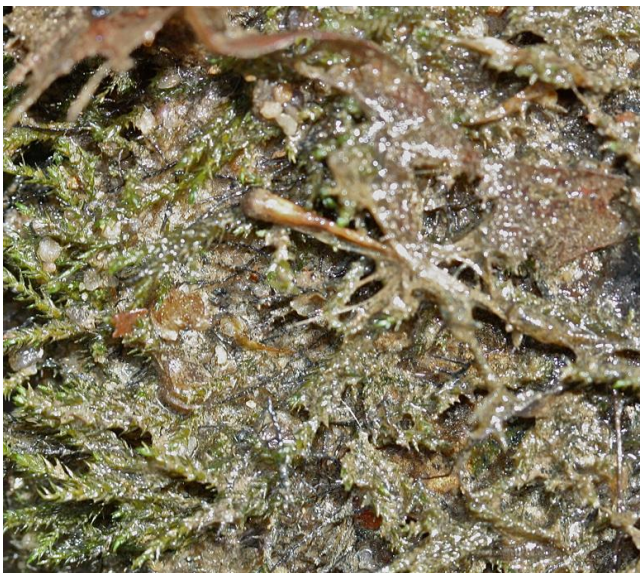


Figure 82. *Ephemerella* on rock with mosses. The mayflies blend with the algal-detrital mat on the mosses. Photo by D. N. Bennett, with permission.

Bengtsson (1981) found that *Ephemerella mucronata* (Figure 83) demonstrated a steady growth rate throughout winter in Sweden. This species has an interesting niche in the River Rajcianska, Slovakia, where it occurs among the wet emergent bryophytes but not among the submerged ones (Krnó 1990).



Figure 83. *Ephemerella mucronata*, a mayfly that continues to grow throughout winter in Sweden. Photo by Biodiversity Institute of Ontario, through Creative Commons.

### *Serratella*

*Serratella tibialis* (Figure 84) is a collector-gatherer, feeding on detritus (Aquatic Insects 2008). Both early instars and mature naiads are common among mosses, including *Platyhypnidium riparioides* (Figure 39) and *Fontinalis antipyretica* (Figure 47) (Langford & Bray 1969). *Serratella teresa* occurs on mosses and other vegetation in swiftly-flowing streams (Allen & Edmunds 1963). In the McKenzie River, Oregon, USA, Hawkins (1984) found that 85% of the individuals of this species sampled were in clumps of *Fontinalis* sp. (Figure 79). Furthermore, 17% of the food for *S. teresa* in Oregon was mosses (Hawkins 1985).



Figure 84. *Serratella tibialis*, a naiad common among mosses in both its young and older stages. Photo by Bob Henricks, with permission.

In Straffan, UK, Frost (1942) found that *Serratella ignita* (Figure 67) lived among mosses. Percival and Whitehead (1929) found that mosses form the primary habitat for *S. ignita*, and that the moss also is its dominant food, an observation consistent with that of López-Rodríguez *et al.* (2008). Langford and Bray (1969) found this species among *Fontinalis antipyretica* (Figure 47) and *Platyhypnidium riparioides* (Figure 39) as well as on bare sand and tracheophytes in Britain.

Macan (1957) found that among the streams he studied in Ford Wood Beck, UK, the abundance of *Serratella ignita* (Figure 1, Figure 67) increased as the flow became more sluggish and the vegetation became thicker. In all



streams, this species was more common when either tracheophytes or mosses were present. In faster streams, this relationship with mosses might explain the presence of this species. Furthermore, this species is able to move about in the wet moss mats above the water level (Krnó 1990). *Serratella ignita* is among the species that not only live among mosses, but it also eats them (Percival & Whitehead 1929).

*Serratella ignita* (Figure 1, Figure 67) usually lays its eggs where moss is present in fast-flowing water (Elliott 1978). The development time for the eggs depends on the temperature, with hatching time decreasing with increasing water temperature in the range of 5.9-14.2°C. However, at higher temperatures the hatching time increases with temperature. Correlations of naiad numbers with moss coverage may be a correlation with temperature.

*Serratella ignita* (Figure 67) prefers a flow of 10-30 cm sec<sup>-1</sup> (Macan 1962). Willoughby and Mappin (1988) were unable to find it in upland streams of the River Duddon where the pH was low (4.8-5.2), but it did occur in lowland streams with pH values of 6.6 and higher. But it appears that the pH was not the direct cause of its absence. In the lab, it was very tolerant of low pH and low ion content, and growth rates were equally good whether food supplied was that available in low pH streams (liverwort *Nardia compressa* (Figure 85) plus the filamentous alga *Klebsormidium subtile* (Charophyta; see Figure 86) or that available in high pH streams [moss *Platyhypnidium riparioides* (Figure 39) with the epiphytic diatom *Cocconeis placentula* (Bacillariophyta; Figure 87). Nevertheless the absence of *K. subtile* as a food at the higher pH seems to account for the absence of *S. ignita* there. Percival and Whitehead (1929) found mosses in the guts of *Serratella ignita* in Great Britain. But are the mosses really a preferred food? In preference experiments, Rosillon (1988) found that *S. ignita* preferred diatoms over detritus. In these experiments, the growth rate was significantly higher on the diatom diet than that on the detritus diet, no matter what the temperature. In fact, larvae reared on the detritus diet had slower development and usually failed to reach the adult stage. If diatoms are the preferred food, eating the moss may simply be the most efficient means of obtaining them.



Figure 85. *Nardia compressa*, a leafy liverwort in low pH streams where *Serratella ignita* feeds. Photo by David T. Holyoak, with permission.



Figure 86. *Klebsormidium flaccidum*, a congener of *K. subtile* that is an important food for *Serratella ignita* in the bryophyte habitat. Photo by Sarah Kiemle, with permission.

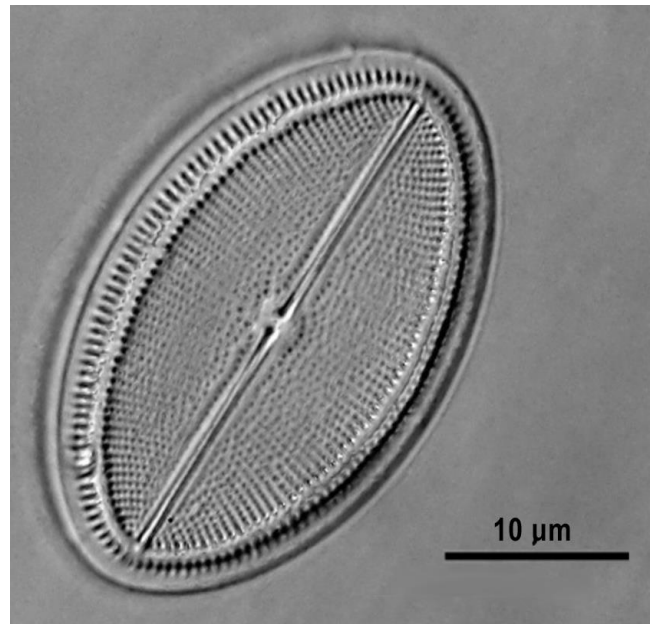


Figure 87. *Cocconeis placentula*, a common epiphyte on aquatic bryophytes and important food for *Serratella ignita*. Photo by Ralf Wagner, with permission.

Rosillon (1988) demonstrated that temperature was an important factor in determining mortality for *Serratella ignita* (Figure 67). Furthermore, as the temperature increased, mortality was higher on the detritus diet than on the diatom diet. The bryophytes are more likely to be abundant in the cooler habitats, often being overtaken by algal and microbial growth where it is warmer.

*Serratella serratoides* (Figure 88) occurs primarily among *Hygroamblystegium fluviatile* (Figure 68) – *Platyhypnidium riparioides* (Figure 39) mats in Appalachian Mountain, USA, streams (Glime 1968). In the southeastern USA it burrows into the moss mats a few cm below the surface (Berner & Allen 1961).



Figure 88. *Serratella serratoides* naiad. Photo by Bob Henricks, with permission.

Even for this common moss-dwelling genus, other substrata are often acceptable as well. *Serratella spinosa nevadensis* (as *Ephemerella ikonovici nevadensis*) only occurred in soft water in Spain, living at margins or midstream where roots, moss, algae, or other form of vegetation, along with detritus, was present (Alba-Tercedor 1990; López-Rodríguez *et al.* 2008). Unlike most of the **Ephemerellidae** that increase moss consumption with size, the naiads of *S. spinosa nevadensis* increase the percentage of detritus in the diet as they grow larger.

Some **Ephemerellidae** take advantage of ecosystem engineering by other insects. They are poor swimmers that need to cling to vegetation or other objects for support in the current (DEP 2014). *Serratella setigera* prefers slow flow (Nakano *et al.* 2005). In field experiments on artificial substrata, this species took advantage of the flow reduction in retreats of the net-spinning caddisfly *Hydropsyche orientalis* (Figure 89). In the experiments, those living on experimental plates with no caddisflies were mostly lost during high flow events, whereas none of the naiads in the caddisfly retreats were lost. It is likely that bryophytes provide similar retreats on rocks for some members of this genus. The researchers suggested that in the complex habitat created by mosses, the advantages provided by the *Hydropsyche* retreats would weaken. *Hydropsyche orientalis* occurs in moss mats of *Platyhypnidium riparioides* (Figure 39) in Japan (Takemon & Tanida 1992), but I could find no documentation that *Serratella setigera* likewise occurs there.



Figure 89. *Hydropsyche orientalis* larva, provider of retreats for *Serratella setigera*. Photo by Takao Nozaki, with permission.

### **Teloganopsis**

*Teloganopsis* (= *Serratella*) *deficiens* (Figure 90- Figure 91) is known from bryophytes in eastern North America (Allen & Edmunds 1963; Glime 1968). In the southeastern states it lives primarily among mosses and other plants in rocky, swift streams, but in Michigan it also occurs among detritus (Allen & Edmunds 1963). Among the mosses they are protected from the current and find a sufficient food supply.



Figure 90. *Teloganopsis deficiens* naiad, a *Fontinalis* inhabitant. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.



Figure 91. *Teloganopsis deficiens* naiad, a *Fontinalis* inhabitant. Photo by Bob Henricks, with permission.

### **Cincticostella**

In Japan, the narrowly distributed *Cincticostella nigra* (Figure 92) occurs in mats of *Platyhypnidium riparioides* (Figure 39) (Takemon & Tanida 1992). This species is restricted to Honshu, Japan (Allen 1971).



Figure 92. *Cincticostella nigra* naiad. Photo from Shiiba Research Forest. Permission pending.



### ***Drunella***

Allen and Edmunds (1962) did not report any bryophyte dwellers among the North American species of *Drunella* they examined. But Muttkowski and Smith (1929) did find *Drunella* twice among the mosses of strong rapids in Yellowstone National Park, USA. Hawkins (1984) found only 2% of two *Drunella* (Figure 93) species [*D. pelosa*, *D. coloradensis* (Figure 93)] among mosses in western Oregon, USA. But *D. spinifera* (Figure 94) was collected primarily (54%) in mats of *Fontinalis* (Figure 79). *Drunella allegheniensis* (see Figure 95) occurs among bryophytes in the Appalachian Mountain, USA, streams (Glime 1968). Gilpin and Brusven (1970) found *D. grandis* (Figure 96) among *Fontinalis* clumps in Idaho, USA, as well as in other habitats with protective cover. *Drunella spinifera* was common on *Fontinalis*. And Barton (1980) found the latter species to be abundant on moss-covered stones in riffles and rapids of a stream in northeastern Alberta, Canada.



Figure 95. *Drunella tuberculata*, a species very similar to *Drunella allegheniensis*. Photo by Bob Henricks, with permission.



Figure 93. *Drunella coloradensis* naiad, a genus sometimes found among bryophytes. Photo by Bob Henricks, with permission.



Figure 96. *Drunella grandis* naiad, a *Fontinalis* dweller. Photo by Bob Newell, with permission.

*Drunella grandis* (Figure 97) was a characteristic species among clumps of the leafy liverwort *Porella* (Figure 98) in California, USA (Corona 2010). This species seems to be adapted to its bryological habitat by large dorsal projections on the head, thorax, and abdomen. These projections reduce the chance of being swept away by rapid current in the locations of the liverwort, hooking the mayfly on the branches (Hora 1930).



Figure 94. *Drunella spinifera* naiad, a *Fontinalis* dweller. Photo by Joseph Fortier, through Creative Commons.



Figure 97. *Drunella grandis* naiad, a leafy liverwort dweller in California, USA. Photo by Bob Newell, with permission.





Figure 98. *Porella pinnata*. This genus provides a home for *Drunella grandis* in California, USA. Photo by Des Callaghan, with permission.

### **Caudatella**

Although the records of the members of this genus inhabiting bryophytes are limited, Hawkins (1985) reported that four species of *Caudatella* had three of the four highest percentages of bryophytes in the gut among all the **Ephemerellidae** in Oregon, USA. The moss percentage in the diet of these species, which we must presume were associated with mosses, were *C. hystrix* (Figure 99-Figure 100) (15% + 20% listed as *C. cascadia*), *C. edmundsi* (Figure 101) (19%), and *C. heterocaudata* (15%).



Figure 99. *Caudatella hystrix* naiad, a mayfly for which mosses comprise 35% of the diet in Oregon, USA, streams and rivers. Photo by Bob Newell, with permission.



Figure 100. *Caudatella hystrix* adult. Naiads live in fast riffles in Idaho, USA, clinging to *Fontinalis*. Photo by Bob Newell, with permission.



Figure 101. *Caudatella edmundsi*, a naiad that sometimes occurs exclusively on *Fontinalis*. Photo by Bob Newell, with permission.

In the St. Maries River of Idaho, USA, *Caudatella hystrix* (Figure 99-Figure 100) typically occurred in fast riffles where it would cling to *Fontinalis* (Figure 79) or the alga *Prasiola* (Maurer & Brusven 1983). These substrata did an effective job of concealing the naiads. *Caudatella edmundsi* (Figure 62, Figure 101) occurs in streams with lower mean summer temperatures at higher elevations and coincides with higher moss coverage (Jacobus *et al.* 2006; Hogue & Hawkins 2008). Hawkins (1984) found *Caudatella edmundsi* exclusively among *Fontinalis* in western Oregon, USA.

### **Attenella**

I am only aware of two species in this genus that live among the bryophytes. *Attenella margarita* (Figure 77) is a detritus shredder that also eats bryophytes and lives among them. In Appalachian Mountain streams, *A. attenuata* lives among the bryophytes, particularly *Fontinalis dalecarlica* (Figure 69), but its use of bryophytes for food is unknown (Glime 1968).

### **Torleya**

This is one of the many genera that have been split off from *Ephemerella*. *Torleya major* is a bryophyte dweller in the River Rajciana in Slovakia, where it lives below the surface but is not found among the emergent wet bryophytes (Krno 1990).

### **Leptohyphidae – Little Stout Crawler Mayflies**

This is a family of small mayflies (3-10 mm) that are clingers and sprawlers (Leptohyphidae 2015). They are widespread in North America, but most are not common among bryophytes. They do crawl about on plants.

*Tricorythodes* (Figure 102) burrows among the stems and rhizoids of mosses (Armitage 1961). In North America Berner (1959) found it in streams with a perceptible current where it lived among mosses or other plant growth on large stones or amid fine sand and gravel. They eat mostly plants (Leptohyphidae 2015). These naiads rarely swim, but rather move by crawling (Berner 1959). Their gill covers protect the gills, keep them clean, and move water across them when the current is insufficient to provide the needed oxygen.





Figure 102. *Tricorythodes* sp. naiad, a genus that burrows among moss stems and rhizoids. Photo by Bob Henricks, with permission.

## Suborder Pisciforma

### Ameletidae – Combmouthed Minnow Mayflies

Unlike the **Leptophlebiidae**, the **Ameletidae** are fast swimmers. They are mostly limited to clean, cold water (Henricks 2011) of North America and Europe (Ameletidae 2015) where they feed by scraping algae (Zuellig *et al.* 2006). Some members of this univoltine family may be **parthenogenetic** (reproducing with an unfertilized egg). They range 7-21 mm in length (Zloty & Pritchard 1997).

*Ameletus* (Figure 103) is not generally a moss dweller, preferring more open waters with a stream substrate free of silt (Schwiebert 2007). Nevertheless, mosses can play a role in its location. It is among the few mayflies able to tolerate acid water, permitting it to live downstream from a lake acidified by *Sphagnum* (Figure 51) (Bauernfeind & Moog 2000). *Ameletus inopinatus* (Figure 104) lives in such a habitat at higher altitudes. In my Appalachian Mountain streams it was an infrequent occupant of the bryophytes (Glime 1968).



Figure 103. *Ameletus ludens* naiad. Some members of this genus are able to tolerate the acidified outflow from *Sphagnum* lakes. Photo by Jason Neuswanger, with permission.



Figure 104. *Ameletus inopinatus* naiad, a species that is able to live in the pH extremes of outflow from *Sphagnum* fens and bogs at higher elevations. Photo by André Wagner, with permission.

### Baetidae – Blue-winged Olives

The **Baetidae** are distributed throughout the cooler (but not polar) parts of both the Northern and Southern Hemispheres (Hebert 2012). They are among the smallest mayflies, usually <10 mm, and mostly members of the open water column, hanging out on the stream bottom or darting into the flow (Baetidae 2013). They are strong swimmers, but feed mostly on algae. Nevertheless, the youngest naiads can be found sheltered among the bryophytes, out of the flow that is beyond their ability for controlled swimming at that early stage (Hynes 1961; Glime 1968). They leave the bryophytes when their swimming skills develop, but when it is time to emerge, the **Baetidae** may once again use the bryophytes to facilitate their break through the surface tension safely. And once above water, they may cling to bryophytes to escape their naiad skin (Figure 105).



Figure 105. **Baetidae** newly emerged adults on wet moss. Photo by Jason Neuswanger, with permission.

Despite their open water nature, *Baetis* species are common among bryophytes in the River Rajcianka in Slavakia (Krno 1990). Those on submerged bryophytes include *Baetis alpinus* (Figure 106), *B. fuscatus* (Figure 107), *B. lutheri*, *B. muticus* (Figure 108), *B. rhodani* (Figure 111), *B. scambus*, *B. vardarensis* (Figure 109), and *B. vernus* (Figure 110). Among these, naiads of *Baetis lutheri*, *B. muticus*, *B. rhodani*, and *B. scambus* are also able to move about among the wet emergent bryophytes.



Figure 106. *Baetis alpinus* naiad. Photo by Andrea Mogliotti <www.euroflyangler.com>, with permission.



Figure 110. *Baetis vernus* adult. Photo by Walter Pfliegler, with permission.



Figure 107. *Baetis fuscatus* adult. Photo by Andrea Mogliotti <www.euroflyangler.com>, with permission.



Figure 108. *Baetis muticus* naiad, a species sensitive to low water pH. Photo by Andrea Mogliotti <www.euroflyangler.com>, with permission.



Figure 109. *Baetis vardarensis* naiad, a dweller of submerged bryophytes. Photo from Zoologische Staatssammlung Muenchen through Creative Commons.

In a Welsh mountain stream Hynes (1961) found the very small (under 3 mm) members of *Baetis* (Figure 105-Figure 112) among mosses. I found a similar relationship of early instars among the mosses in Appalachian Mountain, USA, streams (Glime1968). Macan (1980) found that naiads of *Baetis rhodani* (Figure 111) in the River Lune, England, were common and abundant in the moss-covered area of the stream in winter. Naiads of four species of mayflies lived there spring to autumn, then overwintered in the egg. Hence, in the summer these other species appeared to displace *Baetis rhodani* from the mossy area. Wallace and Gurtz (1986) found that the biomass and production of *Baetis* were more than twice that of the weighted stream biomass and production. They suggested that part of this surge in biomass might be due to the large diatom count on mosses. Galdean (1994) further supported the importance of food among the mosses. On boulders where the velocity had increased in a stream, and the mosses on these boulders formed a felt that lacked detritus, *Baetis rhodani* was rare.

The mayfly *Baetis* (Figure 105-Figure 112) is well adapted to living where water levels fluctuate in streams. It can crawl to deeper water as the water level recedes, and it can relocate by entering the drift (Corrarino & Brusven 1983). When *Baetis* is in the drift, it swims to the surface, does a somersault, and hopefully is able to establish a hold on a substrate (Hughes 1966). Its streamlining makes it a good swimmer, and it is among the few insects that can swim against a current. It is positively phototactic and exits from its dark enclosures when there is light.

In their experiments on effects of pH on mayflies, Willoughby and Mappin (1988) found that *Baetis muticus* (Figure 108) and *Baetis rhodani* (Figure 111) are directly sensitive to the low pH of the water, whereas *Serratella ignita* (Figure 1) was tolerant but absent in low pH water due to an inadequate food supply. Water acidity accounted for the absence of these *Baetis* species in the Upper Duddon, UK.





Figure 111. *Baetis rhodani*, a species that is sensitive to low pH. Photo by J. C. Schou, with permission.



Figure 112. *Baetis tricaudatus* naiad, a common mayfly among *Fontinalis neomexicana* in Idaho, USA. Photo by Tom Murray, through Creative Commons.

Frost (1942) found that *Baetis*, including the common *B. rhodani* (Figure 111), often makes its naiad home among mosses. In their study of colonization of *Fontinalis neomexicana* (Figure 79) in an Idaho stream, Maurer and Brusven (1983) found *Baetis tricaudatus* (Figure 112) to be common among the mosses.

The food of *Baetis* is typically diatoms, desmids, and filamentous algae (Butcher 1933; Percival & Whitehead 1929). But Brown (1961) found that detritus was the primary food of *B. rhodani* (Figure 111), a sometimes moss-dweller. Food of *B. rhodani* varied somewhat with habitat and season, also including algae. On the other hand, *Baetis* is frequent prey for fish. Frost (1942) found that 71% of the fish examined at Ballysmuttan and 59% at Straffan had *Baetis* in their guts. Such consumption is likely because of their frequent ventures into the open water.

Lee and Hershey (2000) found that *Baetis* (Figure 105-Figure 112) did not increase in numbers in fertilized reaches of the Kuparuk River in Alaska when the moss *Hygrohypnum* (Figure 43-Figure 44) increased in density. However, they grew larger in the fertilized zone, a fact Lee and Hershey attributed to greater abundance of epiphytic diatoms.

Wulfhorst (1994) compared naiads of *Baetis* (Figure 105-Figure 112) on mosses and in the **interstitial** spaces (spaces between individual sand grains in the soil or aquatic sediments) in the **hyporheic** zone (region beneath and alongside a stream bed) of two streams in the Harz Mountains, West Germany. There the mosses were home to many more of these mayflies than the interstitial spaces of the stream bed (Figure 113). On the other hand, Arnold and Macan (1969) found that *Baetis*, in addition to inhabiting mosses, occurred on unstable bare stones on the stream bottom.

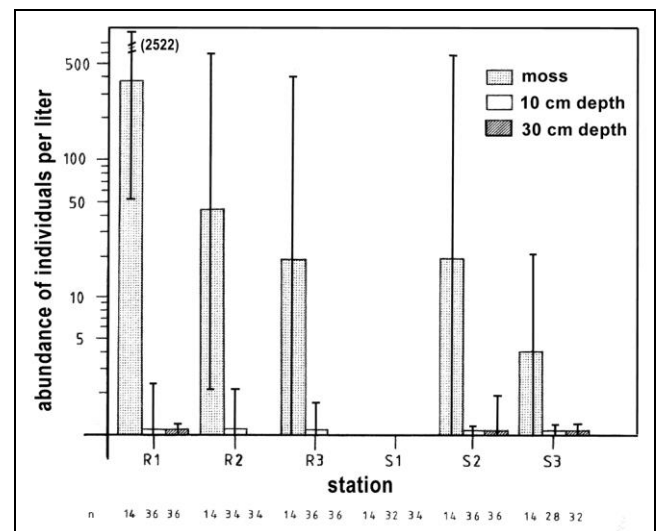


Figure 113. Mean abundance  $\pm$  95% CI of *Baetis* naiads in moss clumps in two streams in the Harz Mountains, West Germany. Redrawn from Wulfhorst 1994.

In the Arctic, conditions that favor mosses do not always favor the insects. Cold temperatures require life cycles that protect them in the winter. Among those species known to occupy mosses elsewhere, Giberson *et al.* (2007) found *Ephemerella aurivillii* (Figure 45) and *Baetis tricaudatus* (Figure 112) in the Arctic streams of Nunavut, Canada. The **Baetidae** was the most common family there. *Baetis bundyae* (Figure 114) naiads hatched within 2-3 weeks of ice-out and completed their development in 2.5-4 weeks. Giberson *et al.* considered the female-biased sex ratio to be an indication they might experience parthenogenesis. The Arctic **Baetidae** species are able to survive by having freeze-tolerant eggs, good dispersal, and a female-biased sex ratio that promotes greater reproduction.



Figure 114. *Baetis bundyae* naiad, a species with a female-biased sex ratio that is possibly parthenogenetic. Photo by Donna Giberson, with permission.

When we enter the Southern Hemisphere, the fauna changes, but major groups tend to remain the same. In Africa, baetid *Acanthiops elgonensis* (= *Afroptilum erepenscan*) attaches to mosses, barely covered by water, in the spray of water falls (Gillies 1990).

### Siphonuridae - Primitive Minnow Mayfly

This family generally occurs in slow water. In St. Maries River in Idaho, USA, Gilpin and Brusven (1970) found *Siphonurus occidentalis* (Figure 115) typically clinging to *Fontinalis* (Figure 47) growing at the stream margins.



Figure 115. *Siphonurus occidentalis* naiad. Photo by Bob Newell, with permission.

### Heptageniidae – Clinger Mayflies

This family is widespread in the Holarctic, Oriental, and Afrotropical regions, as well as Central American Tropics and extreme northern South America (Heptageniidae 2014). Most of them occur in very fast flow where they anchor themselves on rocks by using their collective gills as a suction cup.

Because of this suction cup arrangement, bryophytes are not friends to the **Heptageniidae**. For example, when mosses increased in growth downstream from impoundments, the **Heptageniidae** diminished or were eliminated completely (Brittain & Saltveit 1989). Bottová and Derka (2013) reported that *Rithrogena semicolorata* avoided mosses in a karstic spring in the West Carpathians,

despite its high coverage of mosses. But in the moderately eutrophic River Rajcanka in Slovakia *Rithrogena ferruginea* did occur among the bryophytes, despite the family's adaptations for smooth rock surfaces.

This is a family of flattened mayflies adapted to living on rock surfaces, typically with gills arranged along the abdominal segments to form a suction cup. Nevertheless, Jones (1949, 1950) found all of the guts with identifiable contents from 22 *Ecdyonurus venosus* naiads (Figure 116) contained the moss *Fontinalis antipyretica* (Figure 47). Winterbourn *et al.* (1986) likewise found that this species ate mosses in two British river systems. In the St. Maries River of Idaho, USA, *Cinygmula* sp. (Figure 117) occasionally occurred in clusters among *Fontinalis* (Gilpin & Brusven 1970). Among bryophytes in mid-Appalachian Mountain, USA, streams, I only found *Epeorus* (Figure 118-Figure 119) representing this family (Glime 1968).



Figure 116. *Ecdyonurus venosus* naiad, a mayfly that eats *Fontinalis antipyretica*. Photo by Guillaume Doucet <<http://guillaume.doucet.free.fr/>>, with permission.



Figure 117. *Cinygmula subaequalis* naiad, member of a genus with moss-dwelling members. Photo by Donald S. Chandler, with permission.





Figure 118. *Epeorus* sp. naiad showing flattened body and legs. Photo by Tom Murray, through Creative Commons.



Figure 119. *Epeorus* sp. naiad showing ventral arrangement of gills into a suction cup. Photo from NABS through NSF funding public domain.

### Isonychiidae

The **Isonychiidae** are mostly North American, with scattered records in Asia (Isonychiidae 2015). These active swimmers are 8-17 mm long and occupy rapid currents (Waterbugkey 2015). They filter algae and diatoms from the water by using the long hairs on their forelegs, but they also eat smaller insects.

In the Appalachian Mountain streams I (Glime 1968) found *Isonychia* (Figure 120-Figure 121) occasionally among the bryophytes.



Figure 120. *Isonychia bicolor* naiad, member of a genus that sometimes occurs among bryophytes. Photo by Jason Neuswanger, with permission.



Figure 121. *Isonychia bicolor* naiad, showing fibrillate gills with gill covers. Photo by Jason Neuswanger, with permission.

### Oligoneuriidae – Brushleg Mayflies

This is mostly a river family, but occasionally they are associated with bryophytes. In the Sierra Nevada Mountains in southern Spain, young naiads of *Oligoneuriella marichuae* (Figure 122) require physical support and a way to capture food in the absence of a well developed filtering device (Alba-Tercedor 1990). For this they use roots, filamentous algae, and mosses. After they grow, they are able to move into the current.



Figure 122. *Oligoneuriella rhenana* naiad, a congener of *O. marichuae* that lives among mosses. Photo by Guillaume Doucet <[www.guillaume.doucet.free.fr](http://www.guillaume.doucet.free.fr)>, with permission.

### Suborder Carapacea

#### Baetiscidae – Armored Mayflies

This small family of North American mayflies has a distinctive morphology (Figure 123) – the **notum** (Figure 124) covers the thorax and part of the abdomen (Edmunds 1960). These mayflies are medium sized (4-14 mm long) and live in pools or flowing water of sandy streams (Baetiscidae 2015b). Hence their occurrences among bryophytes are rare. Their feeding strategies are gatherers and scrapers (Baetiscidae 2015a). When they swim, they tuck their legs under the body and move by undulating the abdomen and caudal filaments (Baetiscidae 2015b).

I am delighted to report this unusual-looking family as having at least occasional moss dwellers. In fact, both *Baetisca obesa* (Figure 123) and *B. rogersi* (Figure 124) are moss dwellers. Berner (1955, 1956) found *B. obesa* among mosses that grew on submersed parts of trees in slow streams in North America. Later, Pescador (1973) found *B. rogersi* early instars in thick mats of the moss *Leptodictyum riparium* (Figure 125), likewise in slow water. In Appalachian Mountain, USA, streams, I found *B. callosa* and *B. carolina* among bryophytes, but infrequently (Glime 1968).



Figure 123. *Baetisca obesa* naiad, a species that lives on mosses in slow water. Photo by Jason Neuswanger, with permission.



Figure 124. *Baetisca rogersi* naiad, whose early instars occur in thick mats of the moss *Leptodictyum riparium*. Note the large **notum** that covers the thorax and part of the abdomen. This one has a large spine on each side. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.



Figure 125. *Leptodictyum riparium* in shallow root pit. Photo by Betsy St. Pierre, with permission.

## Summary

The **Collembola** are no longer considered insects and are now placed in the class **Entognatha**. Few live in the water and small numbers may mean they have fallen in. But some can occur in large numbers on the water surface, wet bryophytes of bogs, fens, and streambanks, and emergent bryophytes. They possess a **furcula** that propels them forward like a spring. The **collophore** facilitates respiration and absorption of water. Antennae recognize light intensity, wind direction, and heat.

The **Isotomidae** is the most frequent aquatic family, especially *isotomurus palustris*. This species is **viviparous**.

The **Hemimetabola** have **incomplete metamorphosis** with egg, nymph or naiad, and adult. Naiads typically have gills.

**Ephemeroptera** (mayflies) live only about one day as adults, emerging, mating, and dying, but not eating. Mating is accomplished in swarms. All the immatures (*naiads*) are aquatic. Some are **univoltine** (one brood per year) and some are **bivoltine** (two broods per year).

Most mayflies have high oxygen requirements. Mayfly naiads have gills, and those with gill covers are able to increase movement of water and oxygen across the gills by beating the gill covers. Some use body undulations to increase contact with oxygenated water.

The most common mayfly family among bryophytes is the **Ephemerellidae**. This is the family that most commonly eats bryophytes, and consumption of mosses increases as the naiads age. However it is not clear if they eat the mosses to assimilate them or if they only assimilate the attached algae and bacteria.

*Baetis* (**Baetidae**) seems to use bryophytes as a nursery and a stopping point when they enter the drift, a usage common among a number of other families.

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# **CHAPTER 11-5**

## **AQUATIC INSECTS: HEMIMETABOLA – ODONATA**

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# CHAPTER 11-5

## AQUATIC INSECTS: HEMIMETABOLA – ODONATA



Figure 1. *Lanthus vernalis* (Gomphidae) exuviae on the terrestrial moss *Thuidium* sp. Photo by Richard Orr, with permission.

### ODONATA – Dragonflies and Damselflies

This order contains both dragonflies (**Anisoptera**; Figure 2-Figure 4) and damselflies (**Zygoptera**). You can recognize adult dragonflies by their wings at rest (Figure 2) – they are spread horizontally; the term *anisoptera* means uneven wings. The damselflies, by contrast, usually fold the wings together above the body at rest (Figure 5); their wings are of equal size (**Zygoptera**). Both dragonflies and damselflies have an aquatic stage, the **naiad** (gilled nymph). Dragonflies can be recognized in the naiad stage by having internal anal gills and relatively stout bodies (Figure 3). Damselflies have three blade-like external anal gills and slender bodies (Figure 6).

Both groups are predators (Thorpe & Covich 1991) and the naiads have a large, scooplike **labium** (mouth part; Figure 4 & Figure 8, Figure 7) that extends to capture the prey. These giant jaws are formidable and the **Odonata** are efficient in catching prey.

The naiads climb out of the water and must climb up rocks or vegetation before they split their exoskeleton and emerge (Figure 1). They must then pump fluids into their wings before they fly away. Unlike the mayflies, the dragonfly naiads live as long as 5-6 years and adults for 5-6 months (Dragonfly 2015). Dragonflies are among the strongest fliers in the insect world – just try to catch one!





Figure 2. Dragonfly adult with spread wings. Photo by Eileen Dumire, with permission.



Figure 3. *Anax junius* (dragonfly; **Aeshnidae**) naiad showing stout body and anal opening that surrounds internal gills. Photo by Tom Murray, through Creative Commons.



Figure 4. *Diplacodes* (dragonfly; **Libellulidae**) young naiad showing extended labium. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 5. *Enallagma cyathigerum* (**Coenagrionidae**) Blue Damselfly adult illustrating the wings folded above the abdomen. Photo by Umberto Salvagnin, through Creative Commons.



Figure 6. *Argia* (**Coenagrionidae**) naiad showing three external anal gills typical of damselfly naiads. Photo by Bob Henricks, with permission.



Figure 7. *Lestes* (damselfly; **Lestidae**) showing extended labium. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.





Figure 8. *Cordulegaster boltonii* (dragonfly; **Cordulegasteridae**) jaws on exuvia. Photo by Tim Faasen, with permission.

Bryophytes are not the usual homes of **Odonata** naiads in lakes, ponds, and streams. In a Québec, Canada stream, **Odonata** preferred gravel to the moss *Fontinalis dalecarlica* (Figure 9) (Cattaneo *et al.* 2004). These carnivores preferred places where they could remain hydrated as the water level decreased and were not tied to the bryophytes for obtaining the periphyton required by many other orders.



Figure 9. *Fontinalis dalecarlica*, a moss often less preferred than sand, at least in Quebec streams. Photo by J. C. Schou, with permission.

But bryophytes do seem to hold importance for some **Odonata**. In my studies of Appalachian Mountain, USA, streams, the dragonfly genus *Cordulegaster* (**Cordulegastridae** – spiketail dragonflies; Figure 10) was occasionally present among bryophytes (Glime 1968). The gomphids *Gomphus* (**Gomphidae** – clubtail dragonflies; Figure 11) and *Octogomphus* (**Gomphidae**; Figure 12) also occurred among the bryophytes, both rarely, representing the dragonfly naiads (Glime 1968).

The presence of exuviae provides indirect evidence that the **Odonata** use bryophytes for emergence (Needham *et al.* 1901). Both *Gomphus exilis* (dragonfly; **Gomphidae**) (Figure 13) and *G. spicatus* (Figure 14) exuviae (Figure 15) appeared in layers among mosses at the edge of a pond in the Adirondack Mountains of New York, USA.



Figure 10. *Cordulegaster erronea* (dragonfly; **Cordulegastridae**) naiad, an occasional dragonfly genus among bryophytes in mid-Appalachian Mountain streams. Photo by Richard Orr, with permission.



Figure 11. *Gomphus lividus* (dragonfly; **Gomphidae**) naiad, a genus that is a rare bryophyte inhabitant in the mid-Appalachian Mountain streams. Photo by Richard Orr, with permission.



Figure 12. *Octogomphus specularis* (dragonfly; **Gomphidae**) naiad, a genus that is a rare bryophyte inhabitant in the mid-Appalachian Mountain streams. Photo by Mark Melton, with permission.





Figure 13. *Gomphus exilis* (dragonfly; **Gomphidae**) female adult, a species that uses mosses for emergence. Photo by Sheryl Pollock through Discover Life, with permission.



Figure 14. *Gomphus spicatus* (dragonfly; **Gomphidae**) adult, a species that uses mosses for emergence. Photo through Creative Commons



Figure 15. *Somatochlora tenebrosa* (dragonfly; **Corduliidae**) exuvia. Photo by Richard Orr, with permission.

## Suborder Zygoptera – Damselflies

Specific records of damselfly naiads living among bryophytes outside of bogs and fens are few, partly because they do not tend to inhabit the types of habitats where many of the aquatic bryophytes grow. But it seems more likely that the bryophytes do not afford a suitable habitat for their elongate labium to catch prey.

In the Red Cedar River, East Lansing, MI, I found a number of damselfly naiads early in the spring in large clumps of *Fontinalis* (Figure 16). *Teinobasis ponapensis* (see Figure 17), in the **Coenagrionidae** – narrow-winged damselflies, a damselfly from the eastern Caroline Islands

of Micronesia, occurred as adults only near mosses (Paulson & Buden 2003).



Figure 16. *Fontinalis antipyretica*, home for damselfly naiads in early spring. Photo by Michael Lüth, with permission.



Figure 17. *Teinobasis sjupp* (damselfly; **Coenagrionidae**) adult, relative of *T. ponapensis* that is known as adults only near mosses in the Caroline Islands of Micronesia. Photo by V. J. Kalkman, through Creative Commons.

But there appear to be interesting relationships still waiting for us. Two new species of the genus *Argiolestes* (**Argiolestidae** or **Megapodagrionidae**; damselflies; Figure 18) in Papua New Guinea are known only from shaded areas of water courses; *Argiolestes fornicatus* avoids sunny areas of the watercourses and occurs primarily in areas with high moss cover (Michalski & Oppel 2010). *Argiolestes tuberculiferus* (Figure 19) and *A. verrucatus* were discovered only recently in Papua New Guinea. Other bryophyte relationships most likely remain for discovery in less studied parts of the world.



Figure 18. *Argiolestes ornatus* (damselflies; **Megapodagrionidae**) male adult from Papua, Indonesia. Note that the wing position at rest is spreading, unlike other members of **Zygoptera**. (**Lestidae** hold them at 45° angles.) Photo by Vincent J. Kalkman.



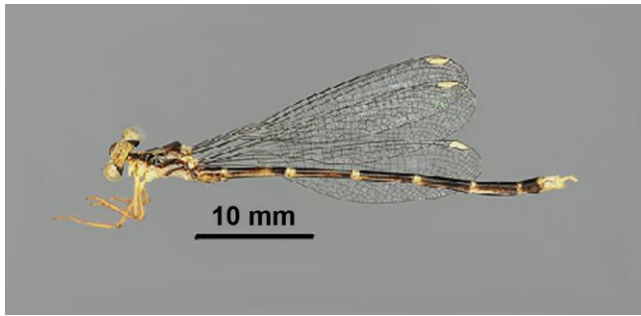


Figure 19. *Argiolestes tuberculiferus* adult. Photo by Naturalis Biodiversity Centre through Creative Commons.

## Suborder Anisoptera – Dragonflies

Direct usage of bryophytes by **Odonata** naiads is not well documented, but there seems to be more usage for the dragonflies than for the damselflies. It appears that mosses, as well as other protective pond locations, can protect some species when their ponds dry up. *Somatochlora semicircularis* (Corduliidae – emerald dragonflies; Figure 20-Figure 21) uses mosses, as well as rocks, logs, and deep in the bases of sedge clumps, to escape the drying conditions of exposure when their Colorado, USA, ponds dry up in late August and September (Willey & Eiler 1972). This species has the further advantage that it loses water more slowly than other dragonflies such as *Aeshna interrupta interna* (Figure 79-Figure 80) and *Libellula quadrimaculata* (Figure 22), neither of which seems to live among bryophytes.



Figure 20. *Somatochlora semicircularis* (dragonfly; Corduliidae) adult whose survival could depend on naiads seeking shelter in mosses when their ponds dry up. Photo by Belinda Lo through Creative Commons.

Even if **Odonata** are unable to live among bryophytes where their large size would make movement and prey capture more difficult, they may still take advantage of them for cover. *Somatochlora provocans* (dragonfly; Corduliidae) (Figure 23) occurred in a small lake inlet in southeastern USA, where *Sphagnum* (e.g. Figure 24) provided a border (Tennessen 1975). The naiads were common in the flowing water, but were hanging out near that *Sphagnum* cover.



Figure 21. *Somatochlora linearis* (dragonfly; Corduliidae) naiad. Some species in this genus retreat to bryophytes when their water body dries up. Photo by Richard Orr.



Figure 22. *Libellula quadrimaculata* (dragonfly; Libellulidae) naiad, a species that loses water rapidly and cannot survive when its aquatic habitat dries up. Photo by Tim Faasen.



Figure 23. *Somatochlora provocans* (dragonfly; Corduliidae) adult. Naiads of this species stay near the *Sphagnum* cover in pools. Photo by Mike Ostrowski through Creative Commons.





Figure 24. *Sphagnum* peatland in Alaska, USA. Photo by Vita Plasek.

*Oplonaeschna armata* (Figure 25), a member of the **Aeshnidae** – hawkers or darners, may not live among mosses, but the species still finds them useful. Some individuals of this dragonfly left traces of their behavior behind as exuviae clinging to mosses 0.8-1.25 m above the water on vertical rocky walls of a canyon (González Soriano & Novelo Gutiérrez 1998).



Figure 25. *Oplonaeschna armata* (dragonfly; **Aeshnidae**) adult, a species that climbs to mosses a meter above water to emerge from the naiad state. Photo by Greg Lasley through Creative Commons.

## Life Cycle Considerations

Bryophytes can actually provide several functions for **Odonata**, from wet habitats in waterfalls to safe sites or cover at the margins of streams, ponds, and lakes. The most important of these uses seems to be for egg depositories.

### Mating and Egg-Laying

Mosses may not house naiads in many habitats, but they are a preferred site for egg deposition in many bogs and fens. *Aeshna subarctica* (dragonfly; **Aeshnidae**) (Figure 27) in northwestern Wisconsin flies along the northwest shoreline, the sunny side, where there is a mat of

floating mosses and sedges (DuBois *et al.* 1999). While they submerge the ends of their abdomens into the moist *Sphagnum* (Figure 27) they are not ready for a quick getaway. Naiads of this species require submerged mosses in their habitat. *Aeshna sitchensis* (Figure 61) does not distinguish between *Sphagnum* bog pools and pools of fens with *Drepanocladus* (Figure 59) (Cannings *et al.* 2004). In the muskeg, *Aeshna coerulea septentrionalis* (dragonfly; **Aeshnidae**) (Figure 62) uses wet moss patches between tufts of scant grass as well as the muskeg "slime" as deposition sites in small pools, or in the creamy-pink muskeg slime bordering small pools (Whitehouse & Walker 1941). During mating and oviposition is a good time to catch the **Odonata** because they are occupied in laying eggs and not in flying.

The female of *Argia moesta* (damselfly; **Coenagrionidae**; Figure 26), in Ohio, USA, deposits her eggs on submerged mosses, logs, and algae-covered stones (Kellicott 1899). *Tanypteryx hageni* was once thought to insert eggs into plant tissues, but in a closer examination Svihla (1959) found that these were deposited below the water among mosses, liverworts, and other bog plants.



Figure 26. *Argia moesta* adult, a species that lays its eggs on submerged mosses. Photo by Richard Murphy through Creative Commons.

Corbet (1999) specifically reports naiads of *Thaumatoneura inopinata* (**Megapodagrionidae**), the giant water damselfly, as moss dwellers. This species oviposits among mosses that grow adjacent to, but not within, the main current.

*Leucorrhinia hudsonica* (dragonfly; **Libellulidae** – skimmers; Figure 29) at a black spruce *Sphagnum* bog (Figure 30) in Québec, Canada, uses that habitat for egg deposition (Hilton 1984). The males first establish territories, then perch there except for short attack flights against intruders. Females visit those sites to deposit eggs and are intercepted by the males who enter into tandem formation and copulate with them. Unlike many of the other **Odonata**, they perch near the egg-laying sites during copulation. Once copulation is completed, the females dip their abdominal tips in rapid succession into the small pools of water associated with the saturated *Sphagnum* (Figure 51). Males hover nearby to guard the females during this process, chasing off competing males. In Illinois, USA, when females of *Leucorrhinia* are pursued by too many males, they land on the mosses and deposit their eggs (Needham & Hart 1901).





Figure 27. *Aeshna subarctica* (dragonfly; **Aeshnidae**) female laying eggs in *Sphagnum*. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

Some species use terrestrial mosses for egg deposition. For example, one female *Tetracanthagyna plagiata* (**Aeshnidae**; Figure 28), the heaviest of all extant **Odonata**, deposited eggs on a moss-covered log adjacent to a stream, arching its abdomen to insert its ovipositor into the soft substrate (Leong & Tay 2009).



Figure 28. *Tetracanthagyna plagiata* (dragonfly; **Aeshnidae**) adult in Malaysia. Photo by Keith Wilson, through Creative Commons.



Figure 29. *Leucorrhinia hudsonica* (dragonfly; **Libellulidae**) female adult. Photo by Richard Orr, with permission.



Figure 30. Spruce bog in Pennsylvania, USA. Photo by Nicholas A. Tonelli, through Creative Commons.

One smart dragonfly in Oregon, USA, used mosses to make egg-laying a safer venture. Using her legs to cling to streambank mosses, *Octogomphus specularis* (dragonfly; **Gomphidae**) (Figure 31) dipped her ovipositor into the stream water, avoiding the danger of being washed away and helpless against the current (Opler 2013).



Figure 31. *Octogomphus specularis* (dragonfly; **Gomphidae**) clinging to moss while ovipositing in the water. Photo by Jim Johnson, with permission.

Temperature plays a major role in the timing and coordination of emergence in *Somatochlora alpestris* (dragonfly; **Corduliidae**) (Figure 34) and *S. arctica* (Figure 35-Figure 36) (Sternberg 1995). Eggs can hatch the same season or go into diapause and remain in their aquatic habitat throughout the winter. This is a facultative response that causes eggs deposited late in the season to increase from 0 diapausal eggs early in the season to 37% later in the season in *S. alpestris* and from 0 to 18% in *S. arctica*. Depending on the temperature during development, egg development requires 17 to 38 days. Dark mosses and dark bog water help to increase the ambient temperature and hasten development.

Few studies have identified egg-laying locations in streams. Bryophytes would seem to be ideal, even if the naiads leave soon after hatching to chase food items in open water. Askew (1988) did in fact observe *Caliaeschna microstigma* (**Aeshnidae**; Figure 32-Figure 33) depositing eggs in mosses on boulders of a stream in Europe.





Figure 32. *Caliaeschna microstigma* adult. Photo by Cosmin O. Mancu, with permission.



Figure 33. *Caliaeschna microstigma* exuvia. Photo by Cosmin O. Mancu, with permission.

### Emergence

Donnelly (1990) reported with implied amazement a finding of naiads of a species of the damselfly *Nesobasis* (Coenagrionidae; Figure 37) crawling over wet mosses near a stream in the Fijian Islands, but it was not clear if they lived there or were seeking an emergence site to climb. It appears that mosses are among the sites used for emergence (Walker 1923). Exuviae from several species of the dragonfly *Ophiogomphus* (Gomphidae; Figure 38-Figure 40) were present on mosses under underhanging foliage at Godbout, Quebec, Canada, where they were a meter or more from the present waterline.



Figure 34. *Somatochlora alpestris* (dragonfly; Corduliidae) adult, a dragonfly whose egg maturation time depends on the temperature. Photo by Gilles San Martin, through Creative Commons.



Figure 35. *Somatochlora arctica* (dragonfly; Corduliidae) adult male, a species whose egg maturation time depends on temperature, permitting it to keep its niche separate from that of *S. alpestris*. Photo by Piet Spaans, through Creative Commons.



Figure 36. *Somatochlora arctica* (dragonfly; Corduliidae) naiad exuvia. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.





Figure 37. *Nesobasis erythropis* (damselfly; **Coenagrionidae**) adult, a genus whose naiads climb across wet mosses in the Fijian Islands. Photo by Mark O'Brien, through Creative Commons.



Figure 38. Adult *Ophiogomphus cecilia* (dragonfly; **Gomphidae**) that has just emerged from its exuvia, a genus that sometimes emerges on overhanging mosses by streams. Photo by Tim Faasen, with permission.



Figure 39. *Ophiogomphus cecilia* (dragonfly; **Gomphidae**) exuvia, a genus with some members that crawl onto overhanging mosses to emerge. Photo by Tim Faasen, with permission.



Figure 40. *Ophiogomphus cecilia* (dragonfly; **Gomphidae**) adult, a genus that apparently uses mosses for emergence. Photo by Varel, through Creative Commons.

*Somatochlora elongata* (dragonfly; **Corduliidae**) (Figure 41) sometimes sheds its exuvia on mosses at the edge of ponds (Needham *et al.* 1901). *Somatochlora semicircularis* (Figure 20) faces imminent danger as it emerges. First, it must find a suitable site for climbing out of the water, and if these sites are scarce, they may all be occupied (Willey 1974). Then, it is vulnerable while it is emerging because it can neither fly nor return to the safety of cover. At this time it is especially vulnerable to birds, and its relatively large size can make a hearty meal. Once free of its nymphal skin, its maiden flight easily draws the attention of hungry predators. At this time, it gains the advantage of safety in numbers. Emergence is highly synchronized, and although many die, the emergence of 50% of the adults within the first three to six days prevents birds from capturing all of them. Considerable space is needed for catching these strong fliers in the air, limiting the number of predators. Life cycle processes from naiad to adult to egg laying can be seen in Figure 42-Figure 48.



Figure 41. *Somatochlora elongata* (dragonfly; **Corduliidae**) male adult, a species that may shed its naiad exuvia on mosses bordering ponds. Photo by Denis A. Doucet, with permission.



## Life Cycle Stages of the Damselfly *Coenagrion scitulum*



Figure 42. *Coenagrion scitulum* naiad, illustrating the three anal gills of the **Zygoptera**. Photo by Tim Faasen, with permission.



Figure 43. Naiad climbing up a plant to emerge to adulthood. Photo by Tim Faasen, with permission.



Figure 44. Adult emerging from exuvia. Photo by Tim Faasen, with permission.



Figure 45. Exuvia of emerged adult. Photo by Tim Faasen, with permission.



Figure 46. Adult *Coenagrion scitulum* ready to mate. Photo by Tim Faasen, with permission.



Figure 47. Mating *Coenagrion scitulum* pair, male on top, female below. Photo by Tim Faasen, with permission.



Figure 48. Male (left) and female (right) *Coenagrion scitulum* in tandem following copulation. They are most likely looking for a suitable site to lay eggs. Photo by Tim Faasen, with permission.

### Safety in Numbers

The dragonfly *Sympetrum vicinum* (Libellulidae – skimmers; Figure 49) typically uses wet mosses at the edge of a lake for depositing eggs (Whitehouse & Walker 1941). Mating and egg laying can be particularly dangerous for the **Odonata**. These able fliers are at a disadvantage when coupled during mating and when dipping into the water to lay eggs. One strategy for reducing chances of becoming frog dinner is for the mating pair to join other mating pairs, with up to seven pairs of *Sympetrum vicinum* (Figure 49) grouping together in a single 1 m<sup>2</sup> plot (McMillan 2000). Interestingly, frogs attacked lone pairs more frequently than they attacked pairs in aggregations. On the other hand, the presence of multiple pairs may have signalled a safe site against the predation.



Figure 49. *Sympetrum vicinum* (dragonfly; Corduliidae) adults mating. Photo by Phil Myers, through Creative Commons.

*Sympetrum danae* (dragonfly; Corduliidae) (Figure 50-Figure 52) does not remain in tandem pairs (compare to Figure 48) like *S. vicinum* (Figure 49). In the field, 14% of females that started oviposition while still in tandem and 10% of those that had separated from the males were killed by frogs (Michiels & Dhondt 1990). A curious observation is that separated ovipositing females were attacked less often by the frogs than were those females that were not observed mating previously. Females of this species preferred sites with *Sphagnum* (Figure 24), but when non-aquatic mosses with a similar structure were substituted, they were selected equally, suggesting that selection was based on surface characteristics of the mosses. Within the bog, temperature played a role in oviposition location. In the cooler part of the season the females selected the south-facing side of a hummock, whereas in the warmer part of the season they selected the cooler north-facing side of the hummock.



Figure 50. *Sympetrum danae* (dragonfly; Corduliidae) naiad. Photo by Tim Faasen, with permission.



Figure 51. The male dragonfly *Sympetrum danae* (dragonfly; Corduliidae) resting on *Sphagnum* in the habitat it prefers for mating. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.





Figure 52. *Sympetrum danae* (dragonfly; **Corduliidae**) mating. Once mating is completed, this species separates and does not fly in tandem. Photo by Tim Faasen, with permission.

## Bogs and Fens

Bogs and fens in many ways offer ideal conditions for adult **Odonata**. These strong fliers prefer bright sunshine and become quiet when the weather is cloudy. Sunny, open bogs are thus best suited for them, compared to other kinds of habitats. As discussed earlier regarding bog habitats (Chapter 11-2), the adults are easily seen flying about in bogs (Boudot *et al.* 1990).

Some **Odonata** seem to prefer bogs as adults, using them as a place to forage and for "sport" (Needham *et al.* 1901). One such dragonfly is *Cordulia shurtleffi* (American emerald – **Corduliidae**; Figure 53) in the Adirondack Mountains of eastern North America.



Figure 53. *Cordulia shurtleffi* (American emerald dragonfly) adult, a species that forages and plays around bog pools. Photo by Richard Orr, with permission.

But is this habitat equally suitable for the naiads? As Krebs (2001) reminded us, habitat heterogeneity provides more ecological niches, and bogs fit that heterogeneity of moisture and temperature as well as differences in microtopography. Some of these may use the mosses as occasional cover in the naiad stage (Figure 54).



Figure 54. *Cordulia aenea* (downy emerald dragonfly) naiad with mosses. This species is a relative of *C. shurtleffi*, a bog species. Photo by Tim Faasen, with permission.

In Ontario, Canada, naiads of *Williamsonia fletcheri* (**Corduliidae**; Figure 55) live among the dead *Sphagnum* stems (Charlton & Cannings 1993). They matched the *Sphagnum* and rarely moved, giving them excellent camouflage. In Maine, USA, the males perch on *Sphagnum* hummocks in spruce bogs.



Figure 55. *Williamsonia fletcheri*, a species whose naiads live among dead *Sphagnum* stems. Photo by Diana-Terry Hibbitts, through Creative Commons.

**Odonata** can have a strong impact on the communities where they live. The naiads are efficient carnivores with highly specialized scoops for capturing prey. Larson and House (1990) concluded that they may be the principal organism determining abundance and distribution of potential prey organisms in the bog pool system.

Normally bogs and fens have rather different flora and fauna from each other. But Cannings and Cannings (1994) concluded that there were no clear differences between the **Odonata** in these two habitat categories. Rather than responding to acidity or nutrient levels, they seem to respond to the form and structure that is similar in these two habitats.

In a study of the northern Cordilleran peatlands, Cannings and Cannings (1994) found that of 40 species there, 8 are obligate peatland inhabitants and another 4 almost always occur there. The most common genera there are *Aeshna* (**Aeshnidae**; Figure 56-Figure 62) – 11 species) and *Somatochlora* (**Corduliidae**; Figure 20-Figure 21) – 10 species, both dragonflies. The peatlands serve as **refugial** habitats (having isolated populations of once more widespread species, *i.e.* **relict populations**), with 25



species that are restricted to boreal regions and six that are **Holarctic** (majority of habitats found throughout the northern continents of the world).



Figure 56. *Aeshna juncea* (dragonfly; **Aeshnidae**) depositing eggs among the *Polytrichum* plants. It is common in small acid pools of bogs. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.

*Aeshna juncea* (dragonfly; **Aeshnidae**) (Figure 56-Figure 57) prefers the acid water of bog pools and lays its eggs among the bog bryophytes (Figure 56). *Aeshna subarctica* (Figure 27) likewise lays its eggs among *Sphagnum* (Figure 24), but in the northern Cordilleran peatlands, *A. subarctica* (Figure 58) is more commonly associated with *Drepanocladus* (*s.l.*) (Figure 59) and *Scorpidium* (Figure 60) (Cannings & Cannings 1997). Its males patrol only the floating mats in search of females; the females lay their eggs directly on these mats. *Aeshna sitchensis* (Figure 61) lives where the peatlands have filled-in depressions. The mossy fen ponds of the Yukon include *Aeshna septentrionalis* (Figure 62) and *A. subarctica* among their fauna. *Aeshna septentrionalis* females use the sedge-moss habitat for oviposition.



Figure 57. *Aeshna juncea* (dragonfly; **Aeshnidae**) naiad, a species of acid bog pools, with mosses. Photo by Tim Faasen, with permission.



Figure 58. *Aeshna subarctica* (dragonfly; **Aeshnidae**) adult, a bog dweller. Photo by Arnold Sennhauser, through Creative Commons.



Figure 59. *Drepanocladus aduncus* var. *polycarpon*, home for species of *Aeshna*, *Somatochlora*, and *Leucorrhinia* in the Yukon. Photo by Michael Lüth, with permission.



Figure 60. *Scorpidium scorpioides*, home for species of *Aeshna*, *Somatochlora*, and *Leucorrhinia* in the Yukon. Photo by Michael Lüth, with permission.





Figure 61. *Aeshna sitchensis* (dragonfly; **Aeshnidae**) adult, a bog dweller. Photo by Five Acre Geographic, through Creative Commons.



Figure 62. *Aeshna caerulea* (dragonfly; **Aeshnidae**) male adult. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

In the Czech Republic, *Aeshna caerulea* (Figure 62) is a relict, living in bogs that are drying up, suffering from nitrogen deposition, suffering from global warming – all factors contributing to the disappearance of the bogs that serve as its habitat (Dolný 2013).

Mossy fen ponds in the Yukon, Canada, provide us with some idea of the dominant **Odonata** in northern habitats (Cannings & Cannings 1997). In addition to *Aeshna* species, their distinctive fauna includes the damselfly *Coenagrion interrogatum* (**Coenagrionidae**; Figure 63-Figure 64) and dragonfly *Somatochlora sahlbergi* (**Corduliidae**; Figure 65; see Figure 66 for *Somatochlora* naiad). *Coenagrion interrogatum* is only common where the aquatic mosses are abundant. Where the peatlands have filled in depressions the habitat is characterized by *Aeshna sitchensis* (Figure 61), *Somatochlora franklini* (Figure 67), *S. kennedyi* (Figure 82), *S. whitehousei* (Figure 83), and *Leucorrhinia patricia* (**Libellulidae**; Figure 84). These dragonfly males patrol the floating mats of mosses that include *Drepanocladus* (*s.l.*) (Figure 59) and *Scorpidium* (Figure 60). *Leucorrhinia patricia* (Figure 84) is restricted to water bodies that have aquatic mosses either floating or near the surface. In Sweden, *Leucorrhinia rubicunda* (Figure 85-Figure 86) hunts for its food in bogs as adults (Scholl 2002). In the boreal ecosystems this species occurs only in transitional mires, but in the Netherlands it is the most abundant species of **Odonata** in the spring in degraded and rewetted mires (Desrochers & van Duinen 2006).



Figure 63. *Coenagrion interrogatum* (dragonfly; **Coenagrionidae**) adult, an inhabitant of mossy fen ponds in the Yukon, Canada. Photo by Jim Johnson, with permission.



Figure 64. *Coenagrion* (damselfly; **Coenagrionidae**) naiad, genus that sometimes lives in mossy fen ponds. Photo by Gerard H. Visser <www.microcosmos.nl>, with permission.





Figure 65. *Somatochlora sahlbergi* (dragonfly; **Corduliidae**) adult, a bog dweller. Photo by Mark Zekhuis, with online permission.



Figure 66. *Somatochlora metallica* (dragonfly; **Corduliidae**) naiad. Several species in this genus live in bogs. Photo by Tim Faasen, with permission.



Figure 67. *Somatochlora franklini* (dragonfly; **Corduliidae**) adult, a bog dweller. Photo by Larry deMarch, through Creative Commons.

In northern British Columbia, Canada, species are similar to those of the Yukon. In standing open water with submerged mosses provides a suitable naiad home for many species with wide ecological tolerances: *Coenagrion interrogatum* (Figure 63-Figure 64), *Aeshna septentrionalis* (Figure 62), *A. subarctica* (Figure 27), *Somatochlora kennedyi* (Figure 82), *S. septentrionalis*, *Leucorrhinia patricia* (Figure 84). In slender sedge fens with *Drepanocladus* (Figure 59), one can find *Lestes disjunctus* (Figure 101), *Coenagrion interrogatum*, *C. resolutum* (Figure 68), *Nehalennia irene* (Figure 69), *Aeshna juncea* (Figure 56-Figure 57), *Aeshna subarctica*, *Leucorrhinia hudsonica* (Figure 29), *L. proxima* (Figure 70), and *Sympetrum obtrusum* (Figure 71-Figure 72) (Cannings *et al.* 2004). In shallow sedge-moss fens, typical of patterned fens with *Drepanocladus*, *Lestes disjunctus*, *L. congener* (Figure 73), *L. forcipatus* (Figure 102), *Enallagma boreale* (Figure 74), *Coenagrion resolutum*, *Nehalennia irene*, *Aeshna septentrionalis*, *A. sitchensis* (Figure 61), *A. tuberculifera* (Figure 75), *Somatochlora brevicincta*, *S. franklini* (Figure 76), *S. kennedyi*, *S. semicircularis* (Figure 87), *S. whitehousei* (Figure 83), *Leucorrhinia hudsonica*, and *Sympetrum danae* (Figure 50-Figure 52) occur. The outer coastal bogs have a communities of *Pinus contorta* – *Empetrum nigrum* – *Sphagnum austini* (Figure 77) and *Juniperus communis* – *Trichoporum cespitosum* – *Racomitrium lanuginosum* (Figure 78). These are suitable habitats for *Lestes disjunctus*, *Enallagma boreale*, *Aeshna interrupta* (Figure 79-Figure 80), *Aeshna sitchensis*, *Cordulia shurtleffii* (Figure 53), *Somatochlora albicincta* (Figure 88), *Leucorrhinia hudsonica*, *Libellula quadrimaculata* (Figure 22), and *Sympetrum danae*. The seepages and springs of coastal fen associations with *Eriophorum angustifolium* and *Sphagnum* are typical habitats for *Tanypteryx hageni* (Figure 81), which burrows into the seepage.



Figure 68. *Coenagrion resolutum* laying eggs. Photo by D. Gordon E. Robertson, through Creative Commons.





Figure 69. *Nehalennia irene* male adult. Photo by Rsbernard, through Creative Commons.



Figure 72. *Sympetrum obtrusum* male, a species that occurs in sedge fens with *Drepanocladus*. Photo by D. Gordon E. Robertson, through Creative Commons.



Figure 70. *Leucorrhinia proxima* adult, a fen species. Photo by Ed McAskill, through Creative Commons.



Figure 73. *Lestes congener* adult. Photo by Richard Orr, with permission.

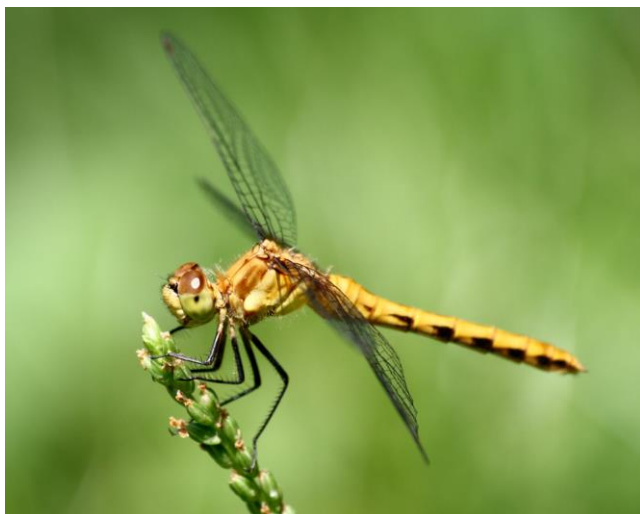


Figure 71. *Sympetrum obtrusum* female in central Connecticut. Photo by Sage Ross, through Wikimedia Commons.



Figure 74. *Enallagma boreale* adult, a species of patterned fens with *Drepanocladus*. Photo by Mike Ostrowski, through Creative Commons.





Figure 75. *Aeshna tuberculifera* adult flying, a species of patterned fens with *Drepanocladus*. Photo by Mike Ostrowski, through Creative Commons.



Figure 77. *Sphagnum austinii*, outer coastal species that is home to a number of **Odonata** species. Photo by Michael Lüth, with permission.



Figure 76. *Somatochlora franklini* male adult. Photo by Denis A. Doucet, with permission.



Figure 78. *Racomitrium lanuginosum*, outer coastal species that is home to a number of **Odonata** species. Photo by Juan Larrain, with permission.



Figure 79. *Aeshna interrupta* naiad, a species that lives in habitats with *Sphagnum austinii* and *Racomitrium lanuginosum*. Photo by Donald S. Chandler, with permission.





Figure 80. *Aeshna interrupta* adult, a species that lives in habitats with *Sphagnum austini* and *Racomitrium lanuginosum*. Photo by Kam's World, through Creative Commons.



Figure 82. *Somatochlora kennedyi* (dragonfly; Corduliidae) male adult, a species that patrols the *Sphagnum* mats to find a female. Photo by Denis A. Doucet, with permission.



Figure 81. *Tanypteryx hageni* adults mating. Photo by Roy J. Beckemeyer, with permission.



Figure 83. *Somatochlora whitehousei* (dragonfly; Corduliidae) adult, a species that patrols the *Sphagnum* mats to find a female. Photo by Jim Johnson, with permission.



Figure 84. *Leucorrhinia patricia* (dragonfly; Libellulidae) adult male, a species restricted to water bodies with mosses near the surface. Photo by Denis A Doucet, with permission.

*Somatochlora franklini* (Figure 76) patrols over *Sphagnum* (Figure 24) in bogs and over water-soaked mosses in fens, preferring spring-fed *Sphagnum* fens. *Somatochlora sahlbergi* (Figure 65) naiads (see Figure 66) live where the water is underlain with mosses. As adults they drop their eggs into the water, but again in sites underlain with mosses. Both *S. semicircularis* (Figure 87) and *S. albicincta* (Figure 88) prefer mossy substrata, the former in a sedge-moss marsh and the latter in mud-bottomed, mossy fen ponds. *Somatochlora semicircularis* (Figure 89) flies low over bogs in search of egg-laying sites among the pools; naiads develop in the spring pools and swamps (Usinger 1974).





Figure 85. *Leucorrhinia rubicunda* (dragonfly; **Libellulidae**) male, a species that hunts in bogs. Photo by Guido Gerding, through GNU Free Documentation.



Figure 86. *Leucorrhinia rubicunda* (dragonfly; **Libellulidae**) naiad on *Sphagnum*. Photo by Tim Faasen, with permission.



Figure 87. *Somatochlora semicircularis* (dragonfly; **Corduliidae**) adult, a species that prefers a mossy fen-marsh. Photo by Leslie Flint, through Creative Commons.



Figure 88. *Somatochlora albicincta* (dragonfly; **Corduliidae**) adult, an inhabitant of mud-bottomed, mossy fen ponds. Photo by Chuunen Baka, through Creative Commons.



Figure 89. *Somatochlora artica* (dragonfly; **Corduliidae**) adult; the female flies low over bogs to find a suitable place to lay eggs. Naiads develop in pools there. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

Dragonflies often deposit their eggs among bryophytes (Macan 1963), with the naiads subsequently living there (Gerson 1982). These bryophyte dwellers include *Leucorrhinia dubia* (**Libellulidae** – skimmers; Figure 90-Figure 93) from Europe (Matthey 1971) and *Calicnemia miles* (**Platycnemididae** – white-legged damselflies; Figure 94) from the Himalayan Mountains (Kumar & Prasad 1977).

Macan (1962) attempted to explain why (and how) *Leucorrhinia dubia* (Figure 90-Figure 93), a **Libellulidae** dragonfly, chose bog pools for laying eggs. He found that this genus was attracted to a white surface on the ground, but that hardly explained anything since *Leucorrhinia* species lay eggs by flying and dipping to deposit the eggs in the water during flight. Schiemenz (1954) found that it preferred a *Sphagnum* (Figure 51) pool (68%) to tap water, but considered this to be inconclusive. It is likely that water chemistry plays a role.





Figure 90. *Leucorrhinia dubia* (Libellulidae) naiad, a dragonfly species that changes color in late naiad stages to blend with the surrounding *Sphagnum* (Figure 51). Photo by Tim Faasen, with permission.



Figure 91. *Leucorrhinia dubia* (Libellulidae) emergent adult dragonfly and exuvia. Photo by Tim Faasen, with permission.



Figure 92. Female white-faced darter, *Leucorrhinia dubia* (dragonfly; Libellulidae). Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.



Figure 93. Male white-faced darter, *Leucorrhinia dubia* (Libellulidae), a bog-dwelling dragonfly. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.



Figure 94. *Calicnemis miles* (Platynemididae) adult female damselfly who often lays eggs among wet mosses in the Himalayas. Photo by Davidvraju, through Creative Commons.

The dragonfly *Leucorrhinia dubia* (white-faced darter; dragonfly; Libellulidae) (Figure 90-Figure 93) is so well adapted to the *Sphagnum* (Figure 24) habitat that the late instar naiads (immature stages) actually change color to blend with the brown and green color of *Sphagnum* (Figure 95) (Henrikson 1993). These naiads show preference for the *Sphagnum* substrate over debris in laboratory tests, a behavior that seems to permit them to be more successful in preying on aquatic pillbugs, *Asellus aquaticus* (Figure 96). Henrikson suggested that the complex habitat of *Sphagnum* serves both as shelter and as a foraging site; the *Sphagnum* apparently provides a safe habitat against predators – where large mats of this moss exist, *Leucorrhinia dubia* is able to coexist with the fish without becoming dinner.





Figure 95. *Sphagnum angustifolium* showing brown and green colors that *Leucorrhinia dubia* dragonfly naiads can mimic. Photo by Michael Lüth, with permission.



Figure 96. *Asellus aquaticus*, food of *Leucorrhinia dubia*. Photo by Niels Sloth, with permission.

*Tanypteryx hageni* (Figure 97-Figure 99) (dragonfly; **Petaluridae** – petaltails) adults are most common in alpine bogs. Naiads have been found in mosses in seepage along the west coast of USA (Usinger 1974).



Figure 97. *Tanypteryx hageni* (dragonfly; **Petaluridae**) naiad clinging to mosses. Photo by Greg Courtney, with permission.



Figure 98. *Tanypteryx hageni* (**Petaluridae**) adult, a dragonfly that lives in alpine bogs; naiads can be found among mosses in seepage. Photo by Dana Kenneth Johnson, through Creative Commons.



Figure 99. *Tanypteryx* (dragonfly; **Petaluridae**) burrows amid mosses and swamp litter. Note the holes. Photo by Greg Courtney, with permission.

Damselflies (**Zygoptera**) seem less common among the bog fauna than dragonflies. The common genus *Lestes* (**Lestidae** – spreadwings; Figure 100-Figure 102), a damselfly, includes bogs among its many habitats. In British Columbia, Canada, *Lestes disjunctus* (Figure 101) is common in several bog types whereas *L. forcipatus* (Figure 102) is uncommon in one type and absent in the others (Cannings & Simaika 2005). *Lestes forcipatus* is most common in the cold sedge and moss fens and is relatively rare in warmer habitats.



Figure 100. *Lestes viridis* (damselfly; **Lestidae**) naiad, a bog inhabitant, among *Sphagnum* mosses. Photo by Tim Faasen, with permission.





Figure 101. *Lestes disjunctus* (damselfly; **Lestidae**) adult, a species common in several types of bogs in British Columbia, Canada. Photo by Phil Myers, through Creative Commons.



Figure 102. *Lestes forcipatus* (damselfly; **Lestidae**) pair mating; the upper male clasps the female at the neck. Note the posterior ovipositor on the female. Photo by Richard Orr, with permission.

## Summary

The **Odonata** are **hemimetabolous**, having egg, naiad, and adult stages. They are comprised of dragonflies (**Anisoptera**) and damselflies (**Zygoptera**). Neither is common among bryophytes, most likely due to their large labium used for catching prey and to their large size. Nevertheless, some occur among the bryophytes as naiads, some lay their eggs there, and some gather on bryophytes to emerge to the adult stage.

The **Odonata** are common in bogs and fens, with naiads living among the many pools, sometimes darting into the dangling mosses for cover. The form and structure of the bryophytes may be important determinants in where they live. At mating time, some of the **Odonata** increase the safety of the species by forming aggregations – safety in numbers. *Aeshna* and *Somatochlora* are the most common genera in the bogs. In both the naiad and adult stages the **Odonata** are voracious carnivores and thus have a major impact, especially in the bog ecosystem.

The typical bog inhabitants include members of **Aeshnidae**, **Coenagrionidae**, **Corduliidae**, **Lestidae**, **Libellulidae**, **Platycnemididae**, and **Petaluridae**. Other families that may be found among bryophytes include **Argiolestidae**, **Cordulegastridae**, and **Gomphidae**.

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# CHAPTER 11-6

## AQUATIC INSECTS:

### HEMIMETABOLA – PLECOPTERA

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# CHAPTER 11-6

## AQUATIC INSECTS:

### HEMIMETABOLOUS INSECTS –

### PLECOPTERA



Figure 1. *Taeniopteryx* sp. naiad, a common inhabitant of stream bryophytes, especially in early stages. Photo by Bob Henricks, with permission.

#### PLECOPTERA – Stoneflies

Like the other **hemimetabolous** (incomplete metamorphosis with egg, naiad, and adult) aquatic orders, the **Plecoptera** (Figure 1) have an aquatic immature stage known as a **naiad**. They differ from the **Ephemeroptera** (Chapter 11-4) in that they consistently have only two tails (**caudal filaments**). Their gills occur in various locations but are not found in the middle of the abdomen. The gills are usually not extensive and are absent in many (Dodds & Hisaw 1924; Pennak 1953), so **Plecoptera** naiads require water with high oxygen levels (Needham 1901; Dodds & Hisaw 1924; Macan & Worthington 1951; Pennak 1953; Ward & Whipple 1959), making them good indicators of relatively clean water.

The naiads reach their greatest numbers in fast, cold mountain streams (Thorpe & Covich 1991). Although most occur in streams, a few occur in cold, **oligotrophic** (low nutrient) lakes. The naiads must climb out of the water to emerge from their exoskeleton and become adults. The adults are short-lived, but live longer than mayflies, usually several days to two weeks (Thorpe & Covich 1991). The

naiads are largely night active and appear most often in the night-time drift (Elliott 1967).

Krno and Žiak (2012) found that the number of stoneflies in West Carpathian calcareous **submontane** (ecological zone pertaining to lower slopes of mountains) rivers increased with an increase in mosses, with several genera maintaining their highest density on mosses. **Plecoptera** can use bryophytes in a number of ways. The most obvious is their use as a substrate and shelter from the flowing water. They are especially common there as young instars when the bryophytes can protect these less able swimmers from the flowing water. Many are able to obtain food there, either by preying on smaller invertebrates, by using the collected **detritus** (dead organic matter and debris) and **periphyton** (attached algae and other microorganisms), or less often by eating the mosses themselves. When it is time to emerge, they can use the bryophytes to help them climb through the surface tension and sometimes even provide a surface on which to emerge from naiad to adult, spread their wings, and fly away (Figure 2). Finally, these adults may return to the mosses to lay their eggs (Figure 3).





Figure 2. *Isoperla* sp. emerging, using emergent vegetation for support and to pump fluids into its wings. Photo by Richard Bartz, through Creative Commons.



Figure 3. **Plecoptera** eggs, laid here on a rock. Photo by Wendy Brown <[www.gunnisoninsects.org](http://www.gunnisoninsects.org)>, with permission.

But the presence of some stoneflies as major inhabitants among bryophytes may be the preference of both the stonefly and the bryophyte for the same habitat. Two of the most common families, **Leuctridae** and **Nemouridae**, prefer cooler upstream stations in a southern Ontario, Canada, stream (Harper 1973), a habitat type also very suitable for bryophytes. Both benefit from clean, cool water with rapid flow and a rocky substrate.

### Predation Retreat or Restaurant?

Many of the stoneflies are carnivores on a microscale. Since they are small, living in water torrents, they need a food source that is close by. For many, bryophytes can provide that habitat, a place where they can move about, safe from the current, and find an abundance of yet smaller prey items. For them, it is a restaurant with an impressive menu, but it is also a retreat from larger predators. For the yet smaller insects – well, it might be easier to escape predators, but it might also be a trap where they are eaten.

Elliott (2003) used *Baetis* naiads as experimental prey items to determine the effect on stonefly interactions, including three known bryophyte dwellers [*Perlodes microcephalus* (Figure 80), *Isoperla grammica* (Figure

75), *Dinocras cephalotes* (Figure 42)]. They found that feeding was density dependent, with the number of *Baetis* being eaten dependent on the number provided (between 20 and 200). Handling time was not affected by predator density or presence of other predators. However, attack rate decreased as predator density decreased. As expected, prey consumption also decreased as predator density decreased, with the severity of competition with a paired species being similar to that with the same species.

### Food Relationships

Gerson (1982) suggested that **Plecoptera** may feed on aquatic bryophytes, but Stern and Stern (1969) found that detritus was the most common food for stoneflies, and detritus is common among the mosses. Jones (1950) examined the gut contents of **Plecoptera** naiads in the River Rheidol. Four of the six species studied had mosses (*Fontinalis antipyretica*, Figure 4) in the gut: *Chloroperla tripunctata* (see Figure 15-Figure 16), *Leuctra hippopus* (Figure 5), *Protonemura meyeri* (Figure 20), *Amphinemura sulcicollis* (= *A. cinerea*; Figure 19). The highest number with mosses in the gut was 12 out of 100 for the species *Protonemura meyeri*. But the question remains, were the mosses digested or just eaten for their adhering periphyton and detritus?



Figure 4. *Fontinalis antipyretica*, food for a number of **Plecoptera** naiads. Photo by Kristian Peters, with permission.



Figure 5. *Leuctra hippopus*, member of a genus that is common among stream bryophytes. Photo by Niels Sloth, with permission.



Small streams in the Tolvajärvi region of the Russian Karelia are characterized by higher nutrient and iron concentrations as well as a large amount of organic matter compared to the lake outlet. These small streams are dominated by the mosses *Fontinalis* (Figure 4) and *Hygrohypnum* (Figure 6) like the lake outlet habitats, but also the leafy liverworts *Scapania* sp. (Figure 7), *Marsupella* spp. (Figure 8), and *Jungermannia* sp. (Figure 9). The dominant moss inhabitants are stonefly shredders in the genera *Nemurella* (Figure 10-Figure 11), *Nemoura* (Figure 12-Figure 13), and *Leuctra* (Figure 5). Shredders typically eat leaf litter. Unfortunately, we have no data to indicate what they were shredding among the bryophytes.



Figure 6. *Hygrohypnum alpinum*, habitat for stonefly shredders in the Russian Karelia. Photo by Michael Lüth, with permission.



Figure 7. *Scapania undulata*, a common emergent liverwort in streams and home for a number of insects. Photo by David T. Holyoak, with permission.



Figure 8. *Marsupella aquatica*, a stream insect habitat. Photo by Michael Lüth, with permission.



Figure 9. *Jungermannia exertifolia* ssp. *cordifolia*, home for stream insects. Photo by Michael Lüth, with permission.



Figure 10. *Nemurella pictetii* naiad, a bryophyte inhabitant. Photo by Urmas Kruus, with permission.



Figure 11. *Nemurella pictetii* adult, a stonefly whose naiads live among bryophytes. Photo by Tim Faasen, with permission.

## Typical Fauna

When I examined the bryophytes from the Appalachian Mountain streams in Pennsylvania, Maryland, and West Virginia, USA, I found that the stoneflies were mostly small members in the genera *Nemoura* (Figure 12-Figure 13), *Allocapnia* (Figure 14), and *Leuctra* (Figure 5). Berthélemy (1966) found the moss-dwelling species generally to be smaller than those living among stones. Stern and Stern (1969) likewise found that the bryophytes



served the smaller stoneflies, especially *Nemoura* (Figure 12), and acted as a nursery for the young of other Plecoptera.



Figure 12. *Nemoura* sp. naiad, a common bryophyte inhabitant in streams. Photo by Bob Henricks, with permission.



Figure 13. *Nemoura* cervical gills that enable the species to live in somewhat low oxygen. Photo by Bob Henricks, with permission.



Figure 14. *Allocapnia* naiad, common among stream bryophytes in its early (small) stages. Photo by Bob Henricks, with permission.

Frost (1942) found that the moss fauna differed between acid and alkaline waters of the River Liffey, Ireland. In the acid areas, *Protonemura* (Figure 20),

*Amphinemura* (Figure 19), *Leuctra* (Figure 5), and *Chloroperla* (Figure 15-Figure 16) dominated the mosses, whereas in the alkaline waters only *Isoperla* (Figure 17) was common. This is consistent with my finding of *Nemouridae* and *Leuctra* among bryophytes in the acidic Appalachian Mountain, USA, streams (Glime 1968).



Figure 15. *Chloroperla* adult, a genus whose naiads are common in acid stream water. Photo by G. Böhne, through Creative Commons.



Figure 16. *Chloroperlidae* naiad, a group dominant among mosses in acid water. Photo by Bob Henricks, with permission.



Figure 17. *Isoperla* naiad, the only genus common among mosses in alkaline streams. Photo by Bob Henricks, with permission.



In a study of a cool mountain stream of central Japan, Tada and Satake (1994) found that the density of many **Plecoptera** was greater among bryophytes than in bare rock areas. These included *Scopura* sp. (**Scopuridae**; Figure 18) (also known from glaciers), *Amphinemura* (Figure 19), *Protonemura* (Figure 20), *Isoperla towadensis* (see Figure 21), and *I. nipponica*.



Figure 18. *Scopura longa*, a species whose naiads live on bryophytes in cold mountain streams in Japan. Photo by Shiro Kohshima, with permission.



Figure 19. *Amphinemura sulcicollis* adult; naiads of this genus are common among bryophytes in cool mountain streams of Japan. Photo by James K. Lindsey, with permission.



Figure 20. *Protonemura meyeri* naiad, member of a genus that is common among bryophytes in cool mountain streams in Japan. Photo by James K. Lindsey, with permission.



Figure 21. *Isoperla carbonaria* adult, member of a genus that occurs among stream mosses in Japan. Photo through Creative Commons.

## Reproductive Use

Stoneflies can use bryophytes for emergence and egg laying. But in some cases the bryophytes are used in mating behavior. Some stoneflies have an interesting way to attract females. They wait on the shoreline of streams or lakes for the females to emerge from the water and escape their naiad skins. Then they drum their abdomens on such available objects as rocks, dry leaves, and mosses, presumably to attract females (Erman 1984). Mating takes place on the ground (Brinck 1949).

Life cycles are typically attuned to the climate, permitting the insects to overwinter or survive dry spells. These life cycle needs thus dictate part of the required niche. Hynes and Hynes (1975) reported that the life cycle of Australian species were less rigid than those of stoneflies in the Northern Hemisphere. Hence, they tend to have broader ecological niches.

## Capniidae – Small Winter Stoneflies

This family of medium-sized stoneflies (usually 5-10 mm) is poorly represented among bryophytes, despite being one of the largest families with about 300 species (Capniidae 2014). In the mid-Appalachian Mountains I found only *Allocaenia* (Figure 22) represented among the stream bryophytes (Glime 1968). *Allocaenia* adults (Figure 23-Figure 24) emerge in winter (Ross & Ricker 1971). The males are wingless, and these stoneflies often can be seen on the snow (Figure 23), wandering as much as 100 m from their naiad stream. Even the females have reduced wings, poorly developed wing venation, and reduced **thoracic sclerites** (plates forming the outer cover of an arthropod thorax) associated with the flight muscles, so their dispersal ability may be more limited than in other genera. Nevertheless, they do have the ability to disperse downstream, with **gravid females** (females carrying eggs) occurring in the drift and riding on floating ice. And adults may disperse upstream by **planing** – climbing up trees and structures, then gliding to a new location.





Figure 22. *Allocapnia pygmaea* male naiad, member of a genus that spends young instars among mosses. Photo by Donald S. Chandler, with permission.



Figure 23. *Allocapnia pygmaea* male adult, a winter emerger. Photo by Donald S. Chandler, with permission.



Figure 24. *Allocapnia pygmaea* female adult, a winter emerger that can ride the ice downstream. Photo by Donald S. Chandler, with permission.

Bryophytes can be an important location for finding food for some members of the **Capniidae**. Production of *Capnia vidua* (Figure 25) naiads in the High Tatra of

Slovakia is dependent on the detritus collected by the mosses, making the mosses a suitable habitat for them (Krnó & Sporka 2003). This genus also contains members that emerge and flit about on the snow (Figure 26).



Figure 25. *Capnia* naiad, a frequent bryophyte dweller. Photo by Jason Neuswanger, with permission.



Figure 26. **Capniidae** adult on snow. Photo by Bob Armstrong, with permission.

### Leuctridae - Rolled-winged Stoneflies

This is likewise a family of medium size (5-13 mm). They are long, narrow stoneflies of streams. Berthélemy (1966) suggested that *Leuctra* (Figure 5, Figure 30-Figure 31) might be a **muscirole** (living in association with mosses). The genus is known as the rolled-wing stoneflies because of the manner in which the wings curve around the adult body (Figure 27). However, a number of species are **apterous** (without wings) as adults.



Figure 27. *Leuctra fusca* adult showing rolled wings. Photo by Malcolm Storey <[www.discoverlife.org](http://www.discoverlife.org)>, through Creative Commons.

The genus *Leuctra*, along with the **Nemouridae**, are among the most common naiads among the European bryophytes (Carpenter 1927; Frost 1942; Illies 1952).

In the mid-Appalachian Mountain, USA, streams, *Leuctra* was a fairly common bryophyte inhabitant, occurring among *Fontinalis dalecarlica* (Figure 78), *Hygroamblystegium fluviatile* (Figure 89) – *Platyhypnidium riparioides* (Figure 62), and most abundant on the leafy liverwort *Scapania undulata* (Figure 7) (Glime 1968). These naiads are relatively small, and those on bryophytes tend to be the youngest, *i.e.* smallest, making species identification nearly impossible. In Toliver Run, Garrett Co., MD, USA, this genus reaches a peak in June, but reaches a secondary peak in December, suggesting the presence of two different species. Mackereth (1957) likewise reported seasonal peaks that differed among species in this genus. I also found one adult in my collections, suggesting that they may emerge among the bryophytes (Glime 1968).

Wulfhorst (1994) examined the relative abundance of **Leuctridae** in mosses and in **interstitial** (spaces between individual sand grains in the soil or aquatic sediments) spaces in the **hyporheic** zone (beneath the bed of a river or stream) of two streams in the Harz Mountains of West Germany. She found that the **Leuctridae** were more abundant among the mosses at most collection stations, but that they were also abundant in the interstitial spaces of the **hyporheic** zone at 10 and 20 cm depths (Figure 28).

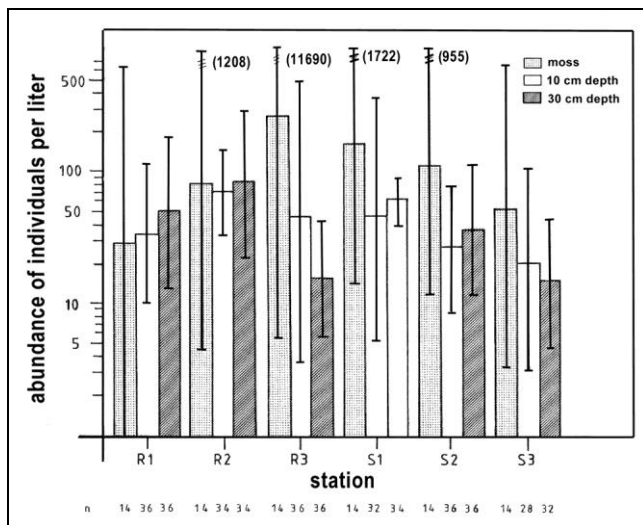


Figure 28. Mean abundance  $\pm$  95% CI of **Leuctridae** in moss clumps compared to depths of the hyporheic zone in two streams in the Harz Mountains, West Germany. Redrawn from Wulfhorst 1994.

Several species of *Leuctra* [*L. armata* (Figure 29), *L. autumnalis*, *L. pusilla*] contribute to the production of Hincov Brook, High Tatra, Slovakia (Krno & Sporka 2003). Krno and Sporka concluded that these detritivorous stoneflies depend on the mosses to trap the coarse **benthic** (bottom) organic matter needed for their diet. The cold period produces higher productivity, attributable to reduction in feeding by brown trout.

In Radíkovský Brook in the Czech Republic, Jezberová (2003) found that substrate explains a large fraction of the data variability for **Ephemeroptera** and **Plecoptera**. Bryophytes play an important role for several species of *Leuctra* in that stream. Among these *Leuctra albida* and *L. teriolensis* highly prefer a bryophyte substratum.



Figure 29. *Leuctra armata* adult, a species whose naiads depend on mosses to trap detritus for their food. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

*Leuctra* is herbivorous (Frison 1929). Jones (1949) found that *Leuctra fusca* (= *L. fusciventris*; Figure 30) and *L. geniculata* (Figure 31) had *Fontinalis antipyretica* (Figure 4) leaf fragments in about half the gut analyses from calcareous streams in South Wales. In the River Rheidol, UK, Jones (1950) found *Fontinalis* fragments in 8 of the 20 guts in which contents could be identified. Percival and Whitehead (1929) reported that several species of UK *Leuctra* had mosses in their guts. Dangles (2002) considered members of this genus to be generalist feeders, including bryophytes among their food choices.



Figure 30. *Leuctra fusca*, a consumer of *Fontinalis antipyretica* in South Wales. Photo by Louis Boumans, through Creative Commons.



Figure 31. *Leuctra geniculata* naiad, a consumer of *Fontinalis*. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

In the River Rajcianka, Slovakia, submerged bryophytes are home to *Leuctra hippopus* (Figure 5), *L. inermis* (Figure 32), and *L. rauscheri* (Krno 1990). Most are restricted to the submerged portions, but *L. rauscheri* is able to live above the water surface among emergent bryophytes.





Figure 32. *Leuctra inermis* adult, a species whose naiads live among bryophytes in River Rajciana, Slovakia. Photo by James K. Lindsey, with permission.

### Nemouridae – Spring Stoneflies

This is a family of small to medium stoneflies (5-20 mm). Wulfhorst (1994) examined the relative abundance of **Nemouridae** in mosses and in interstitial spaces in the hyporheic zone of two streams in the Harz Mountains of West Germany. She found that the **Nemouridae** were much more abundant among the mosses at all collection stations (Figure 33) than on other substrata. Furthermore, she found that most of them avoided 10 and 30 cm depths.

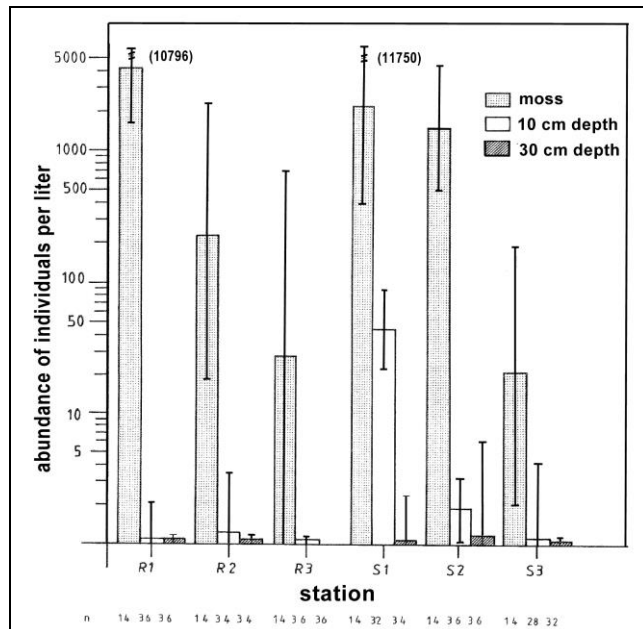


Figure 33. Mean abundance  $\pm$  95% CI of **Nemouridae** (*Amphinemura*/*Protonemura*) in moss clumps in two streams in the Harz Mountains, West Germany. Redrawn from Wulfhorst 1994.

In the Appalachian Mountain streams I studied, **Nemouridae** (Figure 34-Figure 37) were the most frequent and abundant of the Plecoptera, reaching their greatest numbers on turfs of *Scapania undulata* (Glime 1968, 1994). The species included *Nemoura sinuata* (Figure 34), *Soyedina vallicularia*(?) (Figure 35-Figure 36), and *Amphinemura nigritta* (Figure 37). These occurred at all instar stages and most likely emerged to adulthood from the bryophyte mat.



Figure 34. *Nemoura sinuata* adult, a species that lives among bryophytes as naiads in Appalachian Mountain, USA, streams. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.



Figure 35. *Soyedina vallicularia* naiad, a common inhabitant (or a similar species) among bryophytes in Appalachian Mountain, USA, streams. Photo courtesy of the State Hygienic Laboratory at the University of Iowa, with permission.



Figure 36. *Soyedina vallicularia* adults. Photo by R. E. DeWalt, through Creative Commons.



Figure 37. *Amphinemura nigritta* naiad, a common nemourid among Appalachian Mountain stream mosses. Photo by Tom Murray, through Creative Commons.



In subarctic Fennoscandia, some members of *Nemoura*, such as *N. viki*, deposit their eggs on damp mosses, although most are deposited in the water (Lillehammer 1986, 1988). *Nemoura viki* and *N. arctica* differ in their life cycles and in their preferred biotopes, effectively separating their niches. The temperature tolerance range of the eggs of *N. arctica* is wider. For the latter, temperature nevertheless has a profound effect on naiad development time. After 700 days at 4°C, the naiads still are not ready for emergence. On the other hand, at 16°C, the naiads can reach maturity in 120 days.

Wu (1923) reported that *Nemoura* (Figure 12) was a herbivore, eating mostly desmids and diatoms; he never found animal tissue in the diet. On the other hand, Chapman and Demory (1963) found that *Nemoura* in two Oregon, USA, streams consumed mostly detritus. Leberfinger and Bohman (2010) found that *Nemoura* sp. chose algae and shrubby cinquefoil when offered leaves of birch, Swedish whitebeam, shrubby cinquefoil, dead and fresh grass, moss, and algae. The least consumed food was dead grass, despite its being the most abundant food in the stream. Even though the fresh food had the highest carbon to nitrogen content, it was the dead leaves of the shrubby cinquefoil that was the food of choice, suggesting that perhaps fungal or bacterial decomposer organisms might have been important in the diet. A word of caution – the genus *Nemoura* has since been divided into multiple genera, so these generic designations may be misleading; The designation by Leberfinger and Bohman (2010) is recent and is most likely reflective of modern nomenclature.

*Nemoura flexuosa* (Figure 38), *N. marginata*, and *N. monticola* all live among bryophytes in the River Rajciana, Slovakia (Krno 1990). *Nemoura monticola* seems to be restricted to submerged bryophytes, whereas the other two species are able to move about within the wet bryophyte clumps above that water line.



Figure 38. *Nemoura flexuosa* naiad, a bryophyte dweller in Europe. Photo by Niels Sloth, with permission.

*Nemoura cinerea* (Figure 39-Figure 40) survives low oxygen levels better than *Diura bicaudata* (Perlodidae; Figure 41) and *Dinocras cephalotes* (Perlidae; Figure 42) (Benedetto 1970), perhaps explaining the ability of *N. cinerea* to live among mosses with heavy sedimentation. Furthermore, *N. cinerea* was the only species among the four tested that did not display undulations as oxygen levels became low (Benedetto 1970). *Amphinemura* has a cluster

of pompon-like gills in each side of the neck (Figure 43). But *N. cinerea*, like all *Nemoura* species, lacks this group of gills and does not have the ability to acclimate and change its low oxygen response to temperature (Nagell & Fagerstrom 1978).



Figure 39. *Nemoura cinerea* mating, a species whose naiads are unable to acclimate to low oxygen but that is a better survivor in these conditions than *Diura bicaudata* and *Dinocras cephalotes*. Photo by James K. Lindsey, with permission.



Figure 40. *Nemoura cinerea* naiad, lacking cervical gills. Photo by James K. Lindsey, with permission.



Figure 41. *Diura bicaudata* adult, a species that is not able to survive well in low oxygen. Photo by Pentti Ketola, through free usage.





Figure 42. *Dinocras cephalotes* naiad, a species that does not survive low oxygen levels, a factor that may keep it out of some bryophyte clumps. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.



Figure 44. *Protonemura hrabei* naiad, a Slovakian moss dweller. Photo by J. C. Schou, with permission.



Figure 43. *Amphinemura* cervical gills, adapting it to low oxygen levels. Photo by Bob Henricks, with permission.



Figure 45. *Protonemura intricata* adult, a species whose naiads live among bryophytes. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

**Nemouridae** (Figure 39-Figure 43) are very tolerant of low temperatures, achieving a growth rate of 1.6% per day at a mean water temperature of only 0.6°C in a subalpine lake in the Jotunheimen Mountains of southern Norway (Brittain 1983). This is also a typical stream temperature in northern Appalachian Mountain streams of New Hampshire in winter (Glime, unpubl data).

Krno (1990) reported several species of *Protonemura* on submerged bryophytes in the River Rajcianka, Slavakia: *Protonemura auberti*, *P. autumnalis*, *P. hrabei* (Figure 44), *P. intricata* (Figure 45), *P. praecox* (Figure 46-Figure 48). Of these, *Protonemura auberti*, *P. autumnalis*, *P. hrabei*, and *P. intricata* also occurred on emergent wet bryophytes. Krno and Žiak (2012) reported that *Protonemura* was one of the taxa that was greatest on bryophytes in calcareous submontane rivers of the West Carpathians. *Protonemura* is likewise abundant among mosses in the Pyrénées (Berthélemy 1966), causing Berthélemy to consider *P. pyrenaica* to be a **muscirole** (living in association with mosses).



Figure 46. *Protonemura praecox* emergent female adult before wings are inflated. Photo by Walter Pfliegler, with permission.





Figure 47. *Protonemura praecox* emergent female adult attempting to inflate her wings. Photo by Walter Pfliegler, with permission.



Figure 48. *Protonemura praecox* female adult with fully inflated wings. Photo by Walter Pfliegler, with permission.

*Protonemura meyeri* (Figure 20) is common on *Fontinalis* (Figure 4) and other mosses in Europe (Hynes 1941; Costello 1988). This is a species that not only lives among bryophytes below the water surface, but also is able to go above the water level in the protective moisture of the bryophytes (Krno 1990). Frost (1942) concluded that *P. meyeri* lives among mosses throughout its entire naiad life. Not only did Hynes (1941) find that moss is the primary habitat for *P. meyeri*, but Frost (1942) found that in the River Liffey it feeds almost entirely on mosses. However, Jones (1950) found *Fontinalis* in the guts of only 12 out of 32 *Protonemura meyeri* and in 2 out of 43 *Amphinemura sulciollis* (Figure 19) in the River Rheidol, UK. Availability of moss vs other food choices influence which the stoneflies will eat.

On the other hand, Dangle (2002) considered *Protonemura* to be a generalist, including mosses among its food selections. But Dangle also cautioned against making generalizations from one species to another within a genus, even when the mouth parts were essentially the same. Krno and Sporka (2003) found that mosses were important for *P. montana* and *P. nimborum* because of the coarse benthic organic matter that accumulated there, providing both a stable habitat and a detrital food source.

Kamler (1967) found large numbers of *Protonemura nitida* among mosses in the early naiad stages. Bottová and Derka (2013) found that *P. nitida* was a significant contributor to the biomass in a **karstic** (limestone terrain characterized by sinks, ravines, and underground streams) spring in the West Carpathians. Its numbers reached 13,585 per m<sup>2</sup> in moss there, making them the most abundant stonefly. Steiner (1991) was surprised to find that when the surface film in *Fontinalis antipyretica* (Figure 4) was removed, small *P. nitida* fed on the leaf interior, but larger naiads tore the leaves, becoming moss shredders.

In the calcareous submontane rivers of the West Carpathians, *Amphinemura* was in its greatest abundance on mosses (Krno & Žiak 2012). Percival and Whitehead (1929) found *Amphinemura sulciollis* (Figure 19) would occupy both thick and loose mosses, but it is much more abundant in the tracheophyte *Potamogeton* (Figure 49). Butcher *et al.* (1937) commented that it is probable that all the naiads belonged to this species, alluding to the difficulty in identifying the young instars. Frost (1942) found only two individuals of this species among the mosses in the alkaline station, but over 2000 at the acid water station. In their experiments, Willoughby and Mappin (1988) found that the tolerance of low pH by *Amphinemura sulciollis* from acidic streams in the watershed of the River Duddon was similar to that of the mayfly *Serratella ignita* (Figure 1). It is interesting that *A. sulciollis* slightly increases the percentage of detritus in its diet as it grows rather than increasing the moss component, as is common among other stoneflies and mayflies (López-Rodríguez *et al.* 2008). Nevertheless, mosses appear to be important components of the habitat for *A. sulciollis* as evidenced by its presence in thirteen localities on the Isle of Man where mosses or overhanging grass were present (Hynes 1952). In North America, *A. nigrilla* (Figure 50) occurs among bryophytes in the mid-Appalachian Mountain streams, inhabiting all the major bryophytes there: *Fontinalis dalecarlica* (Figure 78), *Hygroamblystegium fluviatile* (Figure 89) – *Platyhypnidium riparioides* (Figure 62), and *Scapania undulata* (Figure 7) (Glime 1968).



Figure 49. *Potamogeton gramineus*, a genus that is a common home for *Amphinemura sulciollis*, also a moss dweller. Photo by Kristian Peters, with permission.





Figure 50. *Amphinemura nigritta* naiad, a common bryophyte inhabitant in Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

In streamside mosses like *Cratoneuron* (Figure 51), the stonefly *Nemurella pictetii* (Figure 10-Figure 11) may reach 16,500 individuals per square meter in a Danish spring (Lindegård *et al.* 1975), and Thorup (1963) considered it to prefer mosses as a substrate. This species not only occurs in springs, but is among the few moss dwellers that are also common in lakes (Kamler 1967). Its adaptability to climate changes and habitat differences is seen in its ability to have both **bi-** and **trimodal** emergence patterns (having 2 and 3 peaks, respectively), coupled with partial **bivoltinism** (two broods per year), in Central Europe (Wolf & Zwick 1989), representing the only confirmed multivoltinism in a stonefly. Its emergence threshold temperature of 8°C prevents it from emerging when freezing danger is still likely. Rather than relying on seasonal life cycle cues, this species seems to be regulated by temperature, registered as accumulated degree days and an emergence temperature threshold.



Figure 51. *Cratoneuron filicinum* where *Nemurella pictetii* lives on springs and streamside. Photo by Michael Lüth, with permission.

*Zapada cinctipes* (= *Nemoura cinctipes*; Figure 52) was most abundant in the upper reaches of Trout Creek, Utah, USA, where the substrate was densely covered with the moss *Hygrohypnum bestii* (Figure 53) (Hales & Gaufin 1971). *Zapada columbiana* (Figure 54), a native of subalpine streams in Calgary, Canada, has a three-year life

cycle (Mutch & Pritchard 1984, 1986). The naiads live primarily on boulders and cobble among mosses (Clifford 2014). Despite their long life cycle, they only grow during the ice-free season (Mutch & Pritchard 1986). The females do not move upstream to lay eggs (Mutch & Pritchard 1984). Of the six females examined, their egg production ranged 800-1200 eggs each (Mutch & Pritchard 1986). These eggs hatch before winter so that the young naiads spend the first winter living among the mosses. Nevertheless, the eggs of these stoneflies develop best at lower temperatures.



Figure 52. *Zapada cinctipes* naiad, a species common where *Hygrohypnum bestii* is present in Trout Creek, Utah, USA. Photo by Bob Armstrong, with permission.



Figure 53. *Hygrohypnum bestii*, home of the stonefly *Zapada cinctipes*. Photo by Robin Bovey, with permission through Dale Vitt.



Figure 54. *Zapada columbiana* adult on snow. Photo by Bob Newell, with permission.



Although *Zapada columbiana* (Figure 54) lives for three years in the rocky streams of the Alberta, Canada, Rocky Mountains, some naiads may complete their life cycle in two years (Mutch & Pritchard 1984). Important to these naiads is the food available to them. Mutch and Pritchard found that at any time during their growth season (June to November) at least 50% of them were living among the mosses covering the boulders or cobble in riffles. Furthermore, mosses are the predominant food in the gut for these shredders, but during winter highly conditioned conifer detritus becomes the predominant component. In experiments these naiads grow better on a moss diet than on the leaves of the willow *Salix glauca*.

## Notonemouridae

This New Zealand/southern Africa family is another stonefly addition to the moss fauna and is not known from the Northern Hemisphere. All the genera are endemic to New Zealand except *Notonemoura* (McLellan 1991). They are typical of cool, high elevation lakes and rivers (Notonemouridae 2015), but some have terrestrial naiads and others have naiads that spend their early instars in the water and later instars on land, and some live in lowlands (McLellan 1991). They are herbivores and detritivores. Their enlarged hind femora helps them to climb vertical surfaces against flowing water (Notonemouridae 2015). The females lay their sticky eggs in the crevices of logs and rocks. These are small stoneflies (5-8 mm) and are mostly leaf shredders (Picker *et al.* 2004).

*Notonemoura latipennis* occurs in bog pools and bog outlet streams (McLellan 1991). *Spaniocercoides hudsoni* (see Figure 55) naiads live in *Sphagnum* bogs (Figure 56-Figure 57) (McLellan 2005). *Spaniocerca zelandica* naiads live in streams under stones or fallen logs or hidden among mosses or leaf litter (Winterbourn 1968).



Figure 55. *Spaniocercoides philpotti* naiad, member of a genus that lives in bogs and in streams among mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.

## Chloroperlidae – Green Stoneflies

Members of this family are medium in size (10-20 mm) and typically green as adults (Figure 58). *Chloroperla tripunctata* (see Figure 59) occasionally eats fragments of *Fontinalis* (Figure 4), but Jones (1950) reported only 3 specimens out of 113 with this moss in their guts in the River Rheidol, UK.



Figure 56. Bog in Fiordland, NZ. Photo through Creative Commons.



Figure 57. *Sphagnum crispum*, a common *Sphagnum* species in New Zealand. Photo by Janice Glime.



Figure 58. **Chloroperlidae** exuviae (shed exoskeletons) and adults showing the green color of the adults. Photo by Jason Neuswanger, with permission.





Figure 59. **Chloroperlidae** naiad, a family where some members occasionally eat *Fontinalis*. Photo by Bob Henricks, with permission.

In the High Tatra of Slovakia, *Siphonoperla neglecta* (Figure 60) depends on mosses that trap the coarse benthic detritus that serves as their food (Krno & Sporka 2003). The moss helps them to avoid predation by the brown trout until the cold season when the trout cease feeding actively.



Figure 60. *Siphonoperla torrentium* mating; *Siphonoperla neglecta* escapes brown trout predation by hiding among mosses. Photo by James K. Lindsey, with permission.

## Taeniopterygidae – Winter Stoneflies

The Taeniopterygidae are among the small to medium (10-20 mm) bryophyte-dwelling stoneflies. These shredders and detritivores prefer cold, clear running water of large streams and rivers (Entz 2006). They emerge in winter and are not among the bryophytes year-round because they are very sensitive to warm temperatures and require high oxygen levels.

The genus *Taeniopteryx* (Figure 61) commonly develops among mosses (Berthélemy 1966). It is common in some mid-Appalachian Mountain streams among *Hygroamblystegium fluviatile* (Figure 89) – *Platyhypnidium riparioides* (Figure 62) clumps, seemingly either abundant or absent. (Glime 1968). This species disappears from the bryophytes as it grows and is never present in older stages. Krno and Žiak (2012) reported that *Taeniopteryx auberti* is one of the taxa that reaches its greatest abundance on mosses in calcareous submontane

rivers of the West Carpathians. Tiny naiads of *Taeniopteryx nebulosa* (Figure 61) are common among *Platyhypnidium riparioides* in Britain (Langford & Bray 1969). Hubault (1927) considered *Taeniopteryx hubaulti* to be a strong muscicole.



Figure 61. *Taeniopteryx nebulosa* naiad, member of a genus that is common among *Platyhypnidium riparioides* in the UK. Photo by Niels Sloth, with permission.



Figure 62. *Platyhypnidium riparioides*, home of *Taeniopteryx nebulosa*. Photo by Michael Lüth, with permission.



*Brachyptera risi* (Figure 63) in a Dartmoor stream was confined to mosses on the sides of boulders in the stream (Elliott 1967). Costello (1988) found it both widespread and abundant among mosses in Irish streams. Langford and Bray (1969) found larger nymphs of this species throughout the year on the mosses *Platyhypnidium riparioides* (Figure 62) and *Fontinalis antipyretica* (Figure 4), two species that usually did not occur together, in British lowland streams. Dangles (2002) reported *Brachyptera seticornis* as specializing on algae and bryophytes for its food.



Figure 63. *Brachyptera risi* naiad, a species confined to mosses in a Dartmoor stream. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

## Perlidae – Common Stoneflies

The **Perlidae** are larger than members of the previous families, reaching 20-50 mm as adults. Although their distribution is nearly worldwide, they are most abundant in eastern North America (Perlidae 2013). Although they typically occur in cool, clear medium-sized to large streams, they can occur in quiet waters. When water is not moving over their bodies, they undulate the body to increase oxygen exchange. They are predators that engulf their prey.

Krno and Žiak (2012) reported that the perlid genus *Dinocras* reached its greatest abundance among mosses, compared to other substrata, in calcareous submontane rivers of the West Carpathians. Berthélemy (1966) considered *Dinocras* to be a muscicole, suggesting that the mosses help to stabilize the habitat for *Dinocras cephalotes* (= *Perla cephalotes*) (Figure 42). *Dinocras cephalotes* is one of the largest stoneflies in the Shropshire Hill Stream, UK, and is found mostly in streams and rivers where mosses cover stable stones (Arnold & Macan 1969). Hynes (1941) similarly found that it was much more common where the substrate was stable and moss-covered. And *Dinocras cephalotes* occasionally ingests mosses, including *Fontinalis antipyretica* (Figure 4) (Percival & Whitehead 1929; Jones 1949). But more importantly, at least in North Wales, the *D. cephalotes* hung out near where the triclads (flatworms) were abundant, forcing the triclads to live exclusively in dense patches of moss (Wright 1975).

In trout streams of Yellowstone National Park, USA, one could find *Hesperoperla pacifica* (Figure 64) among mosses and the green alga *Cladophora* (Figure 65) (Muttkowski & Smith 1929). This medium-sized species is a carnivore, but Muttkowski and Smith did find mosses in many of the guts, perhaps taken along with a grab for an insect prey.



Figure 64. *Hesperoperla pacifica* naiad, a moss inhabitant in trout streams in Yellowstone. Photo by Arlen Thomason, with permission.



Figure 65. *Cladophora*, habitat, along with mosses, for *Hesperoperla pacifica*. Photo by Yuuji Tsukii, with permission.

In the eastern USA, one can find a different array of **Perlidae** among the stream bryophytes. In the Appalachian Mountains, I found *Acroneuria* (Figure 66), *Agnatina capitata* (Figure 67), *Perlesta placida* (Figure 68-Figure 69), and *Paragnetina* (Figure 70) (Glime 1968). *Acroneuria carolinensis* (Figure 66) in Panther Creek, West Virginia, USA, clings to mosses, sand, rocks, and stems of *Rhododendron* (Schmidt & Tarter 1985). I often found this genus among the bryophytes in Appalachian Mountain streams (Glime 1968).





Figure 66. *Acroneuria carolinensis* naiad, a species that clings to mosses and other things in its native streams. Photo by Bob Henricks, with permission.



Figure 67. *Agnetina capitata* naiad, a species that sometimes occurs among *Fontinalis* species. Photo by Donald S. Chandler, with permission.



Figure 68. *Perlesta placida* adult, a species whose naiads sometimes occur among bryophytes in the Appalachian Mountains. Photo by Jason Neuswanger, with permission.



Figure 69. *Perlesta nelsoni* naiad, a New Hampshire, USA, species in a genus that sometimes occurs among stream bryophytes. Photo by Donald S. Chandler, with permission.



Figure 70. *Paragnetina immarginata* naiad, member of a genus that sometimes occurs among bryophytes in Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

### Perlodidae – Springflies & Yellow Stones

Like the **Perlidae**, the **Perlodidae** tend to be somewhat larger than the previous families (10-50 mm). The adults hatch in April to June and the eggs provide **diapause** (period of suspended development; physiological dormancy) during the warmer months, making the naiads absent from their native streams at that time because they have only one generation per year (Perlodidae 2014). Like the **Perlidae**, they are mostly engulfing predators, but some are scrapers and collector-gatherers. In addition to their diet of small invertebrates, at least some eat plant material, especially when they are young.

This is not a common family among moss dwellers, but in their study of an Idaho, USA, stream, Maurer and Brusven (1983) found a species of *Cultus* (Figure 71) to be common in clumps of *Fontinalis neomexicana* (Figure 72) as well as on the mineral substrate. Naiads climb out of the water and emerge on nearby rocks and vegetation (Figure 73).



Figure 71. *Cultus verticalis* naiad, from a genus that is common among *Fontinalis neomexicana* in Idaho, USA, streams. Bryophytes may also provide emergence sites. Photo by Tom Murray, through Creative Commons.





Figure 72. *Fontinalis neomexicana* in a dry streambed; home of *Cultus verticalis* naiads. Photo by Janice Glime.



Figure 73. **Perlodidae** emerged on rock at edge of stream. Photo by Janice Glime.

Krno and Žiak (2012) reported that *Isoperla* is one of the taxa that is at its greatest abundance on mosses in calcareous submontane rivers of the West Carpathians. *Isoperla petersoni* is abundant in the upper 100 m of a Utah stream where the moss *Hygrohypnum bestii* (Figure 74) provides heavy cover on the substrate (Hales & Gauvin 1971). *Isoperla grammatica* (Figure 75) seems to be more common elsewhere than among mosses, but in her study of the River Liffey, Ireland, Frost (1942) found it to be the dominant moss-dwelling stonefly in the alkaline station of her study. Percival and Whitehead (1929) likewise found it to form denser populations among mosses than among stones. Langford and Bray (1969) reported it to have its largest numbers among the moss *Platyhypnidium riparioides* (Figure 62) in Britain, citing Brinck's (1949) comment that it has the widest ecological amplitude of all Swedish **Plecoptera**. This is a species that is common among submerged bryophytes in the River Rajcianka, Slovakia, but unlike some stoneflies, it is absent among the wet emergent mosses (Krno 1990). The same relationship of confinement to submersed bryophytes is true for *Isoperla oxylepis* and *I. sudetica*. Krno and Sporka (2003) found that *Isoperla sudetica* in the High Tatra of Slovakia depends on the detritus collected by mosses. This stonefly is most productive in winter when the brown trout is not actively feeding.



Figure 74. *Hygrohypnum bestii*, home to *Isoperla petersoni* in a Utah, USA, stream. Photo by Robin Bovey, with permission.



Figure 75. *Isoperla grammatica* naiad, a stonefly whose preference for mosses varies among streams. Photo by Urmas Kruus, with permission.

In the Nearctic, Nelson and Kondratieff (1983) found *Isoperla major* only at the source of a stream where naiads hid under large, moss-covered cobble. In Appalachian Mountain streams, *Diploperla duplicata* (Figure 76) and *Isoperla bilineata* (Figure 77) both occur among mosses (Glime 1968). The former is the most common, occurring among all the major bryophytes [*Fontinalis dalecarlica* (Figure 78), *Hygroamblystegium fluviatile* (Figure 89) – *Platyhypnidium riparioides* (Figure 62), *Scapania undulata* (Figure 7)]. What is surprising here is that these are mature naiads, not the tiny young ones.



Figure 76. *Diploperla duplicata* naiad, a common bryophyte inhabitant in Appalachian Mountain streams. Photo by Bob Henricks, with permission.





Figure 77. *Isoperla bilineata* naiad, a common bryophyte inhabitant in Appalachian Mountain streams. Photo by Royce Bitzer <Iowa State Entomology Image Gallery>, with permission.



Figure 78. *Fontinalis dalecarlica* habitat Highlands, NC. Photo by Janice Glime.

In the Sturgeon River, northern Michigan, USA, *Isoperla signata* (Figure 79) had similar growth above and below a hydroelectric power plant, but the naiads were six times as abundant below the power plant ( $46 \text{ m}^{-2}$  vs  $7 \text{ m}^{-2}$ ) (Mundahl & Kraft 1988). Mundahl and Kraft suggested that the greater abundance below the dam may be from the rich growth of *Fontinalis* below the dam. These mosses were able to trap the detritus released from the dam and thus provide both cover and food for the stoneflies.



Figure 79. *Isoperla signata* naiad, a species that thrives on detritus collected by *Fontinalis*. Photo by Royce Bitzer <Iowa State Entomology Image Gallery>, with permission.

In the High Tatra, Slovakia, *Diura bicaudata* (Figure 41) is dependent on detritus that collects among mosses (Krno & Sporka 2003). This species is common in both stream mosses and in lakes (Kamlet 1967).

In Estonia *Perlodes microcephalus* (Figure 80) occurs in stony and gravelly bottoms where *Fontinalis* (Figure 4) grows (Timm 2000). *Perlodes intricatus* in the High Tatra of Slovakia depends on the detritus that accumulates among mosses in streams (Krno & Sporka 2003). The mosses also provide them with shelter from the predatory brown trout.



Figure 80. *Perlodes microcephalus* naiad, a species that hangs out near *Fontinalis* in stony streams of Estonia. Photo by Niels Sloth, with permission.

*Susulus venustus* from California, USA, is one of the species that drums on mosses and other substrates to attract females (Bottorff *et al.* 1989). The male drumming call is 1-3 groups of bi-beats and is a unique pattern among the **Perlodidae**. After mating, the females fly to the dark detritus and moss substrate, then walk into the shallow water where they release their eggs.

## Peltoperlidae – Roachflies

This family (~8-20 mm) did not appear in any of the published studies I found. This is understandable because their preferred habitat is flowing streams characterized by sediments, vascular plants, and detritus (Peltoperlidae 2014). However, I did find *Peltoperla* (Figure 81) occasionally among all the major bryophytes [*Fontinalis dalecarlica* (Figure 78), *Hygroamblystegium fluviatile* (Figure 89) – *Platyhypnidium riparioides* (Figure 62), and *Scapania undulata* (Figure 7)] I studied in the Appalachian Mountain, USA, streams (Glime 1968). It typically preferred the mat habit.



Figure 81. *Peltoperla* naiad, an occasional dweller among bryophytes in streams in the Appalachian Mountains, USA. Photo by Bob Henricks, with permission.



## Gripopterygidae

This family has become terrestrialized to the degree that the naiads usually live among damp substrata on land (McLellan 1977). But the naiads of *Zelandoperla fenestrata* (10-14 mm; see Figure 82) are widely distributed, especially among mosses, in stony streams in the mountains of New Zealand (Winterbourn & Gregson 1981). This species is most abundant among the *Fissidens rigidulus* (Figure 83) in the torrential water mid stream (Cowie & Winterbourn 1979). These naiads feed on the diatoms and detritus collected there.



Figure 82. *Zelandoperla pennulata* from the Takitimu Mountains, N. Z. Photo by Brian Patrick, with permission.



Figure 83. *Fissidens rigidulus*, home to *Zelandoperla fenestrata* in New Zealand. Photo by Bill & Nancy Malcolm, with permission.

*Cardioperla nigrifrons* occurs in large numbers among surface mosses in a fast waterfall (45° angle) in Tasmania (Dean & Cartwright 1992).

South American Plecoptera, like those from New Zealand and Tasmania, are often different from the ones found in the Northern Hemisphere. *Alfonsoperla flinti* occurs among mosses in high waterfalls in Chile (McLellan & Zwick 2007). Illies (1963) found this species among mosses on the stream beds.

*Zelandobius* (Figure 84-Figure 85) is one of the common small stoneflies in New Zealand, starting its life at about 0.6 mm length, with adults 7-11 mm (Death 1990). It is amphibious and is able to climb out of the water and move about among the emergent wet mosses of streams (Auckland Council 2011).



Figure 84. *Zelandobius* sp. naiad, a genus that can climb out of the water to explore among emergent mosses. Photo from Landcare Research, through Creative Commons.



Figure 85. *Zelandobius illiesi* naiad, a genus that can climb out of the water to explore among emergent mosses. Photo from Landcare Research, through Creative Commons.

## Pteronarcyidae – Giant Stoneflies

This family has the largest members (15-70 mm) among the **Plecoptera**, hence the common name. The largest stonefly I have encountered among mosses is *Pteronarcys biloba* (Figure 86) (Glime 1968, 1994). The large size of older individuals seems to preclude their habitation among smaller mosses like *Platyhypnidium riparioides* (Figure 62) and *Hygroamblystegium fluviatile* (Figure 89). But within the larger spaces among branches of *Fontinalis* species (Figure 4) the genus is able to move about more freely. One feature that may contribute to its ability to hide deep within the streaming *Fontinalis* away from the rapid current is its possession of numerous thoracic tufts of gills that resemble pompoms (Figure 88). These gill tufts facilitate obtaining oxygen and permit the stoneflies to live deep within the clump, out of the rapid flow that brings oxygen to surface dwellers. On the other hand, small individuals (early instars) of *Pteronarcys proteus* (Figure 87-Figure 88) are able to live among the smaller spaces of *Hygroamblystegium fluviatile* (Figure 89).





Figure 86. *Pteronarcys biloba* naiad, a *Fontinalis* dweller in the Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.



Figure 87. *Pteronarcys proteus* naiad, an occasional occupant of *Hygroamblystegium fluviatile* in the Appalachian Mountains. Photo by Jason Neuswanger, with permission.



Figure 88. *Pteronarcys proteus* naiad, an occasional moss dweller, showing well-developed thoracic gills. Photo by Jason Neuswanger, with permission.

Muttkowski and Smith (1929) found mosses, along with diatoms (especially *Epithemia*, Figure 90) in the guts of five out of six *Pteronarcys californica* (Figure 91) examined from among mosses in strong rapids of trout

streams in Yellowstone National Park, USA. The researchers were surprised that this large stonefly was a vegetarian, with only 4% of its diet consisting of animals; instead the guts contained over 50% detritus.



Figure 89. *Hygroamblystegium fluviatile* in the Appalachian Mountains, USA, a moss that provides spaces too small for *Pteronarcys biloba*, but houses smaller individuals of *P. proteus*. Photo by Janice Glime.



Figure 90. *Epithemia* on a filamentous alga. Photo by Jason Oyadomari, with permission.



Figure 91. *Pteronarcys californica* naiad, a bryophyte consumer. Photo by Bob Henricks, with permission.



Several researchers have attempted to explain these diet preferences. *Pteronarcys pictetii* (Figure 92) and *P. californica* (Figure 91) have a diet that is 50-80% detritus during most of the year (Martin *et al.* 1981). Lechleitner and Kondratieff (1983) found that *P. californica* naiads switch from a diet of 40% algae in October to one with more mosses and blackflies in December. However they increase their moss intake when their normal food is insufficient. Martin and coworkers (1981) found that the midgut **proteolytic** (breaking down of proteins into simpler compounds) activity of the naiads is very high, similar to that in other aquatic detritivores. But the conditions differ from those of detritus-feeding **Diptera** and lack the digestive systems that are adapted for digesting proteins that are bound to **polyphenols** (compounds such as tannic acid composed of multiple phenol structures and that have toxic, metabolic, and other biological properties). They furthermore are poorly adapted for digesting the major **polysaccharides** (carbohydrate such as starch, cellulose, or glycogen whose molecules consist of a number of sugar molecules bonded together) present in detritus. Polysaccharide digestion is presumed to be restricted to  $\alpha$ -1,4-glucans, the primary storage polysaccharide of higher plants, algae, and presumably bryophytes. But there seemed to be little enzymatic activity on the major structural polysaccharides of higher plants, suggesting that organisms that accompany the food items may help in the digestion.



Figure 92. *Pteronarcys pictetii* naiad, a detritus feeder. Photo from <Plecoptera.SpeciesFile.org> through Creative Commons.

*Pteronarcella badia* (Figure 93) is generally a detritus feeder in its early stages, but in later instars the naiads make mosses a substantial portion of their diet (Fuller & Stewart 1979). The other eight stonefly species examined from several Colorado, USA, rivers ate predominantly animals – **Chironomidae** (Figure 94), **Simuliidae** (Figure 95), and **Ephemeroptera** (see Chapter 11-4). Even though diets shifted for these other species as they developed, only *Pteronarcella badia* shifted to mosses (Fuller & Stewart 1977).



Figure 93. *Pteronarcella badia* naiad, a species that switches to feeding on mosses as it gets older. Photo by Arlo Pelegrin, with permission.



Figure 94. **Chironomidae** larva, a typical part of stonefly diet. Photo by Bob Armstrong.



Figure 95. **Simuliidae** larvae on rock, common food for stoneflies. Photo by Jason Neuswanger, with permission.

Hassage *et al.* (1988) examined feeding behavior in the shredder species *Pteronarcella badia* and found that in small groups (1-4) the naiads distributed themselves in proportion to the available surface area. However, when the group was increased to 14, they formed aggregations that often involved body contact. Addition of the predator *Claassenia sabulosa* (Figure 96) cause them to exhibit a random distribution. It would be interesting to see if this behavior differs on rocks vs bryophytes.





Figure 96. *Claassenia sabulosa* naiad, a predator on *Pteronarcys badia*. Photo by Bob Henricks, with permission.

## Summary

The **Plecoptera** (stoneflies) are **hemimetabolous**, having eggs, naiads, and adults. Some have gills and others are gill-less, requiring high oxygen concentrations. This requirement for oxygen makes them more common in cold, rapid streams. The naiads are mostly night active. Many of the smaller **Plecoptera** are moss dwellers, especially in young stages, where they eat mostly **detritus** and **periphyton**, but some eat bryophytes.

The stoneflies use the bryophytes for depositing eggs, escaping the drift, protection and food source during early instars, and emergence. Adults of some use the bryophytes as a substrate for attracting females – the males drum their abdomens on the mosses. Some stoneflies, however, emerge in the winter, often climbing out of the water on emergent bryophytes, and can be seen on the snow.

The **Nemouridae** and **Leuctridae** are the most common families among bryophytes, although in some locations the **Taeniopterygidae** are abundant. The **Notonemouridae** is a somewhat terrestrialized moss-dwelling family restricted to the Southern Hemisphere. In New Zealand one can find **Gripopterygidae** among stream mosses, although this stonefly family is mostly terrestrialized. Large stoneflies like the **Pteronarcyidae** are usually absent in the small spaces of most bryophytes, but they are able to maneuver among the larger branches of *Fontinalis*. Other families that include regular moss dwellers are **Capniidae**, **Chloroperlidae**, **Perlidae**, **Perlodidae**, and **Peltoperlidae**.

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# **CHAPTER 11-7**

## **AQUATIC INSECTS:**

### **HEMIMETABOLA – HEMIPTERA**

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# CHAPTER 11-7

## AQUATIC INSECTS: HEMIMETABOLA – HEMIPTERA



Figure 1. *Pachybrachius luridus*, a species of bogs and fens. Photo by Tristan Bantock, with permission.

### HEMIPTERA – True Bugs, Cicadas, Hoppers, Aphids, and Allies

Aquatic bryophyte dwellers are rare in this insect order. Most members are either free swimming or skate on the top of the surface tension. However, bogs and bog pools do provide a suitable habitat for some species. Rédei *et al.* (2003) found no specificity for species among *Sphagnum* (Figure 2) or any species that was characteristic for that moss. *Ceratocombus coleoptratus* (Figure 6-Figure 7) and *Hebrus ruficeps* (Figure 13) had the highest dominance in that habitat, with *Cryptostemma pusillum* (Figure 3), *Saldidae* (Figure 27-Figure 31), and *Miridae* (Figure 4) also occurring here. They considered the similarity of the bog community to that of the soil moss community to be due to the low relative dominance of larvae from the large family *Lygaeidae* (Figure 32-Figure 37) in both habitats.

Members of this family lack gills and their immature stages are nymphs, placing them in the **Hemimetabola**. Some breathe by a **plastron** (mechanism for carrying an air layer next to the body).



Figure 2. *Sphagnum fuscum*, a genus that is home for a few members of the **Hemiptera**. Photo by Michael Lüth, with permission.





Figure 3. *Cryptostemma* sp. *Cryptostemma pusillum* is among the **Hemiptera** with the highest dominance in bogs. Photo by Michael F. Schönitzer, through Creative Commons.



Figure 4. *Campyloneura virgula* (Miridae), a dominant species in bogs. Photo by Valter Jacinto, through Creative Commons.

## Cicadellidae – Leafhoppers

This family was previously placed in the Homoptera, but is now included in the order **Hemiptera**. It is not, however, a true bug.

This is the second largest hemipteran family. The members live primarily on land (Leafhopper 2015). They use the hairs on their legs to facilitate a secretion over their bodies that acts as a water repellent and carrier of pheromones. They obtain their food by sucking sap from a variety of plants.

*Megophthalmus scanicus* (Figure 5; 3-4 mm) is a widespread species in the UK where it overwinters among mosses (Edwards 1874-1879). This is a species of wide habitat variety, including both wet and dry habitats.



Figure 5. *Megophthalmus scanicus* nymph, a species that overwinters among mosses. Photo from <www.biolib.cz>, through public domain.

## Ceratocombidae

The **Ceratocombidae** is mostly tropical and lives primarily in leaf litter along water margins. This is a group of small bugs, 1.5-3.0 mm, mostly dull-colored, from yellowish to dark brown (Livermore & Rider 2015). These insects require permanently damp conditions such as those provided by the wet mosses close to running water. Members of this family overwinter as adults, requiring the permanent wetness of habitats like wet mosses near running water (Howe 2004). *Ceratocombus brevipennis* (see Figure 6) is one of these moss dwellers in central and southern Europe (Michael Münch personal communication 30 October 2014).



Figure 6. *Ceratocombus coleoptratus*, an inhabitant of wet mosses in Europe. Michael Münch <www.insekten-sachsen.de>, with permission.

*Ceratocombus coleoptratus* (Figure 7) was rare in the UK even as early as the 1870's (Edwards 1874-1879). It lives among mosses, perhaps being under-collected and accounting for its presumed rarity. Fortunately it still



exists, living in moss cushions, needle litter, and dead plant material at the edges of forests (Münch 2012). It also occasionally lives in moss beds in swampy meadows.



Figure 7. *Ceratocombus coleoptratus* wending its way through its moss home. Photo by Michael Münch, with permission.

### Dipsocoridae – Jumping Ground Bugs

This family (Figure 3) of tiny bugs (2-3 mm) is found mostly among wet mosses by running water in Wales (Howe 2004). These bugs, despite their small size, are predators with rapid movements that typically live near streams and rivers.

In particular, some species of the genus *Pachycoleus* are closely associated with bryophytes in central and southern Europe (Michael Münch pers. comm. 30 October 2014). In Wales, it is *Pachycoleus waltli* that is common among the wet mosses (Howe 2004). Kment *et al.* (2013) found *P. waltli* among wet mosses that covered dead branches along a stream. This species is typical of permanently wet to very wet moss [*Sphagnum* (Figure 2), *Hypnum* (Figure 8), *Brachythecium* (Figure 9), *Cratoneuron* (Figure 10)] and may stay fully submerged.



Figure 8. *Hypnum cupressiforme*, a home for *Pachycoleus waltli*. Photo by Li Zhang, with permission.



Figure 9. *Brachythecium plumosum*, a home for *Pachycoleus waltli*. Photo by Janice Glime.



Figure 10. *Cratoneuron commutatum*, a wet habitat where one might find members of the genus *Pachycoleus*. Photo by Michael Lüth, with permission.

Using Berlese funnels to sample in Hungarian bogs, Rédei *et al.* (2003) found *Cryptostemma pusillum* (Figure 3) among the common Hemiptera.

### Gerridae – Water Striders

The most distinctive feature of the **Gerridae** is their ability to skate about on the water surface. They are larger (~4-18 mm) than the other surface bugs described here. Their skating ability is possible due to hydrofuge (water-repelling) hairs, retractable claws, and long legs (Ward 1992). The hairs are arranged in hair piles with more than 1000 microhairs per mm. They cover the entire body, repelling water drops that could otherwise weigh them down.

*Gerris* is not a genus that finds mosses important in the water, instead skating on its surface. To my surprise, I read an old report of *Gerris lacustris* (Figure 11) hibernating under a terrestrial moss nearly a km from water! (Butler 1886). This species is a water strider – the spider-like insect that skates on the surface tension of quiet pools of ponds and streams. Furthermore, *Gerris argentatus* (Figure 12) occurs among wet mosses (Edwards 1874-1879).





Figure 11. *Gerris lacustris* on pond, a species that hibernates under terrestrial mosses. Photo by Jakub Rom through public domain.



Figure 12. *Gerris argentatus*, a species that can be found among wet mosses. Photo by Niels Sloth, with permission.

## Hebridae – Sphagnum Bugs, Velvet Water Bugs

The **Hebridae** are small insects (1.3-3.7 mm) of semiaquatic habitats, living mostly in moist detritus or among floating plants, wet moss, or margins of still waters (McClarín 2006). The **Hebridae** are most common among wet mosses (Howe 2004) and the genus *Hebrus* lays its eggs among mosses, hiding them in leaf axils, or between closely spaced leaves, where it uses a gelatinous glue to adhere them (Polhemus & Chapman 1979a). In the bogs and fens of Hungary the diversity of **Hemiptera** is very low when a large spatial area is considered (Rédei *et al.* 2003). This is because one wet moss species, *Hebrus ruficeps* (Figure 13), dominates, comprising 90% of the **Hemiptera** fauna!



Figure 13. *Hebrus ruficeps*, a moss dweller in *Sphagnum* bogs that is able to survive the winter frozen in ice at the water surface. Photo by Ruth Ahlburg, with permission.

Members of *Hebrus* are small bugs, only 1.3-3.7 mm long (Ramel 2014). Their preferred habitat is ponds with *Sphagnum* (Figure 14) or along margins of streams. Although the genus has about 150 species worldwide, mostly in tropical environments of Southeast Asia, the UK has only two species, both moss dwellers.



Figure 14. *Sphagnum cuspidatum*, in a genus that is home to *Hebrus* in ponds. Photo by Blanka Shaw, with permission.

*Hebrus concinnus* was observed laying its eggs between the leaves of mosses where the eggs were partially concealed (Hungerford 1920). Edwards (1874-1879) reported *Hebrus pusillus* (Figure 15) from wet moss. Münch (2013) likewise considered *H. pusillus* a moss dweller, but that it also lives on the water surface and at the edge of the water where it reproduces. Howe (2004) reported that it is associated with *Sphagnum* (Figure 2, Figure 14) and other mosses.



Figure 15. *Hebrus pusillus* on a moss. Photo by Michael Münch, with permission.

But not all members of *Hebrus* live along streams. *Hebrus pusillus* (Figure 15) and *H. ruficeps* (Figure 13) both occur among *Sphagnum* (Figure 2) in bogs (Butler 1886). *Hebrus ruficeps* is able to survive the winter frozen in ice at the water surface (Ramel 2014). Butler (1886) recommended tearing a handful of the moss into small pieces and examining each carefully to find these tiny bugs.

The genus *Merragata* (Figure 16), like *Hebrus*, lays its eggs on moss leaves, or under algae, where they incubate for 8-12 days (Polhemus & Chapman 1979a).



Figure 16. *Merragata hebroides*, a genus that lays its eggs on moss leaves or under algae. Photo by Don Loarie, through Creative Commons.

### Mesoveliidae – Water Treaders

These are small usually greenish or yellowish surface bugs of about 2-5 mm length. *Mesovelia mulsanti* (Figure 17) prefers lakes and bogs with lots of surface vegetation where they live on mosses and other floating plants (Figure 18; Menke 1979). They feed on lily pads and easily run on the surface of the water. *Mesovelia amoena* (Figure 19), on the other hand, occurs on mosses in hot spring caves of Death Valley and avoids the water unless disturbed (Hungerford 1917; Polhemus & Chapman 1979b). At least some populations must be **parthenogenetic** (giving birth without fertilization) because only the female of *Mesovelia amoena* occurs in Hawaii.



Figure 17. *Mesovelia mulsanti*, a bog dweller. Photo by Matt Bertone, through Creative Commons.



Figure 18. *Mesovelia* sp. blending with several floating duckweed species. Photo by Steve Nanz, through Creative Commons.



Figure 19. *Mesovelia amoena*, a moss dweller, including those in a hot spring cave. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

### Veliidae – Small Water Striders, Riffle Bugs

The family **Veliidae** (1-12 mm) is best adapted for surface activity, walking easily on the surface tension. The surface tension facilitates their detection of food items (small arthropods) by vibrating as the prey organisms move about (McLeod 2005).

In my studies of Appalachian Mountain, USA, stream bryophyte inhabitants, *Microvelia* (Figure 20-Figure 22) was the only member of **Hemiptera** that I found (Glime 1968). The genus *Microvelia* has a unique means of locomotion. Instead of clambering about on the water surface by paddling with its middle legs like other **Hemiptera**, it exudes a fluid that reduces the surface tension in the water behind it. This causes the surface there to expand and push it forward.



*Microvelia* and *Paravelia* species lay their eggs on such floating objects as moss, duckweed, and living or dead leaves just above or below the water surface (Polhemus & Chapman 1979d). *Microvelia reticulata* (Figure 20) overwinters as an adult (Ramel 2014). It lays eggs in mosses and feeds on tiny invertebrates, including mosquito eggs.



Figure 20. *Microvelia reticulata*, a species that lays its eggs among mosses. Photo by Niels Sloth, with permission.

*Microvelia buenoi* (Figure 21) lives among mosses at the edge of a pond in Indiana, USA (Bamd 2007), where it was sampled using a Berlese funnel. In Florida, Herring (1950) found *Microvelia hinei* (Figure 22) in mats of *Sphagnum* (Figure 14) in acid swamps and bog streams. This species illustrates a short incubation time of only 6.41 days (mean) (Taylor & McPherson 2003). Nymphal development requires only 25 days for its 5 instars (developmental stages).



Figure 21. *Microvelia buenoi*, a species that occurs among mosses at the edge of a pond. Photo by Tim Faasen, with permission.



Figure 22. *Microvelia hinei*, an inhabitant of *Sphagnum* mats in bogs. Photo from Biodiversity Institute of Ontario, through Creative Commons.

## Macroveliidae – Macroveliid Shore Bugs

This new world family never exceeds 5 mm in length. *Macrovelia hornii* (Figure 23; ~4.2 mm) nymphs and adults live among mosses and other floating vegetation at the water's edge in protected niches behind rocks or logs or among debris (Ussinger 1956; Menke 1979). Polhemus and Chapman (1979c) consider this species to be common among the mosses of California springs and seeps. They lay their eggs glued to wet mosses (Menke 1979).



Figure 23. *Macrovelia* sp. Some species live among mosses in crevices at the water's edge. Photo by Paul A. Rude, through Creative Commons.

## Corixidae – Water Boatmen

This family ranges 2-14 mm and is free-swimming in ponds and slow-moving streams (Corixidae 2014). Thus, they are not typically among the bryophyte dwellers. Unlike most aquatic Hemiptera, they are predominantly herbivores, feeding on algae and aquatic plants. And, Macan and Maudsley (1968) report *Micronecta poweri* (Figure 24) to be associated with vegetation, including *Fontinalis* (Figure 25). The Corixidae inject enzymes into the plants (or animals) through the strawlike mouthparts (Figure 26), then suck the cell contents back through that same straw (Corixidae 2014).



Figure 24. *Micronecta poweri*, a water boatman that sometimes lives among *Fontinalis*. Photo by Urmas Kruus, with permission.





Figure 25. *Fontinalis antipyretica*, a genus that is home to *Micronecta poweri*. Photo by Bas Kers, through Creative Commons.



Figure 26. **Corixidae** eating mosquito pupa. Photo by Bob Armstrong, with permission.

## Saldidae – Shore Bugs

The **Saldidae** are small to medium in size (2-8 mm) (Saldidae 2013). *Salda* (Figure 27) is known as a bog-moss dweller at pond margins (Butler 1886). *Salda morio* and *S. muelleri* live in bog pond margins (Spunġis 2009) among mosses (Michael Münch pers. comm. 30 October 2014). *Salda littoralis* occurs in salt marshes and tidal zones, where it hides under marine algae at low tide and migrates to the edge of the water in high tide, but it also lives in freshwater habitats (Spunġis 2009) where it often associates with bryophytes, including living among *Sphagnum* (Figure 14) in a mountain lake in the Italian Alps (Michael Münch pers. comm. 30 October 2014). It will occasionally submerge into the water (Polhemus 1976).



Figure 27. *Salda lugubris*, member of a genus that has bog moss dwellers. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

*Saldula pallipes* (Figure 28) lays its eggs at the bases of mosses or in between their leaves at the edges of ponds (Usinger 1956).



Figure 28. *Saldula pallipes* lays its eggs at the bases or between leaves of mosses at the edges of ponds. Photo by Charlie Eiseaman, through Creative Commons.

*Chartoscirta cocksii* (= *Salda cocksii*; Figure 29) lives in ponds, mossy areas, and wetlands. Michael Münch (pers. comm. 30 October 2014) found it in a swamp among a taller moss (not *Sphagnum*). In early surveys, *Chartoscirta cocksii* was the primary hemipteran among *Sphagnum* (Figure 2, Figure 29) in the UK (Butler 1886). This tiny black bug has huge eyes and stout antennae, making a striking find. Butler recommends putting mud, mosses, and dead leaves in a box to watch how many saldids will hatch out. This species will also take an occasional dip in the pools of the bog (Polhemus 1976).





Figure 29. *Chartoscirta cocksii* on *Sphagnum papillosum*. Photo by Barry Stewart, with permission.

*Chartoscirta elegantula* (Figure 30) occurs between tide marks, but it also can be common among *Sphagnum* (Figure 2) (Michael Münch pers. comm. 30 October 2014). Like *Gerris lacustris*, it migrates to overwinter in dry moss or leaves on land far from its summer habitat.



Figure 30. *Chartoscirta elegantula elegantula*, a species that often migrates from the intertidal zone to overwinter among dry mosses. Photo by Sanjo, through Creative Commons.

*Ioscytus nasti* (Figure 31) occurs in bogs in North America (Usinger 1956). This is a poorly known genus and may provide some surprises in the bogs.

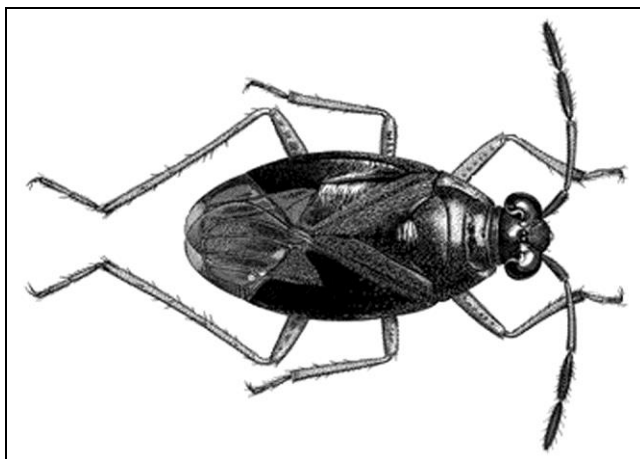


Figure 31. *Ioscytus nasti*, a bog inhabitant. Image from Smithsonian Institution, through Creative Commons.

## Lygaeidae – Seed Bugs, Cinch Bugs

This family of bugs, ranging 4-20 mm (Lygaeidae 2015), feeds primarily on seeds. Hence, bryophytes do not provide an ideal habitat. Nevertheless, the family has several bog and fen dwellers (Michael Münch pers. comm. 30 October 2014). Among these are *Scolopostethus pilosus* (Figure 32) in calcareous fens, *Cymus glandicolor* (Figure 33) in fens, *Ligyrocoris sylvestris* (Figure 34) in hill moors, *Pachybrachius luridus* (Figure 35) in bogs and fens, *P. fracticollis* (Figure 36) rare in bogs, fens, and wet meadows (Spunġis 2009), all among mosses (Michael Münch pers. comm. 30 October 2014). *Scolopostethus puberulus* (Figure 37), on the other hand, lives primarily in deciduous forests, but also in **mesic** meadows (environment with moderate amount of moisture) (Spunġis 2009), as a moss dweller (Michael Münch pers. comm. 30 October 2014).



Figure 32. *Scolopostethus pilosus*, a moss dweller in calcareous fens. Photo by Boris Loboda, with permission.



Figure 33. *Cymus glandicolor*, a moss dweller in fens. Photo by Tristan Bantock, with permission.



Figure 34. *Ligyrocoris sylvestris*, a moss dweller in hill moors. Photo by Tom Murray, through Creative Commons.





Figure 35. *Pachybrachius luridus*, a moss dweller in bogs and fens. Photo by Tristan Bantock, with permission.



Figure 36. *Pachybrachius fracticollis*, a rare moss dweller in bogs, fens, and wet meadows. Photo by Barry Stewart, with permission.



Figure 37. *Scolopostethus puberulus*. Photo by Michael Münch <www.insekten-sachsen.de>, with permission.

## Rhyparochromidae – Dirt-colored Seed Bugs

Like the Lygaeidae, the **Rhyparochromidae** feed primarily on seeds, making bryophytes less than ideal habitats. *Rhyparochromus pini* (Figure 38) has adults 7-8

mm in length (British Bugs 2015). Most in Great Britain live in heathland, often under the heath; others live on sand dunes. However, Spunģis (2009) found that this species also lives in bogs and fens.



Figure 38. *Rhyparochromus pini* nymph, an inhabitant of bogs and fens. Photo by Tristan Bantock, with permission.

## Summary

The Homoptera have been moved into the order **Hemiptera** and the family **Cicadellidae** has a few members that use wet mosses to overwinter.

The true bugs have more aquatic members, but few are true bryophyte dwellers. The families **Ceratocombidae** and **Dipsocoridae** require permanently damp conditions and therefore many live in wet mosses. The surface-dwelling **Gerridae** sometimes spend the winter far from water among bryophytes. The **Hebridae** are frequent bryophyte dwellers among wet mosses and some lay their eggs there; others live in bogs. **Mesoveliidae** occur in lakes, bogs, and among mosses of hot spring caves. Some **Veliidae** lay their eggs on mosses and live among them in pools, acid swamps, and bog streams. Macroveliidae are more terrestrial but may live among mosses as nymphs. The **Saldidae** have some species that prefer bog pond margins among the mosses; others live among the taller bog bryophytes. Even the **Lygaeidae** and **Rhyparochromidae** occur among mosses in bogs. The larger, free-swimming **Corixidae** can occur among *Fontinalis* in slow-moving water.

## Acknowledgments

Allen Knight and Dennis Heiman verified my identifications of the Plecoptera for my mid-Appalachian Mountain study and T. Wayne Porter verified the *Microvelia*. Bob Henricks and Jason Neuswanger have been particularly helpful in contributing images and personal experiences. Michael Munch was very helpful in providing me names of Hemiptera he has found in association with bryophytes, as well as providing a number of images. Eileen Dumire has helped with sorting insects,



maintaining the bibliography records, and reviewing the written chapter.

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CHAPTER 11-8

AQUATIC INSECTS: HOLOMETABOLA –  
NEUROPTERA AND MEGALOPTERA

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# CHAPTER 11-8

## AQUATIC INSECTS: HOLOMETABOLA – NEUROPTERA AND MEGALOPTERA



Figure 1. *Nigronia serricornis* larva (Megaloptera), a species that sometimes pupates in mosses. Photo by Jason Neuswanger, with permission.

### HOLOMETABOLA

The **holometabolous** insects are those with a complete life cycle – egg/embryo > larva > pupa > adult. These insects typically spend only part of the life cycle in the water. Some lay their eggs near water and larvae develop in the water. Some have eggs, larvae, and pupae in the water, but their emerging adults break through the water surface and climb onto land to emerge. For most, adult life and mating occur on land.

### NEUROPTERA – Net-winged Insects

**Neuroptera** literally means nerve wings, so-named because of the prominent wing veins of the adults. This order is not well represented among bryophytes, and only the larvae are associated with aquatic habitats.

#### Osmylidae

On continents other than North America a small family, the **Osmylidae** (Figure 2-Figure 6), occurs among mosses and organic matter in and near streams (Flint 1977). *Osmylus fulvicephalus* (Figure 2) is the only species known in the UK, likewise living among mosses of streambanks (Elliott *et al.* 1996) and seeking food there (NatureSpot 2015). The adults (Figure 3; 25 mm long including wings) don't stray far from water but are not aquatic. The females lay their eggs on overhanging plants, tree trunks, or stones (Osmylidae 2014), and especially on

mosses (Elliott *et al.* 1996) near water, laying about 30 eggs either singly or in pairs. Larvae leave the egg site within 1-3 days to burrow into mosses. Larvae may live in or out of water, but pupation is on land, lasting 7-18 days. If the larvae are submersed, they crawl out of the water (Ward 1965). If the moss is submersed, they burrow deeply into it, but within 8-28 days of submersion they die. Adults live two weeks to three months, depending on species and location.



Figure 2. *Osmylus fulvicephalus* larva, a species that lives among mosses on streambanks and feeds there. Photo by Walter Pflieger, with permission.





Figure 3. *Osmylus fulvicephalus* adult that lays its eggs on overhanging vegetation. Larvae live among streambank mosses. Photo through Creative Commons.

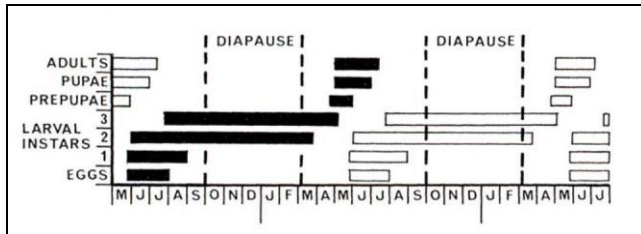


Figure 4. Phenological events (cyclic and seasonal natural phenomena, especially in relation to climate) of the life cycle of *Osmylus fulvicephalus*. From Elliott *et al.* 1996.

*Osmylus fulvicephalus* (Figure 3) is controversial in that its larvae live in wet mosses, but drown in 8-28 days of submersion (Elliott *et al.* 1996). Nevertheless, they do enter the water in search of food. It seems safe to say, however, that their relationship with mosses is damp, but not aquatic. The larva feeds among these mosses. When movement is detected, it jabs at it with the long proboscis, then injects it with a salivary secretion that paralyzes it. A chironomid larva is paralyzed within 10 seconds. The *O. fulvicephalus* then sucks out the interior of the prey. The larvae stop eating during mid autumn and burrow down to the moss rhizoids to hibernate for the winter. Fortunately, in this state they can survive occasional submersion in water, thus surviving **spates** (sudden flood in a river, especially one caused by heavy rains or melting snow). In spring they spin a silken cocoon, sometimes incorporating bits of moss in the cocoon. Just before pupation the long jaws break off (Figure 5). The pupa becomes immobile during pupation. It grows a pair of mandibles that it uses to cut its way out of the cocoon.



Figure 5. *Osmylus fulvicephalus* larva showing large jaws. Photo by Walter Pfliegler, with permission.

Like *Osmylus fulvicephalus* (Figure 2-Figure 5), *Kempynus* sp. (Figure 6) in the Southern Alps of New Zealand is somewhat amphibious, living at the edge between water and land (Cowie & Winterbourn 1979). In springbrooks it lives in clumps of the mosses *Acrophyllum quadrifarium* (= *Pterygophyllum quadrifarium*; Figure 7) and *Cratoneuropsis relaxa* (Figure 8).



Figure 6. *Kempynus* sp larva, member of the small family **Osmylidae** that inhabits mosses near streams. Photo by Stephen Moore, Landcare Research NZ, with permission.



Figure 7. *Pterygophyllum quadrifarium*, a moss habitat for *Kempynus* sp. at stream borders and in springbrooks in New Zealand. Photo by Bill and Nancy Malcolm, with permission.



Figure 8. *Cratoneuropsis relaxa*, a moss habitat for *Kempynus* sp. at stream borders and in springbrooks in New Zealand. Photo by Tom Thekathiyil, with permission.



## Chrysopidae

There are a number of reports of the larvae of the green lacewing *Leucochrysa pavida* (Figure 9-Figure 12) using bits of lichen as camouflage (Tauber *et al.* 2009; Moskowitz & Golden 2012). In fact, Wilson and Methven (1997) found that the larvae at their Illinois, USA, site were somewhat specific in the species of lichens they chose. But Slocum and Lawrey (1976) found that this insect was not totally specific. In addition to the lichens, it also includes pieces of bark, angiosperm pollen, fungal spores, insect debris, and (of course) bryophyte gametophytes. Slocum and Lawrey demonstrated that the lichens, at least, are still alive and that they have photosynthetic rates equal or greater than those same lichen species still growing on a bark substrate. Furthermore, these lichen propagules are still viable when the cocoons are attached to the bark, giving the lichens the opportunity and establish in this new location. Unfortunately, there are no similar studies on the bryophytes in this camouflage arrangement, but it at least provides the possibility for a means of dispersal.



Figure 9. *Leucochrysa pavida* larva with lichen back pack, showing its camouflage against tree bark lichens. Photo by Jim McCormac, with permission.



Figure 10. *Leucochrysa pavida* larva with lichen back pack, showing the legs and mandibles of the larva. Photo by Jim McCormac, with permission.



Figure 11. *Leucochrysa pavida* larva showing ventral side. Photo by Jim McCormac, with permission.



Figure 12. *Leucochrysa pavida* larva showing head and large mandibles of this carnivore. Photo by Jim McCormac, with permission.

## MEGALOPTERA – Dobsonflies and Alderflies

**Megaloptera** means large wing; one adult is known with a wingspan of 21 cm, the largest of any aquatic insect in the world (Megaloptera 2014). The order is relatively small, and is close to the **Neuroptera**. Its members have



aquatic larvae, but they pupate on land in damp soil or under logs. The pupae are fully mobile and can defend themselves against predators with their large mandibles. Female adults lay 1000's of eggs on overhanging vegetation where larvae can drop into the water (Figure 13). The adults often live only a few hours and usually don't eat.

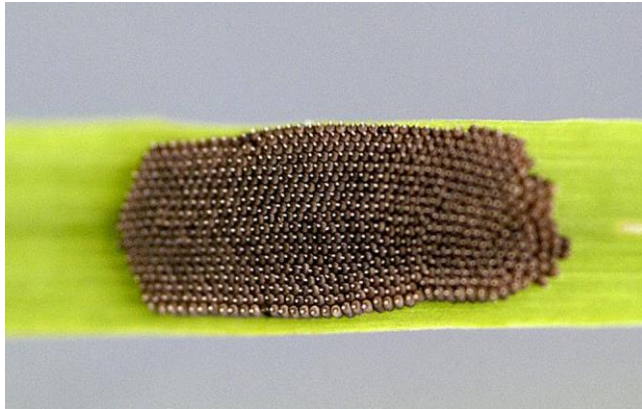


Figure 13. *Sialis fuliginosa* eggs. Photo by James K. Lindsey, with permission.

## Sialidae – Alderflies

This is a small family that can be up to 25 mm long (Alderfly 2014). They occur sparsely worldwide with a concentration of known species in Europe (Sialidae 2015).

I have only found reference to one genus of bryophyte dwellers, *Sialis* (Figure 13-Figure 17) (Lithner *et al.* 1995). I likewise found this genus occasionally among bryophytes in Appalachian Mountain, USA, streams (Glime 1968). It has aquatic larvae, but adults are terrestrial and lay eggs near water (Alderfly 2014). Fully grown larvae of *Sialis* pupate in soil, mosses, under stones, and other locations, usually near water. In Canada, after about one month the adults appear. *Sialis nigripes* prefers mosses for egg laying (Elliott *et al.* 1996). *Sialis lutaria* (Figure 15-Figure 17) was used in a study comparing heavy metal accumulation in mosses (*Fontinalis* spp.; Figure 18), insects, and fish (Lithner *et al.* 1995).



Figure 14. *Sialis* adult, a genus that sometimes pupates and lays eggs among streamside bryophytes. Photo by Patrick Coin, through Wikimedia Commons.



Figure 15. *Sialis lutaria* larva, the aquatic stage that migrates into the water, sometimes from streamside bryophytes. Photo by André Karwath, through Creative Commons.



Figure 16. *Sialis lutaria* adult. Photo ©entomart, through Creative Commons.



Figure 17. *Sialis lutaria* adults mating. Photo by James K. Lindsey, with permission.

On the South African Cape, pupae of **Sialidae** along streams or waterfalls live in *Sphagnum* (Figure 19) and other mosses (Barnard 1931). These pupae require a wet, but not submersed, habitat, so the mosses must be soaking wet.





Figure 18. *Fontinalis antipyretica*, home to numerous kinds of insects and useful for comparing heavy metal accumulation. Photo by Malcolm Storey, through Creative Commons.



Figure 19. *Sphagnum fimbriatum*, a genus that lives in Africa and is a potential home for pupae of *Sialidae*. Photo by Blanka Shaw, with permission.

## Corydalidae- Dobsonflies and Fishflies

This family occurs mostly in the Northern Hemisphere and in South America, including both temperate and tropics (Corydalidae 2014). Their body size is usually greater than 25 mm and ranges up to 80 mm (Penny *et al.* 1997; Bartlett 2004). The larvae are aquatic, are called hellgrammites, and are predators.

*Nigronia*, an aquatic member of the **Corydalidae**, is not typically a moss inhabitant, although I did occasionally find larvae of this genus among Appalachian Mountain stream bryophytes (Glime 1968). But like many other aquatic insects, *Nigronia serricornis* (Figure 20-Figure 21) pupates among mosses as well as under stones and logs (Needham *et al.* 1901). Likewise, *Chauliodes pectinicornis* (Figure 22) and *C. rastricornis* (Figure 24-Figure 24) pupate in these habitats. Pupation lasts about 2 weeks in these **Corydalidae**.



Figure 20. *Nigronia serricornis* larva showing powerful jaws. The aquatic larva often crawls into mosses to pupate. Photo by Jason Neuswanger, with permission.



Figure 21. *Nigronia serricornis* adult. Pupae of this insect often reside in mosses. Photo by Phil Myers, through Creative Commons.



Figure 22. *Chauliodes pectinicornis* adult, a species that lives in the water as larvae and pupates among mosses. Photo by Stephen Cresswell, with permission.



Figure 23. *Chauliodes rastricornis* larva, a species that may move to mosses to pupate. Photo by Tom Murray, through Creative Commons.





Figure 24. *Chauliodes rastricornis* adult, a species that lives in the water as larvae and pupates among mosses. Photo by Stephen Cresswell, with permission.

## Summary

The **Holometabola** have a complete life cycle with egg, larva, pupa, and adult.

The **Neuroptera** are represented among aquatic bryophytes by only one family, the **Osmylidae**. The larvae of *Osmylus* may live among bryophytes in streams or on streambanks and obtain food there. Some species lay their eggs on mosses that overhang streams. Larvae bore into mosses in or out of the water. *Kempynus* species often live among mosses in springbrooks.

The **Megaloptera**, like the **Neuroptera**, have few aquatic bryophyte dwellers. *Sialis* (**Sialidae**) larvae occasionally occur among stream bryophytes; the pupae are often among terrestrial mosses. Some species lay eggs among mosses. Wet *Sphagnum* along streams or near waterfalls serves as a home for some **Sialidae**. Some members of *Nigronia* and *Chauliodes*, both in the **Corydalidae**, pupate among mosses.

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CHAPTER 11-9

AQUATIC INSECTS: HOLOMETABOLA – COLEOPTERA, SUBORDER ADEPHAGA

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# CHAPTER 11-9

## AQUATIC INSECTS: HOLOMETABOLA – COLEOPTERA, SUBORDER ADEPHAGA



Figure 1. *Lancetes angusticollis* adults on moss, South Georgia in the Antarctic. *Lancetes angusticollis* has a two-year life cycle, with overwintering possible in three life stages – aquatic larvae, terrestrial pupae (not proven), and aquatic adults. Note the air supply at the tip of the abdomen. This external air supply makes it necessary for these beetles to cling to vegetation, when they are not swimming, to avoid floating to the surface, hence their use of mosses. Photo by Roger S. Key, with permission.

### COLEOPTERA BACKGROUND

The Coleoptera seem to have a somewhat closer relationship to terrestrial life than other aquatic bryophyte dwellers. First of all, they get their air from the atmosphere or underwater plants where they grab an air bubble (Figure 2). They can accumulate air as bubbles under the **elytra** (hardened forewings; wing covers), through the **plastron** (breast plate breathing apparatus; Figure 3) (Oliveira de Sousa *et al.* 2012), or an anal bubble. The **plastron** is a ventral structure that acts as a physical gill by using various combinations of hairs, scales, and undulations projecting from the cuticle. This apparatus holds a thin layer of air along the outer surface of the body (Figure 3). In all three

of these mechanisms, the nitrogen in the air bubble diffuses into the water slowly while the replacement oxygen diffuses into it 2-3 times as fast (Rich Merritt, pers. comm. 28 January 2015). Thus, as the insect uses up the oxygen from the bubble, the water replaces it by oxygen diffusion for a reasonable period of time. The CO<sub>2</sub> from respiration enters the bubble and rapidly diffuses into the water, having little effect on bubble size. Many beetles attach an anal gas bubble (Figure 1, Figure 18-Figure 19) that uses this diffusion mechanism. They may have hairs that help hold the bubble in place. (See **Elmidae** in Coleoptera, Suborder Polyphaga, for details of the plastron functioning in that family.)





Figure 2. *Berosus luridus* adult on moss where air bubbles from photosynthesis can be used to replenish the air supply. Photo by Tim Faasen, with permission.



Figure 3. *Chaetarthria siminulum* adult with plastron. When the plastron is full of air, the beetle must cling to vegetation in order to descend into the water column. Photo by Gerard Visser <www.microcosmos.nl>, with permission.

Nearly all aquatic **Coleoptera** go to land to pupate (Leech & Chandler 1956; Pennak 1978; Erman 1984), then return to the water as adults. Others clamber about on the surface of the plants. Some of these are associated with floating plants, including *Ricciocarpus natans* (Figure 4) (Scotland 1934). To get below the surface requires muscle action to break the surface tension (Leng 1913).

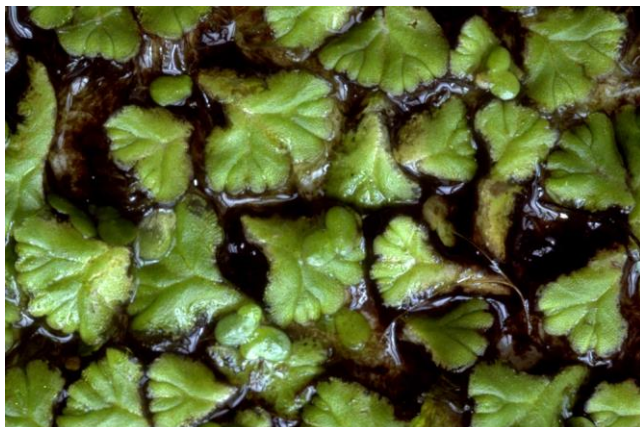


Figure 4. *Ricciocarpus natans*, a floating liverwort. Photo by Jan-Peter Frahm, with permission.

Percival and Whitehead (1930) noted that the mosses in streams in the UK were very important to both larvae and adults of the small **Coleoptera**. In 1949, Badcock indicated that beetles were more common among mosses than associated with stones, especially loose stones. Ogbogu (2000) found **Coleoptera** among the insects associated with *Fontinalis* (Figure 5) in an intermittent reservoir spillway in Ile-Ife, Nigeria. Many of the **Coleoptera** in rivers of northwest Spain prefer moss as a substrate, as indicated by both species richness and abundance (Fernández-Díaz 2003; Sarr *et al.* 2013). They attributed this to the abundance of food available for the herbivores (Passos *et al.* 2003; Sarr *et al.* 2013). This applied particularly to the **Elmidae** and **Hydraenidae**.



Figure 5. *Fontinalis antipyretica* on rocks of a stream bed. Photo by Betsy St. Pierre, with permission.

Among the most common of these bryophyte dwellers are the **Elmidae** (Figure 6), small beetles only a few mm in length (Percival & Whitehead 1930; Glime 1994). But many studies miss the small **Coleoptera** that live among the bryophytes, necessitating special collecting techniques for such habitats as submerged roots, wood, and mosses (Zařovičová *et al.* 2004). Zařovičová and coworkers found 13-61% more species when they used qualitative sampling that included these habitats.



Figure 6. **Elmidae** adult, one of the most common of beetle families among bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Whereas mosses in streams and lakes are not especially important for beetles, bogs and fens have greater



species numbers. Some live in the acidic pools, some burrow into the moss mats, and some run about the surface. The **Dytiscidae** (Figure 18-Figure 55) are particularly important in the pools. These bog dwellers, although often not adapted to a submerged aquatic habitat, will be included here.

Jones (1950) did extensive gut analysis of insects from the River Rheidol and found that none of the **Coleoptera** had mosses (*Fontinalis antipyretica*, Figure 5) in their guts, although **Plecoptera** and **Trichoptera** did. Rather, these **Coleoptera** were all carnivores.

## Suborder Adephaga

This suborder is comprised of a group of highly specialized beetles.

### Carabidae – Ground Beetles

The **Carabidae** forms a large family (>40,000 species) (Ground Beetle 2015), ranging 0.7-66 mm long (Bartlett 2004a). Despite this large number of species, they are mostly either shiny black or metallic and have ridged elytra (Ground Beetle 2015). Their distribution is worldwide, but records from Africa and Asia are scant. Typical homes are under tree bark, under logs, and among rocks or sand by the edge of ponds and rivers. Many expel an especially noxious and painful liquid for their defense. They are predators, often rapidly chasing their prey, usually at night (Bartlett 2004a).

These are not aquatic beetles, but they do live in bogs (Boyce 2011). In Dartmoor, UK, *Agonum ericeti* (Figure 7) prefers mires that have both *Sphagnum* (Figure 7) hummocks and warm, bare peat. Here they run around on the bog surface and are one of the most "important" species in the bog. They occur only where there are abundant bog mosses.



Figure 7. *Agonum ericeti* adult, a mire dweller, on *Sphagnum*. Photo by Niels Sloth, with permission.

*Pterostichus rhaeticus* (Figure 8) prefers to live among *Sphagnum* (Figure 7) of a blanket bog (Boyce 2011). *Pterostichus diligens* (Figure 9) likewise lives in blanket bogs, but lives in litter as well as among mosses. *Acupalpus dubius* is sometimes restricted to the moss *Drepanocladus aduncus* (Kopecky 2001).



Figure 8. *Pterostichus rhaeticus* adult, a blanket-bog dweller. Photo by Niels Sloth, with permission.



Figure 9. *Pterostichus diligens* adult, an inhabitant of mosses and leaves in blanket bogs. Photo by Niels Sloth, with permission.



Figure 10. *Acupalpus dubius* on leafy liverworts and mosses. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 11. *Drepanocladus aduncus*, home for *Acupalpus dubius*. Photo by Bob Klips, with permission.



### Gyrinidae – Whirligig Beetles

This family is aptly named for its behavior of skating in whirling patterns on the water surface. The most unusual feature of this family is the eyes. They are divided so that two eyes are above the water and two are below, protecting the beetles from predators above and permitting them to see what is beneath them (Gyrinidae 2015). Their size ranges 3 to 18 mm long (Whirligig Beetles 2014). They eat insects that fall into the water, sensing the vibrations of their struggles by using their antennae. They are worldwide, with a heavy concentration in Europe.

But even these insects sometimes use mosses. At least some members of the **Gyrinidae** (Figure 12-Figure 14) use mosses as hiding places during the day (Leng 1913). And in the Appalachian Mountain, USA, streams, the mosses may provide a refuge for *Dineutus* (Figure 12-Figure 14) during times of high flow (Glime 1968).



Figure 12. *Dineutus discolor* (whirligig beetles) on the water surface. Photo by Janice Glime.



Figure 13. *Dineutus assimilis* adult showing split eyes. Photo by Joyce Gross, with permission.



Figure 14. *Dineutus* larva, a genus that sometimes occurs among bryophytes when it is resting. Photo by Bob Henricks, with permission.

### Haliplidae – Crawling Water Beetles

The **Haliplidae** are clumsy swimmers, alternating the motion of their legs (Haliplidae 2014). Hence, they move about mostly by crawling. The adults are convex on the dorsal side and range 1.5-5.0 mm long. The hind legs have large coxal plates and are immobile. The primary function of these legs seems to be that of storing air, supplementing the air stored under the elytra. The larvae eat only algae, but the adults are omnivorous. They live among aquatic vegetation around the borders of small ponds, lakes, and quiet streams. Their worldwide distribution is similar to that of the **Scirtidae**, with the greatest diversity known in Europe (Haliplidae 2015).

These are mostly not bryophyte dwellers, but the genus *Haliplus* (Figure 15) still benefits from the presence of *Sphagnum* (Figure 7). *Haliplus variegatus* (Figure 16) in Poland lives in canals that are created by beavers in floating *Sphagnum* mats (Buczyński *et al.* 2014).



Figure 15. *Haliplus* larva. Some members of this genus live in bogs and *H. variegatus* lives in beaver canals in floating *Sphagnum* mats. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.



Figure 16. *Haliplus variegatus* adults, inhabitants of beaver canals in floating *Sphagnum* mats of Poland. These color phases and the spots can help to camouflage the beetles among the mosses. Photo by Stefan Schmidt, through Creative Commons.

In my own studies (Glime 1968) in the Appalachian Mountain, USA, streams, I found the genus *Brychius* (Figure 17). The generic name suggests a possible moss habitat, but I was unable to find additional information on the habitat.



Figure 17. *Brychius elevatus* adult, a genus with moss inhabitants in Appalachian Mountain, USA, streams. Photo by Udo Schmidt, through Creative Commons.

### Hygrobiidae – Squeak Beetles

This small family has only one genus, *Hygrobia*, with six species, and is distributed in Europe, North Africa, China, and Australia (Hygrobia 2014). *Hygrobia* adults make a grating noise, earning them their name of squeak beetles (Pendleton & Pendleton 2014). Their size is moderate (8.5-10 mm). They are most common in stagnant water, where they walk or swim; they do not dive (Watson & Dallwitz 2003a). They obtain their oxygen from the air collected and stored under the elytra. *Hygrobia hermanni* (Figure 18) reaches large populations at pond margins where it lives among the submerged *Sphagnum* (Figure 39) (Denton 2013).



Figure 18. *Hygrobia hermanni* adult, an inhabitant of submerged *Sphagnum*. Note the anal air bubble. Photo by Trevor and Dilys Pendleton, with permission.

### Dytiscidae – Predaceous Diving Beetles and Noteridae – Burrowing Water Beetles

The *Noteridae* are often included with the *Dytiscidae* and I will do so here because it makes the discussion easier. The larvae of *Dytiscidae* are known as water tigers. They

are passive predators, waiting quietly until a prey organism passes nearby (Dytiscidae 2014). On the other hand, several members of the family are eaten by humans in China, Japan, and Mexico, as well as other places in the world. This worldwide family has a large range of sizes (1.2-40 mm long) (Bartlett 2004b). They are distributed throughout the world, but with the best known concentrations in North America, Europe, and Australia (Dytiscidae 2015). The larvae live in the water, but they climb to land and bury themselves in the mud for pupation, returning to the water as adults.

The adult *Dytiscidae*, like other beetles, lack true gills. Instead, they carry a bubble of air with them as they descend down the water column. This bubble is either held against the body or stored under the **elytra** (outer hardened wings) (Figure 1). As oxygen is used up, nitrogen maintains the size of the bubble so that oxygen can diffuse into the bubble. When the bubble becomes too small, they must obtain another bubble from plant surfaces or the water surface by exposing the tip of the abdomen (Figure 19).



Figure 19. *Rhantus suturellus* adult replenishing air supply at surface. Photo by Niels Sloth, with permission.

Based in my own studies on moss-dwelling aquatic insects in the Appalachian Mountains, USA, it seemed that the predaceous diving beetles (*Dytiscidae*) do not typically hang out among the bryophytes. But many of the species occur in mossy wet areas, especially associated with bogs and fens. Usinger (1974) describes three types of ovipositors in the *Dytiscidae*. Those with a long ovipositor are able to inject their eggs into moss mats growing in the water. And some species even ingest mosses occasionally (Jones 1949).

Roger Key (pers. com. 31 October 2014) considers the primary role of bryophytes in the life of the predaceous aquatic beetles to be that of a structural component, a place for cover to escape predators. But these beetles are mostly predators themselves (Figure 20). In some cases the mosses are important as a place to hang or climb to avoid being carried to the surface by their air supply – the plastron apparatus or air layer under the elytra. For example, *Lancetes* in South Georgia may make use of mosses, among other anchored substrata, to get back under the surface or to stay there when it is not actively swimming. In places like South Georgia, mosses are the predominant, if not the only, vegetation at the margins of streams, hence providing these roles for aquatic beetles there.





Figure 20. *Dytiscus* larva eating young fish. Photo by Roger S. Key, with permission.

*Graphoderus zonatus* (spangled diving beetle; Figure 21) occurs where *Fontinalis* (Figure 5) provides the major vegetation in a heathland mire in Hampshire, UK (Roger S. Key, pers. comm. 31 October 2014). This diving beetle is frequently found associated with the mosses and can be collected by shaking the mosses over a container. The bryophyte role, as suggested above, is one of cover.

*Oreodytes davisii* (Figure 22) and *O. sanmarkii* (Figure 23) both live among aquatic bryophytes in a stream in Yorkshire, UK (Gilbert *et al.* 2005). *Oreodytes rivalis* may occasionally even ingest mosses such as *Fontinalis antipyretica* (Figure 5) (Jones 1949), perhaps in their attempts to capture one of the other invertebrates dwelling there.



Figure 21. *Graphoderus zonatus* adult in a heathland mire in Hampshire, UK. Photo by Roger S. Key, with permission.

Foster (1992) found *Hydroporus umbrosus* (Figure 24) among mosses at the edge of a pond in Inner Hordaland, Norway. Usinger (1974) describes the small members of the genus *Hydroporus* as able to occupy moss-covered seepages no bigger than a hand. Buczyński *et al.* (2014) reported *H. incognitus* (Figure 25) from *Sphagnum*

bogs (Figure 26) in Poland. In spring-fed boggy areas one can find *Hydroporus longulus* (Figure 27) among mosses and leaves (Denton 2013).



Figure 22. *Oreodytes davisii* adult, a bryophyte dweller in UK streams. Photo by Udo Schmidt, with permission.



Figure 23. *Oreodytes sanmarkii* adult, a stream bryophyte dweller in the UK. Photo by Christoph Benisch <[www.kerbtier.de](http://www.kerbtier.de)>, with permission.



Figure 24. *Hydroporus umbrosus* adult, a moss dweller at the edge of ponds in Norway. Photo by Niels Sloth, with permission.





Figure 25. *Hydroporus incognitus* adult, an inhabitant of *Sphagnum* bogs in Poland. Photo by Niels Sloth, with permission.



Figure 26. *Sphagnum* blanket bog, home to many kinds of beetles. Photo through Creative Commons.



Figure 27. *Hydroporus longulus* adult, a beetle one can find among mosses in spring-fed boggy areas. Photo by Tim Faasen, with permission.

*Graphoderus zonatus* (Figure 28) in North Hampshire, UK, lives in a variety of habitats, particularly in *Sphagnum*-dominated (Figure 39) lake margins (Denton 2013).



Figure 28. *Graphoderus zonatus* adult with *Sphagnum*. Photo by Niels Sloth, with permission.

### Moors, Bogs, and Fens

These three habitats are partially aquatic, providing wet or damp bryophytes and pools where there may be submerged bryophytes. **Moors**, a term used more commonly in Europe, are upland habitats including heathlands and fens and characterized by low vegetation and acidic soils (Moorland 2014). The term **bog** has a mixed history, with North Americans using a much broader definition than that of the northern Europeans. Until relatively recently, North Americans tended to include any wetland with *Sphagnum* as a bog. English language dictionaries go even further to define a bog as any muddy or spongy wetland. The more restrictive European definition is a habitat that is dominated by *Sphagnum* and receives only precipitation as a source of new nutrients. By contrast, a **fen** may have *Sphagnum* or other dominant bryophytes, but it receives nutrients through surface or ground water in addition to precipitation. Most of the habitats that North Americans have called bogs (including most current definitions and websites on the internet) are actually **poor fens**, *i.e.*, wetland habitats with low nutrients, ground or surface water, and *Sphagnum* species similar to those of true bogs.

Fens and bogs provide habitats for a number of **Dytiscidae** and provide the most common associations with bryophytes. The genus *Agabus* is among these common inhabitants (Nelson 1996). *Agabus affinis* (Figure 29) can be considered a characteristic species, a **tyrphobiont** (species living only in peat-bogs and mires) in high moors (Hebauer 1974), often accompanied by *A. unguicularis* (Figure 30), in the moss lawns of lowland fens and bogs of Ireland (Nelson 1996) and flooded *Sphagnum* (Figure 39) (Denton 2013). In Scotland *A. unguicularis* occurs in peaty water with mosses or other dense vegetation (Knight 2014). *Agabus melanocornis* is less common and occurs in mossy drains, fens, and bogs (Nelson 1996). *Agabus melanarius* (Figure 31) is easily overlooked in North Hampshire, UK, where it lives in shallow water with mosses.





Figure 29. *Agabus affinis* adult with *Sphagnum*. Photo by Tim Faasen, with permission.



Figure 30. *Agabus unguicularis* adult, a common inhabitant of bogs and fens, carrying an anal air bubble. Photo by Niels Sloth, with permission.



Figure 31. *Agabus melanarius* adult, a species from shallow water among mosses. Photo by James K. Lindsey, with permission.

In contrast to other bryophyte habitats, bogs are a mix of terrestrial and aquatic microhabitats that provide homes for a number of **Dytiscidae**. Brink and Terlutter (1983) found *Dytiscus lapponicus* (Figure 32-Figure 34), *Hydroporus tristis* (Figure 35), *H. erythrocephalus* (Figure 36), and *Acilius canaliculatus* (Figure 37), as well as **Noteridae** (burrowing water beetles, sometimes included in the **Dytiscidae**) – *Noterus crassicornis* (Figure 38), to be acid **tyrphophiles** (characteristic of bogs but not confined to them) associated with *Sphagnum cuspidatum* (Figure 39). *Acilius* is one of the genera with a long ovipositor that permits egg-laying among mosses and other substrata (Unger 1956). These eggs are laid in the water and sometimes out of water. From Dartmoor, UK, Boyce

(2011) also reported *Hydroporus tristis* in small, peaty pools that had *Sphagnum* (Figure 39). Boyce also found *Hydroporus gyllenhalii* (Figure 40) among *Sphagnum* in bogs and in small peat pools that likewise had at least some *Sphagnum* in both undisturbed and eroded blanket mires. *Hydroporus obscurus* (Figure 42-Figure 43) was more restricted, living only in relatively pristine blanket bogs where it lived in small *Sphagnum*-dominated peat pools.



Figure 32. *Dytiscus lapponicus* larva, a species associated with *Sphagnum cuspidatum*. Photo by James K. Lindsey, with permission.



Figure 33. *Dytiscus lapponicus* adult with mosses and aquatic plants. Photo by Niels Sloth, with permission.



Figure 34. *Dytiscus lapponicus* adult with mosses and aquatic plants. Photo by Niels Sloth, with permission.





Figure 35. *Hydroporus tristis* adult amid aquatic mosses. Photo by Tim Faasen, with permission.



Figure 36. *Hydroporus erythrocephalus* adult with leaf and *Sphagnum*. Photo by Tim Faasen, with permission.



Figure 37. *Acilius canaliculatus* adult, a species associated with *Sphagnum cuspidatum* (Figure 39). Photo by Niels Sloth, with permission.



Figure 38. *Noterus crassicornis* adult on leaf litter in stream. Photo by Niels Sloth, with permission.



Figure 39. *Sphagnum cuspidatum*, home for some *Dytiscidae* and *Noteridae*. Photo by Jan-Peter Frahm, with permission.



Figure 40. *Hydroporus gyllenhalii* adult, a species that lives among *Sphagnum* in bogs and bog pools. Photo by Niels Sloth, with permission.

In his studies in Central Europe, Hebauer (1974) similarly found *Hydroporus pubescens* (Figure 41) to be a tyrphobiont, as well as such tyrphobionts as *Hydroporus obscurus* (Figure 42-Figure 43) and *H. melanocephalus* in the high moors (Hebauer 1994).

The smallest member of Irish *Hydroporus* is *H. scalesianus* (Figure 44) (Nelson 1996). In the Appalachian Mountain, USA, streams, this genus lives among stream mosses (Glime 1968), whereas in Ireland it lives exclusively among mossy carpets of undisturbed fens, mires, and lake basins.



Figure 41. *Hydroporus pubescens* adult among *Sphagnum*. Photo by Tim Faasen, with permission.





Figure 42. *Hydroporus obscurus* adult on *Sphagnum*. Photo by Tim Faasen, with permission.



Figure 43. *Hydroporus obscurus* adult climbing on a moss. Photo by Niels Sloth, with permission.



Figure 44. *Hydroporus scalesianus* adult, the smallest *Hydroporus*, on *Sphagnum*, from the high moors of Europe. Photo by Tim Faasen, with permission.

Other tyrphobionts in the high moors included *Rhantus suturellus* (Figure 19, Figure 45) (Hebauer 1974), a species also found in Poland in peaty pools (Boyce 2011). In Ireland, *Graptodytes granularis* (Figure 46) lives in mossy carpets of undisturbed fens, mires, and lake basins, but requires permanently wet mosses (Nelson 1996).

*Ilybius crassus* and *I. aenescens* (Figure 47-Figure 48) are tyrphobionts in European high moors (Hebauer 2004). *Ilybius aenescens* also occurs in flooded *Sphagnum* (Figure 39) of heathlands of North Hampshire, UK, but it is rare (Denton 2013). Boyce (2011) found that *Ilybius montanus* usually occur in shallow bog pools where there are dense growths of *Sphagnum*. *Ilybius fuliginosus* (Figure 49) is quite ubiquitous and thus might be found hiding among the mosses (Tim Faasen, pers. comm. 20

October 2014). But *Ilybius* is not restricted to bogs and moors, appearing among mosses in Appalachian Mountain, USA, streams (Glime 1968).



Figure 45. *Rhantus* larva. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.



Figure 46. *Graptodytes granularis* adult, dwelling in the high moors of Europe. Photo by Tim Faasen, with permission.



Figure 47. *Ilybius aenescens* adult among mosses. Photo by Tim Faasen, with permission.



Figure 48. *Ilybius aenescens* adult, a bog dweller. Photo by Niels Sloth, with permission.



Figure 49. *Ilybius fuliginosus* adult, a ubiquitous species that hides among vegetation, shown here on mosses. Photo by Tim Faasen, with permission.

*Laccornis oblongus* (Figure 50) is a flightless beetle that lives in Irish fens that lack open water (Nelson 1996). It occurs among wet moss carpets, especially those associated with clumps of sedges. *Hydaticus seminger* (Figure 51) is a dweller of typical mossy fens. This species is not frequent in North Hampshire, UK, but it does occur among flooded *Sphagnum* and in detritus pools (Denton 2013).



Figure 50. *Laccornis oblongus* adult, a flightless beetle known from moss carpets in Irish fens. Photo by Niels Sloth, with permission.



Figure 51. *Hydaticus seminger* adult, a mossy fen dweller. Photo by Tim Faasen, with permission.

Floating moss carpets are often associated with bogs and fens. *Bidessus grossepunctatus* (Figure 52) is one of the inhabitants of these moss carpets in small lakes, ponds, fen pools, and mires (Nilsson & Holmen 1995).



Figure 52. *Bidessus grossepunctatus* adult, an inhabitant of floating moss carpets, on *Sphagnum*. Photo by Tim Faasen, with permission.

Special techniques can facilitate collecting bog and fen species. Since bryophytes in these habitats are typically underlain by water, these semi-terrestrial beetles can be collected by depressing the mosses, creating a depression until they are covered by water (Nilsson & Holmen 1995; Knight 2014). The beetles can then be swept from the water with a tea strainer. Knight (2014) considers this technique especially useful for sampling **Hydraenidae** and small **Hydrophilidae**.

In the Japanese rice fields, many invertebrates find refuge. Some of these fields even have peat mosses. Such communities include *Cybister japonicus* (Figure 53-Figure 54) (Ohba 2009), a species eaten by humans in Japan (Dytiscidae 2014). These carnivores feed on insects such as Odonata in early instars, but starting in the third instar they feed on small vertebrates such as amphibia as well. In the last larval stage, they burrow into the peat moss and enter the pupation period.





Figure 53. *Cybister japonicus* adult, a species that hides among peat mosses in Japanese rice fields. Photo through Creative Commons.



Figure 54. *Cybister japonicus* larva, a species that hides among peat mosses in Japanese rice fields. Photo through Creative Commons.

*Liodessus cantralli* (Figure 55) lives in small pools in North America, but also lives in moss mats of fens (less often in bogs) (Larson & Roughley 1990). They are particularly associated with *Drepanocladus* s.l. (Figure 56) in depressions in the moss mats.



Figure 55. *Liodessus* adult; *L. cantralli* lives in moss mats of fens. Photo © Stephen Luk through BugGuide non-commercial use, with permission.

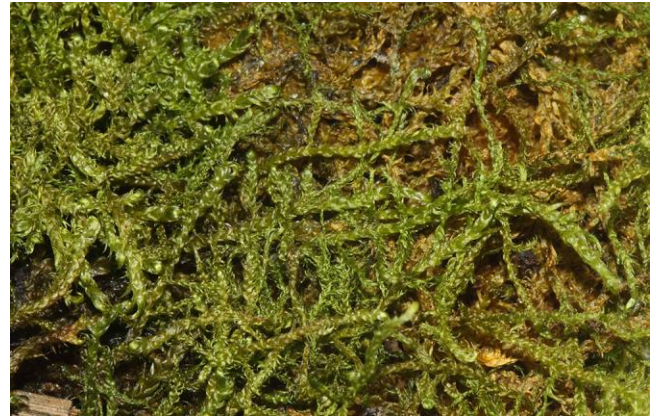


Figure 56. *Drepanocladus aduncus*, home of *Liodessus cantralli* in North America. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University.

## Summary

**Coleoptera** can live in the water as larvae and as adults, but the pupae are generally on land. The aquatic adults gain oxygen by using a **plastron**, accumulating air under the forewings, or from an anal bubble. Some live on the surface and may crawl over plants such as *Ricciocarpus natans*. Smaller beetles live among mosses in streams. But the greatest number of aquatic bryophyte associations for beetles occurs in bogs and fens.

The order **Coleoptera** (beetles) has two sub orders: **Adephaga** and **Polyphaga**. In the **Adephaga** the families **Carabidae**, **Gyrinidae**, **Haliplidae**, **Hygrobiidae**, and **Dytiscidae**. The **Dytiscidae** are especially common and diverse in bog pools and this is the only family of **Adephaga** frequently associated with bryophytes.

## Acknowledgments

Tim Faasen not only gave me permission to use his wide collection of insect images, he also helped me to understand the ecology of some of the species and provided me with additional images I needed. Thank you to Roger S. Key not only for his permission to use his images but for sharing his experiences with me regarding beetle use of bryophytes. Ronald Willson verified my beetle identifications for the mid-Appalachian Mountain study. And thank you to Amy Marcarelli, Wayne Minshall, and especially Rich Merritt for helping me with my query about the anal air bubble in aquatic beetles. Eileen Dumire proofread the chapter and suggested changes to provide more clarity.

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# CHAPTER 11-10

## AQUATIC INSECTS: HOLOMETABOLA – COLEOPTERA, SUBORDER POLYPHAGA

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# CHAPTER 11-10

## AQUATIC INSECTS: HOLOMETABOLA – COLEOPTERA, SUBORDER POLYPHAGA



Figure 1. *Ilybius erichsoni* adult on *Sphagnum*. Photo by Niels Sloth, with permission.

### Suborder Polyphaga

This suborder includes more than 90% of the **Coleoptera** species. As its name suggests, it eats a tremendous variety of foods.

#### Helophoridae

This is a family of North America and Europe and has only one genus, *Helophorus* (Helophoridae 2014). They are relatively small (2-9 mm) (Helophoridae 2014) and live primarily in wetlands (Helophoridae 2015). Most adults live in shallow standing water where they are **saprophagous** (Fikáček 2009) (organism that feeds on decaying organic matter). Larvae, on the other hand, live in terrestrial, but moist, habitats near water and are predators on small invertebrates.

*Helophorus grandis* (Figure 2) occurs among the aquatic mosses in a stream in Yorkshire, UK (Gilbert *et al.* 2005). In Canada, *Helophorus orientalis* (Figure 3) occurs in wet mosses beside small streams (Majka 2008).

*Helophorus strigifrons* (Figure 4) lives in bogs in North Hampshire, UK, among moss and litter (Denton 2013).



Figure 2. *Helophorus grandis*, an inhabitant of stream mosses in the UK. Photo by Tim Faasen, with permission.





Figure 3. *Helophorus orientalis* adult, a species that lives among wet mosses along streams in Ontario, Canada. Photo by Tom Murray, through Creative Commons.



Figure 4. *Helophorus strigifrons* adult, a bog dweller in North Hampshire, UK, among moss and litter. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

### Hydrochidae

Although this family is worldwide, it has only one genus, and most of the records are from Europe (Hydrochidae 2015a). Adults and larvae live in both quiet and flowing water where they are herbivores – shredders (Hydrochidae 2015b). The adults range 4-60 mm long. Some of these are associated with bryophytes.

*Hydrochus ignicollis* (Figure 5), a very rare species in Ireland, appeared in collections only twice between 1988 and 1996 (Nelson 1996). Both finds were from mossy calcareous fens adjacent to **marl lakes** (calcium carbonate or lime-rich lakes. These are alkaline lakes with unconsolidated calcium carbonate or lime-rich mud or mudstone which contains variable amounts of clays and silt (Figure 6-Figure 7).



Figure 5. *Hydrochus ignicollis* adult, a rare inhabitant of mossy calcareous fens in Ireland. Photo by Tim Faasen, with permission.



Figure 6. Marl lake in Jasper National Park, Canada. Photo by Janice Glime.



Figure 7. Marl at margin of marl lake in Jasper National Park, Canada. Photo by Janice Glime.

### Hydrophilidae – Water Scavenger Beetles

This is a worldwide, mostly aquatic family, typically in open water (Cotinus 2005). The larvae often emerge from the water to pupate, usually hanging from moss at the edge of the water (Water Beetles 2014). The final larval skin is found beneath the pupa. The adults (1-40 mm) are mostly scavengers, but some are predators; larvae are often predators (Cotinus 2005).



Some **Hydrophilidae** join the **Dytiscidae** as common beetles swimming in bog waters. *Enochrus* (Figure 8-Figure 9) is a common genus there (Denton 2013). *Enochrus affinis* (Figure 10) is often abundant in *Sphagnum*-dominated (Figure 51) areas of acidic heathland pools (Figure 11) of North Hampshire, UK. *Enochrus coarctatus* (Figure 12) is a mire dweller, preferring older detritus pools but also living in *Sphagnum*-filled large bog pools. *Enochrus ochropterus* (Figure 13) does not occur in areas of pure *Sphagnum* where the *Enochrus* is exclusively *E. affinis*. However, it does occur in richer areas with *E. coarctatus*. The importance of the *Sphagnum* in its habitats may be due to its role in acidification. *Enochrus fuscipennis* (Figure 14) lives in the *Sphagnum*-choked shallow pools of undisturbed blanket bogs in Dartmoor, UK (Boyce 2011). *Enochrus hamiltoni* (Figure 15), on the other hand, lives in wet mosses next to small streams on Prince Edward Island, Canada (Majka 2008). In the Appalachian Mountain streams, eastern USA, the genus *Enochrus* can occasionally be found among mosses, as well as the genus *Tropisternus* (Figure 16-Figure 17) (Glime 1968).



Figure 8. *Enochrus* larva, common among bog bryophytes. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.



Figure 9. *Enochrus* larval head. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.



Figure 10. *Enochrus affinis* adult, an abundant species in *Sphagnum*-dominated heathland pools in North Hampshire, UK. Photo by Christoph Benisch <kerbtier.de>, with permission.



Figure 11. Heathland with a pool. Photo by Jim Champion, through Creative Commons.



Figure 12. *Enochrus coarctatus* adult, an inhabitant of mire pools, often among *Sphagnum*. Photo by Udo Schmidt, with permission.





Figure 13. *Enochrus ochropterus* adult, a species of rich mires, often associated with *Sphagnum*. Photo by Niels Sloth, with permission.



Figure 14. *Enochrus fuscipennis* adult, a species that lives in *Sphagnum*-filled shallow pools in blanket bogs. Photo by James K. Lindsey, with permission.



Figure 15. *Enochrus hamiltoni* adult, a dweller of wet mosses next to small streams on Prince Edward Island, Canada. Photo by Tom Murray, through Creative Commons.



Figure 16. *Tropisternus* sp. larva, an occasional moss inhabitant in Appalachian Mountain, USA, streams. Photo by Tom Murray, through Creative Commons.



Figure 17. *Tropisternus natator* adult, an occasional moss inhabitant in Appalachian Mountain, USA, streams. Photo by Donald S. Chandler, with permission.

The genus *Laccobius* (Figure 18-Figure 19) associates with mosses in both stream and mire habitats. *Laccobius reflexipennis* (see Figure 18) live in wet mosses next to small streams on Prince Edward Island, Canada (Majka 2008). *Laccobius atratus* in Ireland and Great Britain occurs in *Sphagnum* (Figure 51) bogs and other peatlands (Friday 1987; Nelson 1996; Denton 2013). *Laccobius ytenensis* adults live among mosses around the tiny pools that occur in the seepage lines of UK bogs (Denton 2013).



Figure 18. *Laccobius* sp. adult, a genus with several species that live in water or bog mosses. Photo by Gerard Visser <[www.microcosmos.nl](http://www.microcosmos.nl)>, with permission.



Figure 19. *Laccobius* adult with open wings showing the membranous wings under the hardened elytra. Photo by Michael Schmidt, through Creative Commons.



*Chaetarthria siminulum* (Figure 20) can be present in "huge" numbers among mosses at the edges of ponds (Denton 2013). It also lives among mosses in fens and in fen litter.



Figure 20. *Chaetarthria siminulum* adult with plastron. When the plastron is full of air, the beetle must cling to vegetation in order to descend into the water column. Photo by Gerard Visser, with permission.

Hebauer (1994) found *Crenitis punctatostrata* (Figure 21) in the high moors, living as a tyrphobiont. *Hydrobius fuscipes* (Figure 22-Figure 23) on Prince Edward Island (Majka 2008) occurs in *Sphagnum* (Figure 51) bogs and other peatlands.



Figure 21. *Crenitis punctatostrata* adult, a beetle that lives in bogs of the high moors. Photo by Udo Schmidt, with permission.



Figure 22. *Hydrobius fuscipes* adult, a species of *Sphagnum* bogs. Photo by Tim Faasen, with permission.



Figure 23. *Hydrobius* larval head showing large mandibles. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Friends are wonderful, and I recently received this story and all the images from Andrea Ares. She found an "amazing place" covered with the leafy liverwort *Jungermannia vulcanicola* (Figure 24-Figure 25) in Chatubomigoke Park, Gunma Prefecture, Japan. Soon she also discovered a small (6-7 mm) black beetle wending its way upon and within the "big, robust carpet" of the liverwort in this acid stream. This beetle was identified by Itouga san as *Hydrobius pauper* (Figure 26-Figure 28), the only member of the genus in Japan. There was not just one, but the bases of the liverworts were "full" of them.



Figure 24. Cushions of *Jungermannia vulcanicola* (chartreuse-colored cushions) in Chatubomigoke Park in Japan. Photo courtesy of Angela Ares.





Figure 25. Habitat of *Jungermannia vulcanicola* (chartreuse-colored cushions) in Chatubomigoke Park in Japan. Photo courtesy of Angela Ares.



Figure 26. Cushion of *Jungermannia vulcanicola* with its inhabitants, *Hydrobius pauper*. Photo courtesy of Angela Ares.



Figure 27. Disturbed cushion of *Jungermannia vulcanicola* showing bases of plants with its inhabitants, *Hydrobius pauper*. Photo courtesy of Angela Ares.



Figure 28. *Hydrobius pauper* adult. Photo by Itago san.

*Berosus luridus* (Figure 29, Figure 30) is tyrphophilic, living among *Sphagnum* (Figure 51), but can also be found in other places (Tim Faasen, pers. comm.). I have found no other records of it living among *Sphagnum*, but it is rare in the Netherlands and may be rare elsewhere. Perhaps the *Sphagnum* provides a relict habitat, a safe site where conditions are still tolerable.



Figure 29. *Berosus luridus* adult on moss, a rare beetle in the Netherlands, but present in bogs among *Sphagnum* there. Note the air bubbles on the moss; these can be used to replenish the air supply. Photo by Tim Faasen, with permission.



Figure 30. *Berosus* larva, a moss dweller in bogs of New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.



In tropical Africa, the genus *Anacaena* is probably more common than is recognized. Komarek (2004) described nine new species. Among these, four were from mosses. *Anacaena capensis* occurs among the mosses and leaf litter of mountain rivulets in South Africa. *Anacaena glabriventris* lives among mosses in small streams; *A. reducta* likewise lives among mosses in small streams, but with steep channels. *Anacaena tenella* lives among **hygropetric** mosses (mosses growing on vertical rock faces where a thin film of water flows) in mountain streams. *Anacaena limbata* (Figure 31) lives in wet mosses next to small streams on Prince Edward Island, Canada (Majka 2008).



Figure 31. *Anacaena limbata* adult, an inhabitant of wet mosses adjacent to streams. Photo by Tim Faasen, with permission.

*Anacaena globulus* (Figure 32) lives among *Sphagnum* (Figure 32) in bogs in Europe and can be collected by squeezing the moss (Buczyński *et al.* 2014). However, Faasen (personal communication) does not find them typically in *Sphagnum* bogs in the Netherlands, but considers them widespread, occasionally occurring in bogs.

Also in Dartmoor, UK, *Helochaeres punctatus* (Figure 33) is an obligate mire species, living among saturated *Sphagnum*, particularly *S. cuspidatum* (Figure 34), of pools and acid flushes.



Figure 32. *Anacaena globulus* adult on *Sphagnum*, one of its many habitats. Photo by Tim Faasen, with permission.



Figure 33. *Helochaeres punctatus* adult on moss. Photo by Niels Sloth, with permission.



Figure 34. *Sphagnum cuspidatum*, home for *Helochaeres punctatus*. Photo by David T. Holyoak, with permission.

Nelson (1996) found several additional species of **Hydrophilidae** in Irish mossy fens. These included *Cercyon convexiusculus* (Figure 35-Figure 36) in mossy fens. In North Hampshire, UK, Denton (2013) found this species to be abundant in detritus and rotting leaf litter, but also among mosses that bordered richly vegetated sites. *Cercyon marinus* similarly occupied mosses or decaying organic matter at the water's edge in Ireland (Nelson 1996). *Cercyon ustulatus* (Figure 37) occurs in mossy areas of ponds and also occurs among mosses growing on sewage filter beds (Denton 2013).



Figure 35. *Cercyon convexiusculus* adult, an inhabitant of mossy fens. Photo by Tim Faasen, with permission.





Figure 36. *Ceryon convexusculus* adult, an inhabitant of mossy fens. Photo by Christoph Benisch <kerbtier.de>, with permission.



Figure 37. *Ceryon ustulatus* adult, an inhabitant of mossy areas of ponds and filter beds. Photo by Tom Murray, through Creative Commons.

*Paracymus scutellaris* (Figure 38) occurs among peat mosses in Ireland (Nelson 1996).



Figure 38. *Paracymus scutellaris* adult, a peat moss dweller in Ireland. Photo by Udo Schmidt, with permission.

## Hydraenidae – Minute Moss Beetles

Adults of **Hydraenidae** (Figure 39), known as minute moss beetles (1-3 mm length), are aquatic, but the larvae drown if completely submersed (Watson & Dallwitz 2012). Even adults are poor swimmers (EOL 2014); most eat plants, but a few are carnivorous or **saprophagous** (feeding on decaying organic matter) (Hydraenidae 2014). They are sparsely distributed worldwide with a concentration in Europe (EOL 2014).

Sarr *et al.* (2013) found that *Hydraena* was correlated with a moss substrate in Northwest Spain. Berthélemy (1966) found this family commonly among mosses in the Pyrénées, including *Hydraena gracilis* (Figure 40), *H. minutissima*, and *H. pygmaea* (Figure 41), with the latter two being considered **musciholes** (thriving among mosses). He also considered *Hydraena pulchella* (Figure 42) and *Hadrenya* to be **musciholes**. Nelson (1996) reported *Hydraena gracilis* as a common and widespread species in Britain where it lives on mossy rocks in fast-flowing streams and rivers.



Figure 39. **Hydraenidae** adult, an aquatic minute moss beetle that commonly lives among mosses in the Pyrénées. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 40. *Hydraena gracilis* adult, a common aquatic moss inhabitant in the Pyrénées. Photo by Tim Faasen, with permission.





Figure 41. *Hydraena pygmaea* adult, a muscicole in the Pyrénées. Photo by Tim Faasen, with permission.

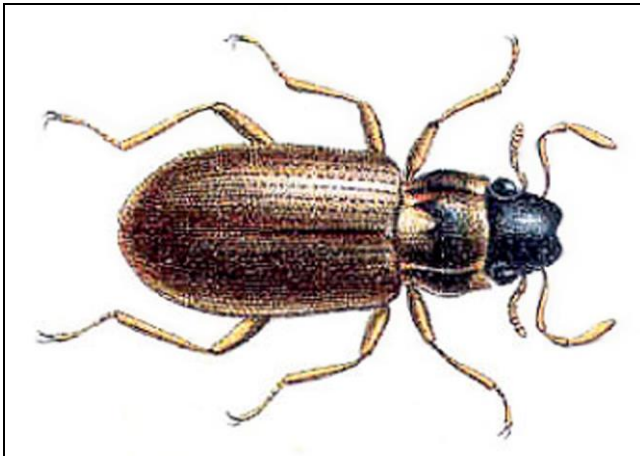


Figure 42. *Hydraena pulchella* adult, a tiny beetle that lives among stream mosses in Europe. Image through Creative Commons.

*Hydraena nigrita* is a tiny beetle that lives among mosses at the edges of streams, but it will climb out if the moss is placed under water (Anderson 2014). It is considered vulnerable because of siltation and loss of habitat (Foster *et al.* 2009). *Hydraena rufipes* (Figure 43) lives among mosses (Nelson 1996; Knight 2014) and fine **shingle** (mass of small rounded pebbles) along rivers (Nelson 1996).



Figure 43. *Hydraena rufipes* adult, a species that lives among mosses along rivers. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Hebauer (1994) found similar species representation from this family in middle Europe. Among the stream mosses he found *Hydraena minutissima*, *H. pygmaea* (Figure 41), and *H. pulchella* (Figure 42). Several more used mosses or algae as a substrate: *Ochthebius granulatus* (Figure 44), *O. metallescens* (Figure 45), *O. exsculptus* (Figure 46), *O. melanescens*, *O. colveranus*, and *O. halbherri*. Eggs of *Ochthebius* are either naked or somewhat covered by loosely applied silk provided by the mother; the eggs hatch in 7-10 days. In rivers in Northwest Spain, Sarr *et al.* (2013) found that *Ochthebius heydeni* was likewise correlated with a moss substrate.

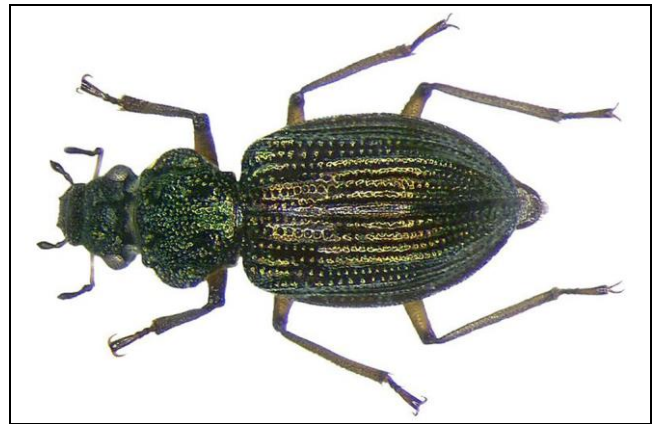


Figure 44. *Ochthebius granulatus* adult, a stream moss dweller in middle Europe. Photo by Magnus Manske.



Figure 45. *Ochthebius metallescens* adult, a beetle that uses mosses and algae as substrates. Photo by Tim Faasen, with permission.

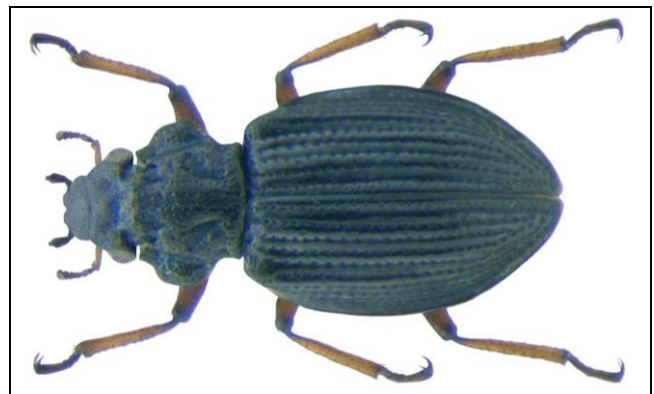


Figure 46. *Ochthebius exsculptus* adult, a European stream moss dweller. Photo by Udo Schmidt, with permission.



*Limnebius nitidus* (Figure 47) is among the smallest of the water beetles and in addition to wet mud, it makes mosses in swamps and at the edges of pools and streams its home (Nelson 1996). Adults are a mere mm long, so these scavengers of dead plants and animals are easily overlooked (Hilsenhoff 1975). Eggs of this genus are either naked or somewhat covered with loosely applied silk and hatch in 7-10 days (Usinger 1956). In my studies in the Appalachian Mountain streams of the eastern US, this genus likewise occurred among submerged mosses (Glime 1968).

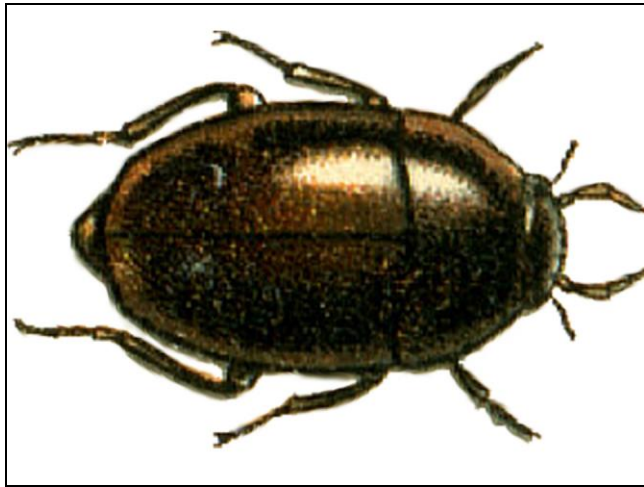


Figure 47. *Limnebius nitidus* adult, one of the smallest of all water beetles and a moss dweller in swamps. Photo through United States public domain.

*Hygrotus decoratus* (Figure 48) lives in shallow, mossy fens in North Hampshire, UK, where mosses may provide safe sites for larvae and adults (Denton 2013). *Hygrotus novemlineatus* was reared with **Chironomidae** larvae as a food source (Nilsson 1983). Mosses were provided in the culture chamber. After a few days, the beetles laid eggs, attaching them to branches of mosses. But is this a normal substrate for egg-laying in nature? The habitat seems suitable, providing lots of **Chironomidae** larvae as food. This genus should be sought among bryophytes in other fens.



Figure 48. *Hygrotus decoratus* adult, a species of shallow mossy fens, at surface getting air. Photo by Niels Sloth, with permission.

## Ptiliidae – Featherwing Beetles

This is a large, worldwide family of minute (0.3-2 mm long) beetles (Ptiliidae 2015). The egg size is half the length of the body and only one is developed at a time, permitting the female to store a large energy supply in the egg. Their wide-ranging habitats include moist leaf litter, under bark of dead trees, along sand and gravel banks of rivers and streams, beneath seaweed on beaches, in mammal nests, on dung, rotting cacti, ant and termite colonies, and other habitats containing rotting or damp organic material. And some seem to live their entire lives in bogs.

The small size of several **Ptiliidae** beetles – *Tychobythinus bythinoides* (Staphylinidae or Ptiliidae; Figure 65), *Ptiliopycna moerens* (Figure 49), *Acrotrichis* (Figure 50) – and other small beetles in bogs seems to correlate with a high incidence of **parthenogenesis** (reproduction from an unfertilized egg) in **relict** (habitat that survived from an earlier period) bogs (Dybas 1978), most likely having poor dispersal as an additional selection factor.



Figure 49. *Ptiliopycna moerens* adult, a parthenogenetic inhabitant of relict bogs. Photo © Stephen Luk for non-commercial use, with permission.



Figure 50. *Acrotrichis* sp. adult, a parthenogenetic inhabitant of relict bogs. Photo by Joyce Gross, with permission.



*Ptiliopycna moerens* is minute, less than 1.0 mm long, and lives in the northeastern United States and adjacent Canada (Dybas 1978). It lives in *Sphagnum* in bogs and swamp forests, confined within the limits of Wisconsinian glaciation. Males are seemingly restricted to the northern part of the range. More southern locations have parthenogenetic females, a common character of small beetles in relict bogs. (See the chapter on Terrestrial Insects – Coleoptera for further discussion of beetles in bogs.)

### Silphidae – Large Carrion Beetles

This family is predominantly in the Northern Hemisphere, although scattered records exist in the Southern Hemisphere (Silphidae 2015a). Ranging in size from 7-45 mm, the family is rare in the tropics where ants might out-compete them (Silphidae 2015b). As the common name implies, the family feeds on decaying organic matter. Because of this feeding behavior, forensic scientists use their stage of development to determine how long a body has been dead.

Despite the need to find new carcasses as their carcass home ages, the **Silphidae** use walking as their primary means of locomotion (Silphidae 2015b). Most of their activity occurs at night.

The **Silphidae** have a variety of defenses (Silphidae 2015b). These include color warnings from **aposematism** (use of bright colors to advertise danger or unpalatability) to **Batesian mimicry** (mimicking coloration or behavior of poisonous or unpalatable species), chemical defenses, and parental care. And many of them use camouflage, having dark colors with a mix of gold, black, and brown to blend with their environment.

Some carrion beetles (**Silphidae**) occur in bogs. Beninger and Peck (1992) described the resource use by *Nicrophorus* species (carrion beetles, **Silphidae**) in a *Sphagnum* (Figure 51) bog near Ottawa, Canada, and found that resource use differed little from resource use in forested habitats. However, *Nicrophorus vespilloides* (Figure 52) used only small carrion (Figure 53) in the bog for reproduction, whereas the closely related *N. defodiens* (Figure 54) went to the nearby forest for reproduction. Likewise, *N. sayi* (Figure 55), *N. orbicollis* (Figure 56), and *N. tomentosus* (Figure 57), also bog inhabitants, were rarely associated with the small carrion of the bog, but rather reproduced mostly in the forest.



Figure 51. *Sphagnum* blanket bog. Photo through Creative Commons.



Figure 52. *Nicrophorus vespilloides* adult, a common carrion beetle that occurs in bogs. Photo by Tim Faasen, with permission.



Figure 53. *Nicrophorus vespilloides* with small carrion, a preferred substrate for its reproduction in bogs. Photo by Niels Sloth, with permission.



Figure 54. *Nicrophorus defodiens* adult, a bog dweller that goes to the forest to reproduce. Photo by Derek Sikes, through Creative Commons.





Figure 55. *Nicrophorus sayi* adult, a bog dweller that goes to the forest to reproduce. Photo by Tom Murray, through Creative Commons.



Figure 56. *Nicrophorus orbicollis* adult, a bog dweller that goes to the forest to reproduce. Photo by Tom Murray, through Creative Commons.



Figure 57. *Nicrophorus tomentosus* adult, a bog dweller that goes to the forest to reproduce. Photo by Tom Murray, through Creative Commons.

## Staphylinidae – Rove Beetles

These beetles are distinctive in having short wings that cover less than half the abdomen (Bartlett 2004). This large family has about 58,000 species, ranging in size from 1 to 35 mm, but mostly 2-8 mm (Rove Beetle 2014). Distribution is worldwide, but records are lacking in vast areas of Asia and Africa. They live in every imaginable type of habitat and likewise eat everything – except living plants! There is now one exception to that – a recent discovery of a herbivore.

Like the *Carabidae*, the *Staphylinidae* are not aquatic, but likewise inhabit bogs (Boyce 2011). In Dartmoor, UK, *Gymnusa brevicollis* (Figure 58) is **stenotopic** (able to tolerate only a restricted range of habitats or ecological conditions). Its preferred habitat is saturated *Sphagnum* (Figure 51) in extremely wet acid mires where they can be found at the edge of bog pools.



Figure 58. *Gymnusa brevicollis* adult, a beetle that lives among saturated *Sphagnum* at the edge of bog pools of wet acid mires. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

*Myllaena kraatzii* (Figure 59), a nationally (UK) rare species, is restricted to very high quality acid mires with abundant bog mosses (Boyce 2011). It is collected by shaking the *Sphagnum* (Figure 51) and litter, suggesting close ties with these two substrates. *Oxypoda procerula* (Figure 60) is likewise sampled by shaking the litter and *Sphagnum*, indicating that it is directly a moss dweller.



Figure 59. *Myllaena vulpina* adult. *Myllaena kraatzii* is a rare species of high quality acid mires in the UK. Photo by Reginald Webster, Jan Klimaszewski, Georges Pelletier, and Karine Savard through Creative Commons.





Figure 60. *Oxyptoda procerula* adult, a *Sphagnum* and litter dweller. Photo by Udo Schmidt, through Creative Commons.

*Philonothus nigrita* (Figure 61) is a characteristic species in *Sphagnum*-dominated (Figure 51) acid mires (Boyce 2011). It can be found by treading on the moss cushions, causing it to float out of the saturated *Sphagnum*. *Stenus brevipennis* (see Figure 62) lives among *Sphagnum* in blanket bogs. *Stenus kiesenwetteri* (Figure 63) is rare in the UK, occurring in very wet *Sphagnum* (Butler 1886).



Figure 61. *Philonothus nigrita* adult, a species that characterizes *Sphagnum*-dominated acid mires. Photo by Marko Mutanen, through Creative Commons.



Figure 62. *Stenus biguttatus* adult. *Stenus brevipennis* lives among *Sphagnum* of blanket bogs. Photo through Creative Commons.



Figure 63. *Stenus kiesenwetteri* adult, a rare beetle inhabiting very wet *Sphagnum*. Photo by Udo Schmidt, through Creative Commons.

Unlike the other *Staphylinidae* discussed here, *Dianous coerulescens* (Figure 64) lives where water trickles over mosses and liverworts (Butler 1886).



Figure 64. *Dianous coerulescens* adult on leafy liverwort. Photo by Malcolm Storey, through Creative Commons.

The *Pselaphinae* beetles are represented along the postglacial fringe in the central and eastern United States where they inhabit *Sphagnum* (Figure 51) bogs (Reichle 1966). More than 20 species of pselaphids characterize these bogs. They are relict species with specific habitat requirements and poor dispersal ability. Some have very specific temperature range requirements: *Tychobythinus bythinoides* (= *Bythinopsis tychoides*; Figure 65),  $21.5 \pm 0.81$ ,  $25.9$ - $15.3^\circ\text{C}$ ; *Decarthron defectum*,  $28.5 \pm 0.55$ ,  $31.4$ - $24.0$ ; *Pselaphus ulkei*,  $19.5 \pm 0.86$ ,  $24.7$ - $13.0$ ; *Reichenbachia borealis* (a short-winged mold beetle; Figure 66),  $21. \pm 0.99$ ,  $26.2$ - $14.4$ ; *Rybaxis clavata* (Figure 67),  $28.3 \pm 0.41$ ,  $29.9$ - $25.1$  (Reichle 1967). The moss microhabitats provide them with both the required near-saturation humidities and the multiple temperature ranges they require. Changes in temperature stratification regimes result in different species occurring at different seral stages in the bogs.





Figure 65. *Tychobythinus bythinoides* adult, a minute beetle that takes advantage of the temperature and moisture stratification in a *Sphagnum* bed to meet its needs. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Figure 66. *Reichenbachia borealis* adult, a minute beetle that takes advantage of the temperature stratification in a *Sphagnum* bed to meet its temperature needs. Photo by Tom Murray, through Creative Commons.



Figure 67. *Rybaxis clavata* adult, a minute beetle that takes advantage of the temperature stratification in a *Sphagnum* bed to meet its temperature needs. Photo by Tom Murray, through Creative Commons.

### Scirtidae (=Helodidae) – Marsh Beetles

This is a worldwide family, but is most diverse in the temperate region (Murray 2005). The larvae live in both stagnant and flowing water where abundant decomposing plant material is present. Adults live on vegetation and on rotting vegetation. The **Scirtidae** are soft-bodied relative to other beetles and are slightly flattened to nearly **subglobular** (almost globe-shaped) (TOL 2011). Their sizes range 1-15 mm long. Some females secrete substances that may be pheromones used to stimulate males into courtship (Ruta 2008).

This is typically a beetle of open water, but in a subalpine springbrook in the southern Alps of New Zealand, **Scirtidae** (Figure 68) are most abundant in the moss *Acrophyllum quadrifarium* (= *Pterygophyllum quadrifarium*; Figure 69) at the edge of the inner spray zone where the mosses are saturated (Cowie & Winterbourn 1979).



Figure 68. **Helodidae** adult, a beetle that is abundant among *Acrophyllum quadrifarium* in the subalpine springbrooks of the southern Alps of New Zealand. Photo from Pybio at <www.pybio.org>, with permission.



Figure 69. *Acrophyllum quadrifarium*, a bryophyte habitat for **Helodidae** in streams in the Southern Alps of Australia. Photo by Jan-Peter Frahm, with permission.



*Cyphon* (Scirtidae; Figure 70-Figure 72) has been collected from wet mosses at the edge of a cold spring (Usinger 1974). *Cyphon hiliaris* (Figure 71) in Dartmoor, UK, prefers bog pools that have *Sphagnum* (Figure 51) (Boyce 2011). In North Hampshire, UK, *C. hiliaris* occurs infrequently in wetlands with peaty soils, acidic bogs, and fens (Denton 2013). *Cyphon padi* (Figure 72), also in North Hampshire, prefers peaty areas in wooded sites where the *Sphagnum* is flooded.



Figure 70. *Cyphon* pupa. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.



Figure 71. *Cyphon hiliaris* adult, a species that occurs among wet mosses at the edge of a spring. Photo by Stefan Schmidt, through Creative Commons.



Figure 72. *Cyphon padi* adult, a species of flooded *Sphagnum* in peaty forested areas. Photo by Miroslav Deml, through Creative Commons.

## Elmidae – Riffle Beetles

These are small beetles (1-8 mm) (Gordon & Post 1965). The **Elmidae** have a distribution similar to that of the **Silphidae**, but there are more known locations, including southern Africa (Harrison 2009). As the common name describes, these beetles usually live in the riffles of cool, rapid streams (Arnett *et al.* 2002; Harpootlian 2005). They feed mostly on decaying plants and algae (Epler 2010).

Only three species of **Elmidae** are considered to be frequent aquatic bryophyte dwellers: *Promoresia tardella* (Figure 73), *Atractelmis wawona* (Figure 74), and *Cleptelmis addenda* (Figure 75) (Brown 1972; Shepard & Barr 1991; Bowles *et al.* 2003; Elliott 2008a), all from North America where the family has many more species (80 species) than in Europe (46 species) (Elliott 2008a). But if one looks among the liverworts in the Pacific states of USA, a fourth genus, *Bryelmis* (Figure 108-Figure 110) is lurking (Bowles *et al.* 2003 – see below); further searching among submerged leafy liverworts may expand this *Bryelmis* distribution. Nevertheless, a number of species use bryophytes at some stage in their lives. Both larvae and adults of some **Elmidae** are able to feed on mosses (Usinger 1974). When disturbed, **Elmidae** may play dead for a number of hours before attempting to relocate (Usinger 1956). *Cleptelmis* (Figure 75) may wait for 12-15 hours before moving. Such patience!



Figure 73. *Promoresia tardella* adult, one of the few frequent bryophyte dwellers in the **Elmidae**. Photo through Creative Commons.



Figure 74. *Atractelmis wawona* adult, a frequent bryophyte inhabitant. Photo through Creative Commons.





Figure 75. *Cleptelmis addenda* adult, one of the few frequent **Elmidae** bryophyte dwellers. Photo by Crystal Maier, through Creative Commons.

**Elmidae** colonize mosses when insect-free mosses are introduced, but some of the elmids may be slow to colonize. This is no surprise since they creep and don't swim. For example, Maurer and Brusven (1983) found that the elmid *Cleptelmis ornata* (Figure 76) was the only insect that was slow to colonize insect-free test clumps of *Fontinalis neomexicana* (Figure 77) during a field experiment in Idaho, USA.

Elliott (2008a) summed up some of the characters that define the bryophyte dwellers. Their larvae have a triangular cross section. Among this group he included *Elmis* (Figure 87-Figure 86), *Esolus* (Figure 84-Figure 85), and *Oulimnius* (Figure 88-Figure 89), none of which were considered by earlier researchers mentioned above to be the frequent bryophyte dwellers. All members of the family have aquatic larvae and most have aquatic adults. The pupae are terrestrial. This means that the newly emerged adults must re-enter the water – no small feat for such a small insect. They must break through the surface tension – easy for us, but nearly impossible for them unless they have something to cling to and provide leverage for them to break through (see Figure 78). Bryophytes, plants, and rocks can help here.



Figure 76. *Cleptelmis ornata* adult, a slow colonizer of *Fontinalis neomexicana*. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 77. *Fontinalis neomexicana*, a moss that is avoided as home for liverwort-dwelling *Bryelmis*. Photo by Belinda Lo, through Creative Commons.



Figure 78. *Dryops auriculatus* (Dryopidae) adult entering water by clinging to a plant. Note the rings in the water and depression of the surface by the beetle body. Photo by Tim Faasen, with permission.

The aquatic adults use the **plastron** for oxygen availability (Thorpe & Crisp 1949) – they are air breathers. The plastron apparatus is seen as a silvery layer (Figure 79) on the ventral side of the beetle. Some members include the antennae as part of the apparatus that holds the air bubble. They groom the plastron with brushes on the femur of the leg and also use these brushes to add air bubbles to the plastron apparatus by smearing bubbles over the plastron. Most do not need to return to the surface, using the mouthparts to capture oxygen bubbles emitted by plants. If the plastron air layer is thick, it has a silvery sheen and is called a **macroplastron** (Figure 116). When air diminishes from the macroplastron to the normal, smaller plastron, air exchange with the water is generally adequate to maintain the duller-looking air bubble and meet their needs. This low need for fresh air is likely possible because these beetles do not swim, requiring less oxygen for their clambering movements.

In a tributary of the Danube, *Elmis maugetii* and *Riolus subviolaceus* (Figure 80) were abundant in high flow areas among coarse mosses, whereas *Esolus parallelepipedus* (Figure 81) and *Limnius volckmari* (Figure 82-Figure 83) were among algae in moderately flowing water (Dietrich & Waringer 1999). *Esolus*



*angustatus* (Figure 84-Figure 85) and *Oulimnius tuberculatus* (Figure 88-Figure 89) were more common in moderate flow with abundant moss-covered pebbles.



Figure 79. *Riolus subviolaceus* adult with thin plastron showing as a silver line where the elytra meets the ventral plastron. Photo by Tim Faasen, with permission.



Figure 80. *Riolus subviolaceus* adult, inhabitants of high flow areas among coarse mosses. Photo by Tim Faasen, with permission.



Figure 81. *Esolus parallelepipedus* adult, a species with a high drift rate. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.



Figure 82. *Limnius volckmari* larva, an elmid that seems to prefer algae to mosses as a substrate. Photo by Urmas Kruus, with permission.



Figure 83. *Limnius volckmari* adult, an elmid that seems to prefer algae to mosses as a substrate. Photo by Urmas Kruus, with permission.



Figure 84. *Esolus angustatus* larva, member of a genus that has the triangular cross section that characterizes many bryophyte dwellers. Photo by Tim Faasen, with permission.



Figure 85. *Esolus angustatus* adult, member of a genus that is common among bryophytes. Photo by Tim Faasen, with permission.



In British streams and rivers, *Elmis aenea* (Figure 86-Figure 87), a moss dweller in rapid streams and rivers (both above and below water), occurred among bryophytes as both adults and larvae, but larvae were more abundant among small stones or under larger ones (Elliott 2008a). In these rivers and streams, *Oulimnius tuberculatus* (Figure 88-Figure 89) preferred tracheophytes.



Figure 86. *Elmis aenea* larva, a species whose distribution is related to elevation. Photo by Niels Sloth, with permission.



Figure 87. *Elmis aenea* adult, a moss dweller in rapid streams and rivers. Photo by Tim Faasen, with permission.

In a 39-month study, Elliott (2008b) examined the effect of density on drift rate. Most of the larvae and adults of **Elmidae** drift at night with very few drifting in daytime. Elliott found that the **Elmidae** in the study, including the bryophyte dwellers, did not drift on the basis of density. Drift losses accounted for only about 0.07% of total losses in the benthos. The exception to this was the high drift, during a heavy rainfall, of early stages of immature adults of *Elmis aenea* (Figure 87), *Oulimnius tuberculatus* (Figure 88-Figure 89), and *Esolus parallelepipedus* (Figure 81), all species known from bryophytes. For *Elmis aenea*, the highest drift density was in the earliest life stage soon after egg hatching; for *O. tuberculatus* it was the start of the larval overwintering period. Frost (1942) found that *Oulimnius tuberculatus* lives among mosses (and other habitats); moving to land for pupation most likely subjects this insect to the drift.



Figure 88. *Oulimnius tuberculatus* adult, a European moss dweller. Photo by J. C. Schou, with permission.



Figure 89. *Oulimnius tuberculatus* larva, an aquatic moss dweller. Photo by J. C. Schou, with permission.

Nelson (1996) described *Elmis aenea* (Figure 86-Figure 87) as a species from moss-covered rocks in rapid rivers and streams. Berthélemy (1966) found larvae (Figure 86) and adults (Figure 87) of *E. aenea* and *E. maugetii* were often abundant among mosses and liverworts in the Pyrénées. The moss-dwelling species were generally smaller than those among stones. Nelson found that the proportion of *E. aenea* vs *E. rioloides* (Figure 90) among mosses was related to elevation.



Figure 90. *Elmis rioloides* adult, a moss dweller whose distribution is affected by elevation. Photo through Creative Commons.

Gurtz and Wallace (1984) found larvae of the elmid *Promoresia* in only one sample in Big Hurricane Branch.



They had learned from J. Haefner (personal communication) that these larvae in Sawmill Branch occurred almost exclusively among aquatic mosses (Haefner & Wallace 1981). I found *Promoresia elegans* (Figure 91-Figure 92) frequently among the bryophytes [*Fontinalis dalecarlica* (Figure 93-Figure 94), *Hygroamblystegium fluviatile* (Figure 95), *Scapania undulata* (Figure 112)] of Appalachian Mountain, USA, streams. This is a genus that exhibits the triangular cross section that Elliott (2008a) suggested to be characteristic of bryophyte dwellers.



Figure 91. *Promoresia elegans* adult, a common stream moss inhabitant. Photo through Creative Commons.



Figure 92. *Promoresia elegans*, a larva that is common among bryophytes. Photo by Erin Hayes-Pontius, through Wikimedia Commons.



Figure 93. Riffles with *Fontinalis dalecarlica*, home for *Promoresia elegans*. Photo by Janice Glime.



Figure 94. *Fontinalis dalecarlica* showing the dangling streamers. Photo by Jan-Peter Frahm, with permission.

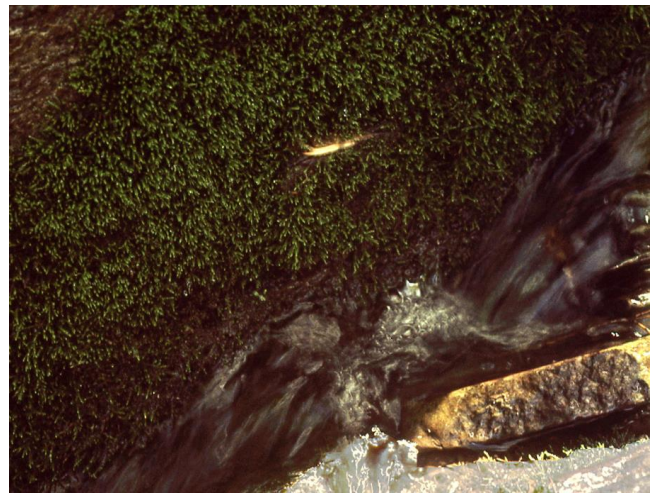


Figure 95. *Hygroamblystegium fluviatile*, home to several species of Elmidae. Photo by Janice Glime.

In addition to *Elmis*, Berthélemy (1966) found *Riolus cupreus* (Figure 96-Figure 97), *Esolus parallelepipedus* (Figure 81), and *Oulimnius tuberculatus* (Figure 88-Figure 89) among mosses in streams in the Pyrénées. *Elmis* and *Oulimnius* were strong **muscoles** (living among or in association with mosses). Hebauer (1994) found *Elmis obscura*, *E. rioloides* (Figure 90), and *Oulimnius tuberculatus* among mosses in streams in Central Europe.



Figure 96. *Riolus cupreus* larva, an inhabitant of Pyrénées stream mosses. Photo by Urmas Kruus, with permission.





Figure 97. *Riolus cupreus* adult, an inhabitant of Pyrénées stream mosses. Photo by Urmas Kruus, with permission.

The **Elmidae** spend their larval life in the water, pupate on land, then after their initial dispersal flight they return to the water. The interesting note here is that once they return to the water, they lose their ability to fly (Ward 1992). This locks them into their habitat no matter what the water conditions. For those inhabiting stream mosses, this means that if the water level drops, they must remain in the habitat of the mosses, unable to disperse for any significant distance. But for them it seems to be no problem because they have a high drought tolerance (Larimore *et al.* 1959; Iverson *et al.* 1978).

Steffan (1961) suggested that the mosses such as *Fontinalis* (Figure 94) were necessary for some **Elmidae** and **Dryopidae** to make the transition from water to land (and back to the water) during their amphibious life. Bryophytes would permit them to gain a firm hold while breaking through the surface tension in either direction.

In Louisiana, USA, the endangered riffle beetle *Heterelmis comalensis* (Figure 98-Figure 99) lives on submerged roots and aquatic mosses (Barr & Chapin 1988). In this same habitat, *Microcyloepus pusillus* (Figure 100-Figure 101) likewise uses these substrata. In the Appalachian Mountain streams, USA, I found a species of *Microcyloepus* among the submerged mosses (Glime 1968).



Figure 98. *Heterelmis comalensis* adult, a moss dweller, as well as living on submerged roots. Photo through Creative Commons.



Figure 99. *Heterelmis comalensis* larva, a moss inhabitant. Photo by Mike Quinn, through Creative Commons.



Figure 100. *Microcyloepus pusillus* larva, an inhabitant of submerged roots and mosses. Photo by Mike Quinn, through Creative Commons.



Figure 101. *Microcyloepus pusillus* adult, an inhabitant of submerged roots and mosses. Photo by Mike Quinn, through Creative Commons.

My experience with **Elmidae** among the stream bryophytes in the Appalachian Mountains, USA, differs from that in many of the reports cited here (Glime 1968). I found six species, and among these only *Microcylloepus* (Figure 100-Figure 101) and *Promoresia elegans* (Figure 91-Figure 92) (both larvae and adults) have been reported in the other studies cited herein. The numbers of *Promoresia elegans* actually exceeded the numbers of **Chironomidae** among bryophytes in one stream in March; in winter I found only two adults. In addition I found two species of *Optioservus* (Figure 102-Figure 103) on *Hygroamblystegium fluviatile* (Figure 95); on *Fontinalis dalecarlica* (Figure 93-Figure 94), I found *Stenelmis crenata* (Figure 105-Figure 104) and one species of *Dubiraphia* (Figure 106-Figure 107).



Figure 102. *Optioservus fastiditus* adult, member of a genus that lives among mosses in Appalachian Mountain, USA, streams. Photo by Sarah McManus, through Creative Commons.



Figure 103. *Optioservus* larva, member of a genus that lives among mosses in Appalachian Mountain, USA, streams. Photo by Joseph C. Fortier, through Creative Commons.



Figure 104. *Stenelmis* larvae, an inhabitant of bryophytes in Appalachian Mountain, USA, streams. Photo by Erin Hayes-Pontius, through Creative Commons.



Figure 105. *Stenelmis crenata* adult, a moss dweller in Appalachian Mountain, USA, streams. Photo by Tom Murray, through Creative Commons.



Figure 106. *Dubiraphia* larva. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.



Figure 107. *Dubiraphia vittata* adult. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

It is no surprise that new species remain to be discovered among the bryophytes. But one such recent discovery in the western states of the USA was not just a new species, but a new genus, widespread, and with multiple species! And these were among aquatic bryophytes, particularly leafy liverworts (Barr 2011). These three species were *Bryelmis idahoensis* (Figure 108), *B. rivularis* (Figure 109), and *B. siskiyou* (Figure 110) from streams and springs in the states of Washington,



Oregon, California, and Idaho. Once Barr alerted her colleagues in neighboring states of her find, they began searching this new habitat, the leafy liverwort *Chiloscyphus polyanthos rivularis* (Figure 111). After searching through 652 adult and over 200 larval specimens from museum and new collections, she distinguished three species, all previously unknown. And now all these people know the difference between a moss and a liverwort – the latter houses *Bryelmis*.



Figure 108. *Bryelmis idahoensis* adult male, a species that seems to be restricted to leafy liverworts. Photo by Traci Grzymala, with permission.



Figure 109. *Bryelmis rivularis* adult male, a species that seems to be restricted to leafy liverworts. Photo by Traci Grzymala, with permission.



Figure 110. *Bryelmis siskiyou* adult male, a species that seems to be restricted to leafy liverworts. Photo by Traci Grzymala, with permission.



Figure 111. *Chiloscyphus polyanthos*, primary home to the recently discovered genus *Bryelmis*. Photo by Jan-Peter Frahm, with permission.

Barr had found *Bryelmis idahoensis* in association with aquatic bryophytes on rocks, but some also occurred on water-soaked wood. *Bryelmis rivularis* preferred *Chiloscyphus polyanthos rivularis* (Figure 111) and *Scapania undulata* (Figure 112) and tended to avoid both of the mosses *Fontinalis neomexicana* (Figure 77) and *Platyhypnidium riparioides* (Figure 113). By targeting aquatic liverworts she discovered another new species, *B. siskiyou*.



Figure 112. *Scapania undulata*, home for some members of *Bryelmis*. Photo by Hermann Schachner, through Creative Commons.



Figure 113. *Platyhypnidium riparioides*, a habitat rejected by *Bryelmis*, a leafy liverwort inhabitant. Photo by Hermann Schachner, through Creative Commons.



In Mexico, Central America, and the West Indies, *Lara avara* (Figure 114-Figure 115) spends 4-6 years as larvae, going through seven instars (Spangler & Santiago-Fragoso 1992). The larvae leave the stream water in spring and move to mosses at the stream bank in their last instar. In their last instar they burrow into small "cells" under mosses at water's edge (Spangler & Santiago-Fragoso 1992) or under mosses on the upper surface of emergent logs (Elliott 2008a). When the moss dries in early summer the larvae begin pupation (Spangler & Santiago-Fragoso 1992). This pupation lasts only two or more weeks.



Figure 114. *Lara avara* adult, a species that pupates among mosses. Photo through Creative Commons.



Figure 115. *Lara avara* larva, a species that crawls out of the water to pupate among mosses at the water's edge. Photo by Arlo Pelegrin, with permission.

### Dryopidae – Long-toed Water Beetles

The **Dryopidae** are mostly Northern Hemisphere (Dryopidae 2015), but the scant records in the Southern Hemisphere may reflect limited collecting rather than absence of beetles. This is an interesting family in that the larvae are mostly terrestrial, living in decaying plant material, rotting wood, and soil, whereas the adults (3.5-5.5 mm long) return to running water to lay eggs (Watson & Dallwitz 2003). They are unable to swim and clamber about by clinging to plants. They eat plants as adults, but larvae may also prey on small animals. The **Dryopidae** occur on every continent except Antarctica and Australia, but they are most common in the tropics (Dryopidae 2015). They use hairs to create a **plastron** apparatus (see introductory information), enabling them to breathe under water.

The **Dryopidae** (Figure 116) seem seldom to be reported among the bryophytes of aquatic habitats. Nevertheless, Percival and Whitehead (1930) found that the **Helminae** (**Dryopidae**) reached 1244 per dm<sup>2</sup> in the mossy area of streams in the UK, whereas among stones with no mosses they reached only 10-15 per dm<sup>2</sup>. Buczyński *et al.* (2014) reported that in Poland *Dryops anglicanus* (Figure 117) lives in canals created by beavers in floating

*Sphagnum* (Figure 51) mats. In rivers of Northwest Spain, *Dryops luridus* preferred moss substrata (Sarr *et al.* 2013). In the Appalachian Mountain, USA, streams, I found a species of *Helichus* (Figure 118) (Glime 1968).



Figure 116. *Dryops luridus* adult with plastron surrounding entire body, a **macroplastron**. Photo by Tim Faasen, with permission.



Figure 117. *Dryops anglicanus* adult, an inhabitant of beaver-made canals in floating *Sphagnum* mats. Photo by Stefan Schmidt, through Creative Commons.



Figure 118. *Helichus lithophilus* adult, member of a genus with bryophyte dwellers in Appalachian Mountain, USA, streams. Photo by Mike Quinn, through Creative Commons.



### Chelonariidae – Turtle Beetles

These are relatively small beetles (adults 2.5-10 mm long) and somewhat resemble turtles in that their heads are hidden and their legs can be tucked into depressions in the abdomen made for them (Harpootlian 2006). They are best known from eastern North America, western South America, and Central America, but there are some records from eastern Asia (Chelonariidae 2015). They reach their greatest diversity in the Neotropics.

Sometimes it is hard to determine if the insects are aquatic or terrestrial. Perhaps it is just a wide niche with a wide water tolerance. In other cases, entrance into the aquatic world may be accidental. Such seems to be the case with *Chelonarium* (Figure 119), a genus that inhabits damp moss (Spangler 1980). From these damp mosses, they may occasionally get washed into the nearby stream by rain or high water (Brown 1972). The larvae, once considered aquatic, lack gills (Spangler 1980). Members of the genus are often associated with the roots of terrestrial **epiphytes** (plants that grow on other plants but are not parasitic) and often feed on ants and termites.



Figure 119. *Chelonarium lecontei* adult, a species once thought to have aquatic larvae. Note how the legs fit into the exoskeleton. Photo through Creative Commons.

### Lampyridae – Lightning Bugs

"When night closes in, fireflies flicker with an ethereal and haunting light" (WWF 2011). This is the family of fireflies (Figure 120) that delighted us as children. And one of them, *Luciola ficta* (see Figure 121), lives in the water as a larva and uses mosses (Ho *et al.* 2010)! The adults court, mate, and females oviposit on mosses (or under leaf litter, in root gaps, or in soil clefts), but on land. The young hatchlings must make their way to the water. This unique Asian beetle is in danger of extinction because its habitat is disappearing. However, the Chinese are attempting to save it by learning its development (Ho *et al.* 2006) and creating small pools for it (WWF 2011).



Figure 120. **Lampyridae** adult showing the portion that lights up. Photo by Andy Deans, through Creative Commons.



Figure 121. *Luciola lusitanica* adult. *Luciola ficta* is a species with aquatic larvae and adults that oviposit on terrestrial mosses. Photo by Tim Faasen, with permission.

### Latridiidae – Minute Brown Scavenger Beetles

Minute it is, with sizes up to 3 mm (McClarín 2005). The family mostly eats fungi and slime molds, frequenting decaying vegetation (Latridiidae 2015). Records of this family are concentrated in Europe, with scattered records in North America, South America, Africa, and Australia. But this family is even present in the Antarctic region.

In South Georgia (southern Atlantic Ocean) bryophytes often play an important role as habitats for insects. One such inhabitant is *Aridius malouinensis* (Figure 122) (Arnold & Convey 1998).



Figure 122. *Aridius malouinensis* adult, a moss dweller on the island of South Georgia. Photo by Roger S. Key, with permission.

### Curculionidae – Weevils

Despite the fact that **Curculionidae** (Figure 123) is the third largest animal family (Curculionidae 2014), its presence is missing among aquatic mosses. Its distribution is worldwide, although records are lacking in vast areas of Asia and Africa (Curculionidae 2015). Adults range 1-40 mm long and are plant feeders.



Figure 123. *Cionus hortulanus* adult, showing one of many thousands of bizarre forms present in this family. Photo by Lukas Jonaitis, through Creative Commons.

This terrestrial family has limited associations with the water. The marine weevil *Palirhoeus eatoni*, on the Prince Edward Islands south of Africa, lives among tufts of algae as larvae (Doyen 1976). When it pupates it goes above the high water level among clumps of the shoreline moss *Grimmia amblyophylla* (Jeannel 1940, 1953).

### Lagriidae

Our records of bryophyte dwellers from Africa seem to be rare, so it is pleasing to see a study on bryophagy in South Africa (Chown 1993). Chown found that members of the **Lagriidae** in the Afromontane forest fed on both green and brown parts of the moss *Braunia secunda*. This is a family with poorly known feeding habits, and the species discovered here was unnamed.



Figure 124. *Lagria hirta* adult, a beetle that eats the moss *Braunia secunda*. Photo by Udo Schmidt, with permission.



Figure 125. *Braunia secunda*, home for some members of the Lagriidae. Photo by Efrain De Luna, with permission.

### Summary

The suborder **polyphaga** includes a number of families of beetles that live among bryophytes, especially the small members.

These include **Helophoridae** that live in both bogs and streams among bryophytes. **Hydrochidae** live among bog mosses. **Hydrophilidae** are common in

bog pools, where diversity is high, but some also occur among stream bryophytes. The **Hydraenidae** are tiny beetles that live primarily among bryophytes in streams and fast rivers. Some small members of the **Ptiliidae** are **parthenogenetic** and live in **relict** bogs. The **Silphidae** are carrion feeders and those in bogs breed on small carrion such as frogs. The **Staphylinidae** are not typical bryophyte dwellers, and are not aquatic, but they live in bogs. The **Scirtidae** find suitable habitat in the saturated mosses of the spray zone of the streambrooks in the Alps of New Zealand.

The best adapted family of the beetle bryophyte dwellers is the **Elmidae**. They use a **plastron** to breathe and are small enough to clamber about among the bryophyte stems and leaves. The **Dryopidae** are similarly adapted and both families can be found among stream bryophytes.

Some species of the **Chelonariidae** live among wet mosses of stream banks and seem to occasionally fall in. The species *Luciola ficta* is a firefly in the family **Lampyridae**. Its larvae live in the water and the adults deposit their eggs on mosses and other substrata near water. The **Latridiidae** are among the insects in South Georgia where one species lives among the bryophytes. The **Curculionidae** are weevils and few are associated with aquatic habitats. Some live on floating plants and one species leaves its water home to pupate among shoreline mosses.

### Acknowledgments

Tim Faasen not only gave me permission to use his wide collection of insect images, he also helped me to understand the ecology of some of the species and provided me with additional images I needed. Thank you to Roger S. Key not only for his permission to use his images but for sharing his experiences with me regarding beetle use of bryophytes. Ronald Willson verified my beetle identifications for the mid-Appalachian Mountain study. Eileen Dumire proofread the chapter and offered suggestions to improve clarity.

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# CHAPTER 11-11

## AQUATIC INSECTS: HOLOMETABOLA – TRICHOPTERA, SUBORDER ANNULIPALPIA

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# CHAPTER 11-11

## AQUATIC INSECTS: HOLOMETABOLA – TRICHOPTERA, SUBORDER ANNULIPALPIA



Figure 1. *Fontinalis antipyretica* in a small stream. This moss is often home to many kinds of insects, including even larger Trichoptera. Photo by Betsy St. Pierre, with permission.

### LEPIDOPTERA – Moths and Butterflies

This predominantly terrestrial order has a number of aquatic members whose larvae live on tracheophytes. These include such families as the **Pyralidae** (Figure 2) and **Noctuidae**. Larvae of some aquatic species possess gills (Bouchard *et al.* 2004). The aquatic **Pyralidae** are the only **Lepidoptera** with aquatic pupae.

I have not been able to find any records of this order on bryophytes. However, on one occasion I found a caterpillar of the **Nymphalidae** in a bed of *Fontinalis* in the Red Cedar River, East Lansing, MI. Unfortunately, I was there for a different purpose and don't have any further details.

### TRICHOPTERA – Caddisflies

The **Trichoptera** are distinguished as adults by the hairs on their wings (Figure 3) and the resting position that looks like a pup tent (Figure 4). Their distribution is worldwide and size varies greatly. Most build cases that serve as retreats for both larvae and **pupae** (immature stages, often immobile) between larvae and adults).



Figure 2. *Petrophila* larva (ventral view), a common aquatic moth that lives among aquatic plants. Photo by Bob Henricks, with permission.





Figure 3. *Brachycentrus appalachia* adult wings showing hairs. Photo by Jason Neuswanger, with permission.



Figure 4. *Limnephilus frijole* adult showing wings folded like a pup tent. Photo by Bob Newell, with permission.

Caddisflies are common inhabitants among mosses (Oswood 1979; Glime 1994; Ogbogu 2000; Ogbogu & Akinya 2001). Berg and Petersen (in Macan 1963) found a mean of 260 Trichoptera in just 1 sq meter of *Fontinalis* (Figure 1) in Lake Gribso. And Frost (1942) found 492,200 individuals per gram of mosses in Ireland. Several families of caddisfly larvae have members that use bryophytes in the construction of their homes (Glime 1978).

In North America, caddisfly larvae are closely associated with mosses such as *Fontinalis* (Figure 1) (Ogbogu 2001a). As the density of these mosses increases, so does the density of the caddisfly larvae. Ogbogu suggested that use of the mosses as part of their life cycle strategy permits these larvae to survive in the unstable habitats of streams.

Krno (1990) found that some Trichoptera were able to climb out of the water to move about among the wet emergent mosses. However, the fauna there was not as rich as that among submerged mosses. Galdean (1994) found that some caddisflies were common on the mosses lining the walls of the Somequell Cald Gorges. These mosses were clean, lacking **detritus** (organic matter produced by the decomposition of organisms), and formed a felt on the walls.

Some insect assemblages even partition the moss into several habitats. The caddisfly *Brachycentrus* (Brachycentridae; Figure 5) uses mosses (as well as rocks

and sticks) for attachment; *Tricorythodes* (Ephemeroptera: Leptohyphidae) burrows among the stems and rhizoids; and the caddisfly *Chimarra* (Philopotamidae; Figure 6) lives in the gravel and sand at the base of the mosses, all in the riffles of one Wyoming river (Armitage 1961).



Figure 5. *Brachycentrus occidentalis* larvae. Photo by Arlen Thomason, with permission.



Figure 6. *Chimarra tsudai* larva, member of a genus that lives in gravel and sand at the bases of mosses in riffles. Photo by Takao Nozaki, with permission.

In the case of *Helicopsyche sperata* (Helicopsychidae; Figure 7), the aquatic surroundings are achieved by living on mossy rocks out of the stream but in the sun in locations kept wet by constantly dropping water (McLachlan 1880).



Figure 7. *Helicopsyche* sp. larva and case, a genus that lives on wet mosses in the splash of streams. Photo by Stephen Moore, Landcare Research, with permission, NZ.



## Drift

Unlike most of the drifting aquatic insect species, many species of Trichoptera are day-active and do most of their drifting during the day (Waters 1972). This makes this group more vulnerable to predation by fish (White 1967), and this would particularly apply to the caseless caddisflies that are the most common caddisflies among bryophytes. However, Brusven (1970) found that among the caseless net-spinning caddisflies, *Arctopsyche* (Figure 8) drifted mostly at night and *Hydropsyche* (Figure 9) was rare in the drift. It is reasonable to assume that the bryophyte habitat may help to keep these caddisflies anchored as they move about, hence offering a safe refuge.



Figure 8. *Arctopsyche ladogensis* (Hydropsychidae) larva, a night drifter. Photo by Donald S. Chandler, with permission.



Figure 9. *Hydropsyche pellucidula* larva (Hydropsychidae), a rare drifter that can be found among bryophytes. Photo by Niels Sloth, with permission.

## Food

Slack (1936) compared the food of twelve species of caddisflies. Among these, all but three had bryophyte leaf fragments in the gut. Those with more than half the larvae having bryophyte fragments were **Limnephilidae**: *Glyptotaelius* sp. (Figure 10), *Limnephilus rhombicus* – an opportunist in using a variety of materials to build its case (Figure 11), *Stenophylax* sp. (Figure 12), and *Halesus* sp. (Figure 13) and **Sericostomatidae**: *Sericostoma personatum* (Figure 14). Among common bryophyte dwellers, *Hydropsyche* sp. (Figure 9) had none and

*Rhyacophila dorsalis* (Figure 15) had bryophyte fragments in only one out of nine larvae. An image on Garden World Images by Dave Bevan (Bevan 2014) suggests that some *Stenophylax* species eat mosses. (The image looks like either protonemata or a filamentous alga.)



Figure 10. *Glyptotaelius pellucidus* larva in its case, a genus known to eat bryophytes. Photo by Niels Sloth, with permission.



Figure 11. *Limnephilus rhombicus* larva showing two very different cases for the same species. This species eats bryophytes. Photo by Niels Sloth, with permission.



Figure 12. *Stenophylax permistus* adult, a genus known to eat bryophytes. Photo by Wouter Bosgra, through Creative Commons.





Figure 13. *Halesus radiatus* larva, a genus which has bryophyte consumers. Photo by Malcolm Storey, through Creative Commons.



Figure 14. *Sericostoma personatum* larva, a genus known to eat mosses. Photo by J. C. Schou, with permission.



Figure 15. *Rhyacophila dorsalis* larva, a common bryophyte dweller that had no moss in the gut of 8 out of 9 individuals. Photo by Walter Pfliegler, with permission.

**Trichoptera** is a large order, surpassing Ephemeroptera, Odonata, and Plecoptera in the number of genera (Wiggins & Mackay 1978). Most of the filter-feeders are in eastern North America in the deciduous forest biome. In addition to filter feeders, they are represented by grazers, especially upstream in the mountains where waters are cool. Shredders, especially in the **Limnephilidae**, can be found in lakes, ponds, streams, and even terrestrial habitats. Shredder-collectors are more common upstream and grazer-collectors are more common downstream. Some are predators.

Cairns (2005) reported that some caddisfly larvae consumed stream mosses. Kalachova *et al.* (2011) used

acetylenic acids as biomarkers of *Fontinalis antipyretica* (Figure 1) to demonstrate consumption of this moss by Trichoptera in the Yenisei River.

### Case Building

**Case building** provides most species of Trichoptera with a mobile home that protects them from predation. Some of these case-builders use bryophytes in their construction, including the New Zealand genus *Zelolessica* (**Helicophidae**; Figure 16) that sometimes uses bryophytes exclusively (Suren 1988). Frost (1942) found that a rather dominant caddisfly in her acid site on the River Liffey, Ireland, made cases from fragments of *Fontinalis* (Figure 1), but the larvae were too small for identification.



Figure 16. *Zelolessica*, a caddisfly that sometimes uses bryophytes in case construction. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Elliot and Spribille found that in a northwest Montana fen caddisfly larvae use living *Scorpidium scorpioides* (Figure 17) to build cases. The larvae harvest small tips of branches (*ca.* 2 cm) of the *S. scorpioides* from plants that grow submerged in shallow water and attach them to their cases. Elliot and Spribille suggested that the moss provides a "buoyant platform" from which the caddisfly can emerge, prey on the invertebrate fauna, and then fly off without being trapped by the surface tension.



Figure 17. *Scorpidium scorpioides*, a moss used for building caddisfly cases. Photo by Malcolm Storey <[www.discoverlife.org](http://www.discoverlife.org)>, through Creative Commons.



## SUBORDER ANNULIPALPIA

### Hydropsychoidea

#### Ecnomidae

This is a relatively small family with worldwide distribution (Holzenthal *et al.* 2007). Although records of this family are worldwide, their main distribution is Gondwanan (Ecnomidae 2014). The larvae are of moderate size (5-10 mm) and live in retreats that they construct of silk in slow-water streams or lakes. They are predators, but some eat algae and detritus.

From Ceylon, Schmid (1958) reported *Ecnomus ceylanicus* (see Figure 18) and a new species, *Ecnomus vaharika*, from large, mossy rocks in the torrent.



Figure 18. *Ecnomus tenellus* adult, member of a genus in which some species live in mossy torrents in Ceylon. Photo by Dick Belgers, through Creative Commons.

#### Hydropsychidae – Net-spinning Caddisflies

This worldwide family occupies a wide range of rivers and streams, always requiring flowing water to obtain its food (Hydropsychidae 2014). For example, in Ceylon Schmid (1958) reported *Pseudoleptonema ceylanicum* (see Figure 19) from a small, mossy creek in the jungle.



Figure 19. *Pseudoleptonema supalak* adult. In Ceylon, larvae of *P. ceylanicum* live in a mossy creek. Photo from Biodiversity Institute of Ontario, through Creative Commons.

The larvae can be relatively large, ranging 5-25 mm (Hydropsychidae 2015). The larvae of this family build retreats from plant and mineral fragments. These retreats open into the nets used to catch their food, including algae, detritus, and small animals. When another caddisfly attempts to occupy the retreat, the current occupant uses its hind legs, rubbing them under the head, to produce stridulations that warn the intruder to vacate (Jansson & Vuoristo 1979).

Larvae of *Hydropsyche angustipennis*, *H. siltalai*, *H. nevae*, and *H. pellucidula* will enter any suitable retreat when forced to leave their own, and it need not be their own species or unoccupied. When it is already occupied, a vigorous fight will ensue. Larger defenders lost more fights as the size of the intruder increased. Stridulation increased the likelihood of a defender winning the fight.

Several researchers have supported the importance of mosses in the habitats of net-spinning caddisflies (Sprules 1947; Tanaka 1968). Oswood (1979) found that in a lake outlet stream in Montana, USA, larvae of **Hydropsychidae** had greater densities on moss-covered substrata (up to >1400 0.2 m<sup>-2</sup>) than elsewhere. In a gorge of the Some River, Galdean (1994) considered the mosses on the walls of the gorge to create the conditions needed for the **Hydropsychidae** to develop. The boulders were cleaned by the river velocity on the concave bank, permitting the mosses, hence the **Hydropsychidae**, to develop there.

*Parapsyche cardis* preferred substrata in the order of mossy rock face > cobble riffle > pebble riffle > sandy reach (Gurtz & Wallace 1986). This relationship held true for all instars (larval stages) in both studied streams. Thus, mossy rock faces accounted for 94.8% of the total production of *Parapsyche* (Figure 20) in Hugh White Creek (with 36.5% rocky channel) and 87.3% in Big Hurricane Branch (with 16.8% rocky channel) in the southern Appalachian Mountains, USA. Haefner and Wallace (1981a, b) likewise found that the distribution of *P. cardis* was highly correlated with the distribution of moss in Sawmill Branch. In several Maryland, USA, streams, *Parapsyche apicalis* occurred among bryophytes, mostly *Fontinalis dalecarlica*, and at the time were new records for Maryland, but it was not one of the more common **Hydropsychidae** represented among the mid-Appalachian bryophytes (Glime 1968).



Figure 20. *Parapsyche apicalis* larva, a species I collected among bryophytes in several Maryland streams. *Parapsyche cardis* distribution is correlated with moss cover. Photo by Donald S. Chandler, with permission.



Wulfhorst (1994) examined the relative abundance of the caddisfly larva *Diplectrona* (Figure 29) in mosses and in **interstitial spaces** (spaces between individual sand grains in soil or aquatic sediments) in the **hyporheic zone** (region beneath and alongside a stream bed, where mixing of shallow groundwater and surface water occurs) of two streams in the Harz Mountains of West Germany. She found that *Diplectrona* was more abundant among the mosses at most collection stations, but that they were also abundant in the interstitial spaces of the hyporheic zone at 10 and 30 cm depths (Figure 21).

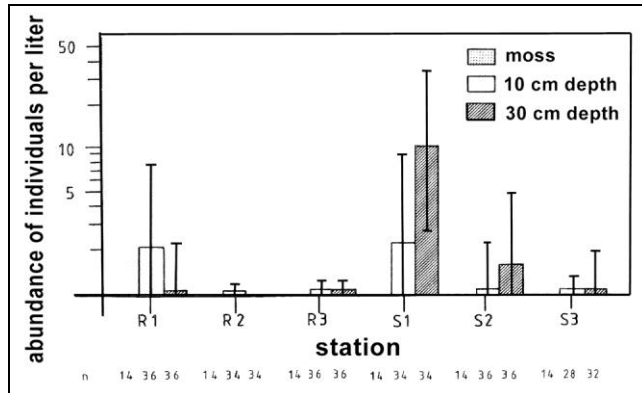


Figure 21. Mean abundance  $\pm$  95% CI of *Diplectrona* spp. in moss clumps in two streams in the Harz Mountains, West Germany. Numbers of samples are shown at the bottom. Redrawn from Wulfhorst 1994.

The high density of **Hydropsychidae** among stream mosses is supported by their ability to colonize that habitat rapidly. Smith-Cuffney (1987) found that artificial mosses reached their capacity of these net-spinning colonizers in only 7 days; Georgian and Thorp (1992) found that 6-9 days provided enough time for them to reach their constant colonization density among the artificial mosses. Mosses provide a particularly easy place to colonize relative to other stream habitats because their rough surface makes it easy to gain a hold that rescues them from the speeding water.

The **Hydropsychidae** can be considered ecosystem engineers (Nakano *et al.* 2005). In Japan, *Hydropsyche orientalis* (Figure 22, Figure 23) make their larval retreats on the upper surfaces of stones. These retreats provide a safe site for naiads of the mayfly *Serratella setigera*, providing them with the slower flow that they prefer. It is likely that in the absence of these caddisflies and their nets that mosses could play a similar role in creating a suitable refuge. And in some cases it appears that the hydropsychids use the mosses in place of some, but not all, nets (Figure 24).

Ogbogu (2000) found **Hydropsychidae** associated with *Fontinalis* (Figure 1) in Nigeria and reported that the density of larvae increased when the moss grew. Both *Cheumatopsyche* (Figure 45) and *Amphipsyche* formed close associations and Ogbogu (2001a, b) suggested that the moss served as a **refugium** (area in which population of organisms can survive through period of unfavorable conditions, even glaciation) during vulnerable life cycle stages.



Figure 22. *Hydropsyche orientalis*, a species that provides shelter used by the mayfly *Serratella setigera*. Photo by Takao Nozaki, with permission.

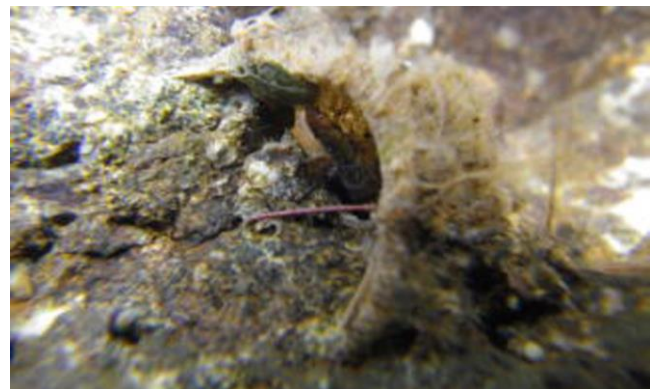


Figure 23. *Hydropsyche orientalis* net where *Ephemera setigera* takes refuge. Photo by Takao Nozaki, with permission.



Figure 24. **Hydropsychidae** nets among mosses. Photo by Janice Glime.

### Pupal Sites

Frost, in her 1942 study of the River Liffey, Ireland, found that few Trichoptera pupae were present among the mosses. She considered this an expected absence because the caddisfly larvae usually seek another type of environment instead of mosses for **pupation** (period of development of pupa). For example, *Ceratopsyche morosa* (Figure 25) lives among moss and algae in young larval stages (Stern & Stern 1969), but just prior to pupation it moves to stones.

Temperature can signal that it is time to pupate. At least some *Hydropsyche* species cannot live below 8°C (Kaiser 1965). Instead, they build loose cases and go into the pupa state in autumn. Sleight (1913) found *Hydropsyche* pupae (Figure 26-Figure 28) among mosses in strong currents in the eastern USA. At maturity, these pupae moved to the surface where the pupal case would split and adults would emerge. The larval hooks made it possible for these caddis larvae to climb over the vegetation to find a suitable place for the pupa.



Figure 25. *Ceratopsyche morosa* larva, a moss dweller that leaves the mosses to pupate among stones. Photo by Bob Henricks, with permission.



Figure 26. *Hydropsyche* pupae, a genus that pupates among the protective mosses in strong currents. Photo by Mark Melton, with permission.

### Crowding and Niche Separation

It appears that mosses might separate the niches of co-habiting net spinners. Late instar *Diplectrona modesta* (Figure 29) has a somewhat uniform occupancy among substrata in Big Hurricane Branch (Gurtz & Wallace 1986). The first three instars are most abundant on the (mossy) rock face and the fourth and fifth are more evenly distributed. But in Hugh White Creek, the rocks have a lower density of moss, and *D. modesta* is less common than in Big Hurricane Branch, where the moss is thicker. In fact, in Hugh White Creek, *D. modesta* is most abundant in the cobble riffle and least abundant in the rock face samples, while first instars are most common on sand. Gurtz and Wallace suggested that the lower density of moss in the Hugh White Creek may not provide enough microhabitats and that differences in available substrata

could account for the differences in productivity. Mosses provide a suitable substrate for attaching the nets (Figure 30) and retreats of these caddisflies while providing a range of current velocities. The nets themselves do not, however, appear to contribute directly to their food; none were found in the gut analysis (Haefner & Wallace 1981a). The larvae are also relatively common among *Hygroamblystegium fluviatile* (Figure 31), *Platyhypnidium riparioides* (Figure 32), and *Fontinalis dalecarlica* (Figure 33) in Appalachian Mountain streams (Glime 1968).



Figure 27. *Hydropsyche* pupae removed from their pebble cases. Photo by Mark Melton, with permission.



Figure 28. *Hydropsyche* pupa, common among mosses in strong currents. Photo by Jason Neuswanger, with permission.



Figure 29. *Diplectrona modesta* larva, a species that is more common among mosses in early instars but is more evenly distributed between mosses and other substrata in later instars. Photo by Bob Henricks, with permission.



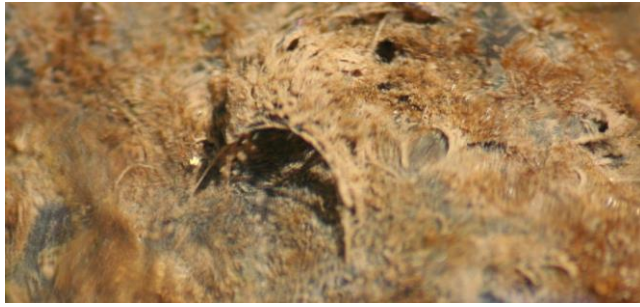


Figure 30. *Cheumatopsyche* larval net. These are often attached to bryophytes and are able to trap detritus and algae. Photo by Justin Montem, through Creative Commons.



Figure 31. *Hygroamblystegium fluviatile*, a home for smaller insects. Photo by Michael Lüth, with permission.



Figure 32. *Platyhypnidium riparioides*, a home for smaller insects, sometimes serving as food and case-building materials. Photo by David Holyoak, with permission.



Figure 33. *Fontinalis dalecarlica*, home to some larvae of *Cheumatopsyche*. Photo by J. C. Schou, with permission.

When *Cheumatopsyche* sp. (Figure 34) reaches high densities it becomes more aggressive (Glass & Bovbjerg 1969). This aggressiveness dictates a pattern of **dispersion** (pattern of distribution of individuals within a habitat) that is a function of density. Hildrew and Edington (1979) found that larvae are able to make ultrasonic sounds to discourage intruders when they approach. Fortunately, for overlapping generations of the same species larval sizes differ at a given point in time, permitting them to use different net sizes (Figure 35-Figure 36) and avoid competition for food.



Figure 34. *Cheumatopsyche* larva, a caddisfly that becomes less aggressive when it has shelter. Photo by Bob Henricks, with permission.



Figure 35. *Hydropsyche* net showing mesh size that can differ in size with species. Photo by Michael Wiesner <[www.waldzeit.ch](http://www.waldzeit.ch)>, with permission.



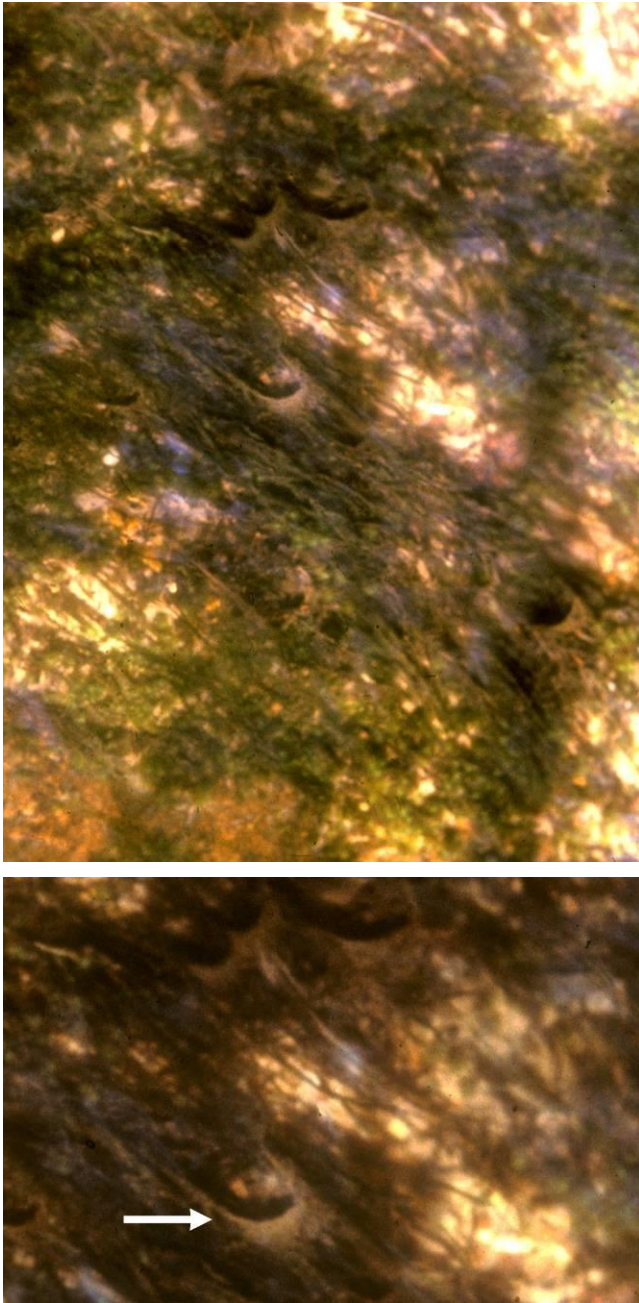


Figure 36. Nets of the net-spinning caddisfly, *Cheumatopsyche*, on *Fontinalis*. The number of larvae usually greatly exceeds the number of nets on the *Fontinalis*, suggesting that they may be using the mosses as nets to gather detritus and diatoms. Photos by Janice Glime.

Williams and Hynes (1973) suggested that mossy habitats provide the greatest number of protected sites. Furthermore, the rapid flow typical of locations where mosses grow will bring more food per unit of time. *Cheumatopsyche* (Figure 37) larvae are common among the mosses *Hygroamblystegium fluviatile* (Figure 31), *Platyhypnidium riparioides* (Figure 32), and *Fontinalis dalecarlica* (Figure 33) in the mid-Appalachian Mountain streams (Glime 1968). And *Cheumatopsyche* (Figure 34) larvae seem to be less aggressive when shelter is readily available (Glass & Bovbjerg 1969). Williams and Hynes (1973) found that the hydropsychids *Cheumatopsyche oxa* (Figure 37) and *Ceratopsyche sparna* (Figure 38) occupied the mossy areas of boulders, whereas the philopotamid

*Chimarra aterrima* (Figure 39), a potential competitor, occupied the spaces under large stones. The two hydropsychid species share the same sites, eat the same foods, and have similar life cycles. In contrast to *Chimarra aterrima*, these net-spinning caddisflies have mechanisms in their gut for crushing diatoms, important constituents of the diet and one that separates their niche from that of *C. aterrima*.



Figure 37. *Cheumatopsyche oxa* larva, an occupant of mossy areas on boulders. Photo by Trevor Bringloe, Biodiversity Institute of Ontario, through Creative Commons.



Figure 38. *Ceratopsyche sparna* larva, a species that prefers mossy areas to those under stones. Photo by Bob Henricks, with permission.



Figure 39. *Chimarra aterrima* larva, a species that occupies spaces under rocks in preference to that of mosses. Photo by Stroud Water Research Center, Stroud Water Research Center, through Creative Commons.



*Hydropsyche pellucidula* (Figure 40-Figure 41) occurs among submerged mosses in the River Rajcianka (Krno 1990). Elsewhere, when *Hydropsyche pellucidula* and *H. siltalai* (Figure 42) occur together, the moss cover is important in permitting these two caddisflies to partition the rocks into two functional feeding (net-spinning) niches and co-exist throughout their larval lives (Hildrew & Edington 1979). In late winter and early spring, there is rapid growth of moss (particularly *Fontinalis antipyretica*, Figure 43) on boulders and bedrock in rapids. *Hydropsyche siltalai* (but not *H. pellucidula*) migrates onto the moss in spring. Although large numbers of *H. siltalai* occupied the moss, not a single *H. pellucidula* could be found there. Plastic artificial grass, similar to moss mats, proved to be a suitable surface for net-spinning.



Figure 40. *Hydropsyche pellucidula* larva, a species that occurs among mosses in the River Rajcianka of Slovakia. Photo by Niels Sloth, with permission.



Figure 41. *Hydropsyche pellucidula* larva showing the large jaws. Photo by Niels Sloth, with permission.



Figure 42. *Hydropsyche siltalai* larva, a species that migrates to mosses to avoid competition from *H. pellucidula*. Photo by Urmas Kruus, with permission.



Figure 43. *Fontinalis antipyretica*. Photo by Bernd Haynold, through Wikimedia Commons.

*Hydropsyche siltalai* (Figure 42) filters its food with a fine-meshed net (mean  $100 \times 70 \mu\text{m}$ ) while *H. pellucidula* (Figure 40-Figure 41) is larger and uses nets with a mean mesh of  $370 \times 240 \mu\text{m}$  (Hildrew & Edington 1979). Migration of *H. siltalai* onto mosses (*Fontinalis antipyretica*; Figure 43) in spring further separates their niches. Englund (1993) observed that whereas small IV instar larvae were able to construct nets on the mosses, the physical structure seemed unsuitable for the larger V instar larvae to do so.

### Food

Although Frost (1942) reported several studies in which *Hydropsyche instabilis* ate primarily Chironomidae, and Slack (1936) found that it ate diatoms, it also ingests mosses. In Great Britain (Percival & Whitehead 1929) and in calcareous streams in South Wales, *Hydropsyche instabilis* (Figure 44) ingested *Fontinalis antipyretica* (Figure 43) (Percival & Whitehead 1929; Jones 1949). Frost (1942) found that *Hydropsyche instabilis* (Figure 44) lived primarily among mosses in an acid stream, but in the alkaline stream it was *Cheumatopsyche lepida* (Figure 45) that was dominant among the mosses, in this case where there was more silt. Jones (1950) did extensive gut analysis of insects from the River Rheidol; among the Trichoptera, only *Hydropsyche instabilis* of the six species examined had fragments of *Fontinalis antipyretica* (Figure 43) in the gut (7 out of 27). Fragments of this moss were present in nine of the 23 analyses with identifiable gut contents (Jones 1949). Algae and detritus were the most common foods.



Figure 44. *Hydropsyche instabilis* adult, a species whose larvae sometimes eat mosses. Photo from Biodiversity Institute of Ontario, through Creative Commons.





Figure 45. *Cheumatopsyche lepida* larva, a dominant caddisfly among mosses with lots of silt in an alkaline stream. Photo through Creative Commons.

On the other hand, occurrence of net-spinning caddisflies among mosses may offer the advantage of a greater number of prey organisms. Although these insects trap their food on finely constructed nets, they are also carnivores. Haefner (1980) found a significantly higher (2x) density of prey organisms (*Baetis* spp., *Ephemerella* spp., *Nemoura* spp., *Hydroptila* sp., and *Chironomidae*) in rock face samples, where mosses were typically dense. These organisms are common among stream mosses – *Hydroptila* less so (Glime 1994), thus the abundance of prey invertebrates may account for the greater productivity of *Parapsyche cardis* (see Figure 20) there.

Although *Diplectrona modesta* (Figure 29) had little correlation with mossy rocks in one of two Appalachian Mountain streams, and few such rocks existed in the other (Haefner & Wallace 1981a,b), this and other studies (Gurtz & Wallace 1986) suggest that the mosses provide a variety of niches that benefit both the potential prey organisms and the net-spinning caddisflies.

In a study to determine the source of foods for aquatic invertebrates, Torres-Ruiz *et al.* (2007) used the distinctive fatty acids for green algae, diatoms, and bryophytes, each of which also differed from fatty acids of terrestrial food sources. They determined that *Hydropsyche* spp. (Figure 40-Figure 42) consumed primarily **autochthonous** (originating from within the stream system) food sources, not the terrestrial **allochthonous** (originating from elsewhere) food such as leaf litter. In Appalachian Mountain streams the **Hydropsychidae**, including species of *Hydropsyche*, seemed to use the mosses instead of constructing nets to capture their food (Glime 1968). There always seemed to be many more larvae than nets.

Gut pH is often important in determining the digestible food sources. *Hydropsyche betteni* (Figure 46-Figure 47) had a gut pH close to neutral but somewhat alkaline (Barlocher & Porter 1986). Hence, this species was unable to **hydrolyze** (break down a compound by chemical reaction with water) proteins of maple leaves that were not yet conditioned by decomposer organisms. They could, however, digest starch and laminarin (storage product in many seaweeds). Unlike those in the crane fly *Tipula*, the fungal **carbohydrases** (enzymes that break down carbohydrates) ingested with decomposing leaves remained active in the guts of this species.



Figure 46. *Hydropsyche betteni* larva, with a gut pH that is alkaline. Photo by Bob Henricks, with permission.



Figure 47. *Hydropsyche betteni* larva showing ventral gills. Photo by Donald S. Chandler, with permission.

### Role of Water Velocity

The larvae of the **Hydropsychidae** are able to partition the niches of the most immature from those of the nearly mature (Osborne & Herricks 1987; Muotka 1990). Osborne and Herricks (1987) found that *Hydropsyche* (Figure 40-Figure 42) species in their study separated the larger larvae into communities at higher velocities, whereas the smaller, less mature larvae sought areas of diminished flow. The same size distribution occurs between species. These larvae seek out depressions where they can gather passing detritus but where sedimentation is minimal. Turbulence seems to play a role in determining distribution, perhaps contributing to food availability and preventing



sedimentation. Larger larvae are apparently able to occupy greater velocities; this is coupled with the construction of a larger mesh size, hence dividing the feeding niche from that of smaller larvae.

The net-spinning caddisflies prefer a habitat with a stable substrate and high water velocity. Georgian and Thorp (1992) showed that 96% of the **Hydropsychidae** larvae selected artificial moss substrates that had high velocity water flowing over them. They estimated that a prey item would be consumed within 5.5 m of travel in the drift. It appears that one advantage afforded these moss dwellers is that they can take advantage of high-flow rates while themselves finding a flow-rate suitable for their own safety.

Current speed also influences net-spinning activity, with a greater percentage of larvae spinning nets at 20 cm sec<sup>-1</sup> (73%) than at 10 cm sec<sup>-1</sup> (10%) (Edington 1965). Edington found that hydropsychid larvae formed tunnels into the moss mats with nets at the moss surface. When the nets were removed (and when they were not) and the flow was artificially reduced, the larvae moved to a different area. When something restricts the flow, the larvae move to a new location and construct new nets (Edington 1965, 1968).

Muotka (1990) considered that it was the flow pattern, rather than the flow velocity itself, that determined the pattern of occupancy by filter-feeding caddisfly larvae. He based this on the ability of multiple sizes of caddisflies, including **Hydropsyche** (Figure 40-Figure 42) to coexist at the same flow rates. Nevertheless, he concluded that species were often ecologically closer to other species than to other instars of their own species. In their study, many of the sites were covered with bryophytes [mosses *Fontinalis antipyretica* (Figure 43), *Cratoneuron commutatum* (Figure 48), leafy liverwort *Jungermannia exsertifolia* (Figure 49)] and the uneven surface of this substrate would create multiple flow patterns. It is noteworthy that in the stream that lacked bryophytes only one filter-feeding caddisfly was present – **Hydropsyche saxonica** (Figure 50) – whereas seven species occurred in the two streams with heavy bryophyte cover.



Figure 48. *Cratoneuron commutatum*, a moss that alters flow patterns, as it is doing here. Photo through Creative Commons.

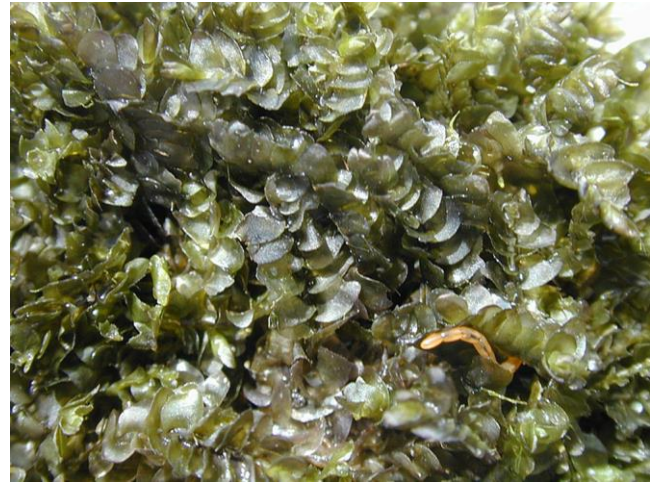


Figure 49. *Jungermannia exsertifolia* ssp. *cordifolia*, contributor to flow patterns that allow niche partitioning for **Hydropsychidae**. Photo by Michael Lüth, with permission.



Figure 50. *Hydropsyche saxonica* larva, the only filter-feeding caddisfly in a stream with no mosses. Photo by Niels Sloth, with permission.

Food capture is important in the location of nets, and water velocity helps to determine the food available. Mosses on the rocks actually prevent some insects from living there. The caddisfly **Leucotrichia** (**Hydroptilidae**; Figure 51) is unable to live on a substrate dominated by heavy moss growth and instead the net spinner **Hydropsyche** (Figure 40-Figure 42) occupies those locations (McAuliffe 1983). The larvae arrange their nets very evenly downstream but are often crowded across the substrate, preventing the water from being filtered by a net above them.



Figure 51. *Leucotrichia pictipes* larva, a genus that cannot live on a substrate with heavy moss cover. Photo by Stroud Water Research Center, through Creative Commons.



As I already noted in the Appalachian Mountain streams, some caddisflies actually use the mosses to help them gather food. Hildrew and Edington (1979) found that favorable situations for net-spinning caddis larvae (**Hydropsychidae**), such as moss covered rocks, often seem to be occupied to capacity. I have observed the same relationship, but it appeared that the caddisflies in some cases took advantage of the collecting ability of the moss and did not make nets. This would be useful for those species that eat primarily small invertebrates living among the bryophytes (Ross & Wallace 1983), but it could also take advantage of the bryophytes as filter traps.

### Role Below Impoundments

Mosses are important habitats at impoundments. In Valley Creek in Minnesota, USA, **Hydropsychidae** caddisflies use mosses and filamentous algae as sites for attachment and building materials for retreats, with the mosses providing an environment that protects the larvae from the abrasive sand deposited by the impoundment (Mackay & Waters 1986).

Ogbogu (2000; Ogbogu & Akinya 2001) likewise found that **Fontinalis** (Figure 1) was important to the **Hydropsychidae** in an impoundment at Ile-Ife, Nigeria. They occupied the spillway, among the **Fontinalis**, in large numbers when sampled in August (1233 m<sup>-2</sup>), September (900 m<sup>-2</sup>), and November (1178 m<sup>-2</sup>). The moss provided refuge from the rapid water of the spillway, protection from predators, and food (epiphytic diatoms and other algae) trapped among the mosses.

### Polycentropodidae – Tube Maker Caddisflies

Members of this worldwide family are relatively small to moderate in size, with the forewing reaching 6-13 mm (Hickin 1967). Larvae live in both quiet and flowing waters and trap their food in a tube (Murray 2006).

**Polycentropus** (Figure 52) is not a caddisfly one thinks of as a moss dweller because of its long, tubular net. But in both Ballysmuttan and Straffan, UK, it does occur among mosses, as well as other locations (Frost 1942). Percival and Whitehead (1929) found that **Polycentropus flavomaculatus** (Figure 52) was most abundant in thick mosses compared to other types of substrate. In mid-Appalachian Mountain streams, larvae of this genus are occasional inhabitants of bryophytes (Glime 1968).



Figure 52. *Polycentropus flavomaculatus* larva, a species that is more abundant in thick mosses than elsewhere. Photo by Dragiša Savić, with permission.

In one location in the Pyrénées Décamps (1967) found that **Plectrocnemia scruposa** (see Figure 53) comprised 4.5% of the **Trichoptera** fauna among mosses. Edington (1965) found that **Plectrocnemia conspersa** (see Figure 53) spun more nets at a flow rate of 10 cm sec<sup>-1</sup> (80% of the larvae) than at 20 cm sec<sup>-1</sup> (4%), a relationship just the opposite of that of **Hydropsyche instabilis**. Furthermore, in both species, those few making nets at the less favorable flow rate had a tendency to construct aberrant nets.



Figure 53. *Plectrocnemia geniculata* larva, member of a genus in which some larvae live among mosses. Photo from Biodiversity Institute of Ontario, through Creative Commons.

From Ceylon, Schmid (1958) reported **Nyctiophylax devanampriya** (Figure 54), **Pseudoneureclipsis watagoda** (Figure 55), and **P. thuparama** from large, mossy rocks in the torrent.



Figure 54. *Nyctiophylax* sp. larva; *N. devanampriya* occurs among mosses in torrents in Ceylon. Photo by Dana R. Denson Florida Association of Benthologists, with permission.





Figure 55. *Pseudoneureclipsis* adult, a genus whose naiads can live on mossy rocks in torrents. Photo by Biodiversity Institute of Ontario, through Creative Commons.

But this family relies primarily on food trapped in its funnel-shaped net. Ross and Wallace (1983) demonstrated that 80% of the food for this family in a southern Appalachian Mountain, USA, stream was fine detritus. Another 15% was diatoms. So why do we find them among bryophytes at all?

### Psychomyiidae – Net Tube Caddisflies

The **Psychomyiidae** are widespread, but are concentrated in the Oriental Region and absent in the Neotropical Region (Kjer 2010a). The adults are of moderate size (5-8 mm long forewings) (Watson & Dallwitz 2003). This family traps its food in a silken tube (Figure 56), with the diet consisting of algae, leaves, and animal matter (Neuswanger 2015). Grazing may occur both on the tubes and nearby, therefore consisting mostly of diatoms and other algae (Holzenthal *et al.* 2007; Kjer 2010a). Females dive to the bottom of the stream to lay their eggs (Neuswanger 2015).



Figure 56. **Psychomyiidae** net. Photo by Janice Glime.

Mosses occurred in the guts of *Psychomyia pusilla* (see Figure 57) and *Tinodes waeneri* (Figure 58-Figure 59) in UK streams (Percival & Whitehead 1929), attesting to their residence among bryophytes.



Figure 57. *Psychomyia flavida* larva. *Psychomyia pusilla* eats mosses. Photo from Stroud Water Research Center through Creative Commons, with permission.



Figure 58. *Tinodes waeneri* larva, a species that consumes mosses. Photo by Niels Sloth, with permission.



Figure 59. *Tinodes waeneri* larval tube. Photo by Niels Sloth, with permission.

## Philopotamoidea

### Philopotamidae – Finger-net Caddisflies

The larvae of this worldwide family build nets that can require more than 1 km of silk (Wallace & Malas 1976); these are used to trap small particles for food (McLeod 2005). To use them, the larvae are restricted to fast-flowing water of rivers and streams. The adult body is 5-9 mm long.



The net-building behavior would seem to preclude mosses as a substrate, but exceptions occur. *Philopotamus montanus* is not typically a bryophyte inhabitant and captures its food with a tube net. But this net can trap bits of mosses travelling downstream, and of the 15 guts with identifiable contents, two had *Fontinalis antipyretica* (Figure 43) (Jones 1949).

*Chimarra* (Figure 39; Figure 60-Figure 65) lives among mosses but prefers the gravel and sand at their bases (Armitage 1961). Williams and Hynes (1973) suggested that the affinity of *C. aterrima* (Figure 39) for moss-covered rocks may have been more related to the large size of those rocks rather than the presence of the moss. For example, in a wooded Ontario, Canada, stream, *Wormaldia moesta* (Figure 66) preferred bare stones, whereas *Rhyacophila minor* (Rhyacophilidae) preferred moss-covered stones in the same area (Singh *et al.* 1984). *Wormaldia moesta* grazed on diatoms when its primary food supply, detritus/ seston (living organisms and non-living matter swimming or floating in a water body), became scarce. In my own studies of the fauna of bryophytes in the Appalachian Mountain streams, *C. aterrima* was occasionally present, but in small numbers, among *Fontinalis dalecarlica* (Figure 33) in larger streams (Glime 1968). It was absent in the other bryophytes.



Figure 60. *Chimarra tsudai* tubes with thallose liverworts at the funnel opening. Photo by Takao Nozaki, with permission.



Figure 61. *Chimarra* pupal case. Photo by Mark Melton, with permission.



Figure 62. *Chimarra* pupa showing on underside of sand case. Photo by Mark Melton, with permission.



Figure 63. *Chimarra* pupa removed from sand case, showing shed sclerotized parts from larva inside the pupal covering. Photo by Mark Melton, with permission.



Figure 64. *Chimarra* pupa removed from case. Photo by Mark Melton, with permission.



Figure 65. *Chimarra tsudai* adult. Takao Nozaki, with permission.





Figure 66. *Wormaldia moesta* larva, a species that prefers bare stones even when mosses are present. Photo by Donald S. Chandler, with permission.

Another occasional visitor to bryophytes in Appalachian Mountain, USA, streams was *Dolophilodes distinctus* (Figure 67) (Glime 1968). In this case, it occurred among all four of the primary bryophytes in the study: *Hygroamblystegium fluviatile* (Figure 31), *Platyhypnidium riparioides* (Figure 32), *Fontinalis dalecarlica* (Figure 33), and *Scapania undulata* (Figure 68), preferring the mats and turfs over *Fontinalis* streamers.



Figure 67. *Dolophilodes distinctus* larva, an occasional visitor to Appalachian Mountain stream bryophytes. Photo by Donald S. Chandler, with permission.



Figure 68. *Scapania undulata*, a leafy liverwort that can modify flow patterns and house insects. Photo by Michael Lüth, with permission.

## Summary

**Lepidoptera** apparently do not use aquatic bryophytes.

**Trichoptera**, on the other hand, are among the common inhabitants. Those that enter the drift may use bryophytes as a means to get out of the drift. Some larvae use the bryophytes for food and many use them as a safe site for capturing food, using both filtering strategies and predation of smaller inhabitants. The mosses themselves may serve as filter traps for caddisfly food, including drifting algae, bacteria, decomposing organic matter, and detritus. For some caddisflies the bryophytes themselves serve as food and may be a seasonal staple when other foods are unavailable. Some build their cases from bryophytes and live among the bryophytes to capture food.

Larvae of most **Trichoptera** are aquatic, and many may also use the bryophytes as a site for pupation and emergence. The most common families among bryophytes are The **Hydropsychidae** and **Rhyacophilidae**. These are both caseless caddisflies, and the bryophytes may provide some of the protection otherwise afforded by cases.

**Hydropsychidae** take advantage of the bryophytes to partition their niches and avoid competition for food. In some cases this is the result of changing diets at later instar stages. Others use differences in flow within the bryophyte mat. They seem to be able to use the bryophytes to trap food, and the bryophytes create locations with a variety of flow regimes. Still other caddisflies are selective about which species of bryophytes they use, with a few selecting leafy liverworts only and others avoiding them.

The importance of the bryophytes as food remains a mystery. It is possible they are ingested along with adhering periphyton and detritus without being digested.

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# CHAPTER 11-12

## AQUATIC INSECTS: HOLOMETABOLA – TRICHOPTERA, SUBORDERS INTEGRIPALPIA AND SPICIPALPIA

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# CHAPTER 11-12

## AQUATIC INSECTS: HOLOMETABOLA – TRICHOPTERA, SUBORDERS INTEGRIPALPIA AND SPICIPALPIA

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Figure 1. *Adicrophleps hitchcocki* (Brachycentridae), a larva that makes its case from mosses. Note the "furry" portion near the opening. Photo by D. N. Bennett, with permission.

### SUBORDER INTEGRIPALPIA

#### Leptoceroidea

##### Odontoceridae – Mortarjoint Casemakers

This worldwide family lives in springs and small to medium streams and rivers, typically with slow flow; some are associated with waterfalls (Holzenthal *et al.* 2010c). Also known as the strong case-maker caddis, the larvae make very strong cases from bits of rock with more than usual amounts of the silk glue (Henricks 2011).

Although I never found *Pseudogoera* in my studies of stream insects among bryophytes in the mid Appalachians, *P. singularis* (Figure 2) is associated with mosses in waterfalls in the southern Appalachians, USA (Wallace & Ross 1971).



Figure 2. *Pseudogoera singularis* larva, a species that lives in mosses of waterfalls in the southern Appalachian Mountains. Photo by BIO Photography Group, through Creative Commons.



In the mid-Appalachian Mountain streams, I found two species of *Psilotreta* (Figure 3) among *Hygroamblystegium fluviatile* (Glime 1968). This genus has forewings of 6-17 mm (Parker & Wiggins 1987), representing one of the larger of the bryophyte dwellers.



Figure 3. *Psilotreta* larva, an inhabitant of *Hygroamblystegium fluviatile* in the Appalachian Mountains. Photo by Bob Henricks, with permission.



Figure 4. *Hygroamblystegium fluviatile*, home of *Adicropheps hitchcockii*. Photo by Michael Lüth, with permission.



Figure 5. *Hygroamblystegium fluviatile* leaf showing strong costa that seems to be used in making the cases of *Adicropheps hitchcockii*. Photo by Michael Lüth, with permission.

## Limnephiloidea

### Goeridae

This family occurs on all continents except Australia and South America (Holzenthal *et al.* 2007). Adults have a forewing length of 6-9 mm and are typically light brown (Figure 6) (Houghton 2012). The larvae (Figure 7) live in cool, flowing water and graze on **periphyton**. Their larval cases consist entirely of rock fragments, sometimes with larger rocks on each side of the case (Figure 8).



Figure 6. *Goera pilosa* adult, demonstrating the light brown wings typical of the family **Goeridae**. Photo from Biopix, through Creative Commons.



Figure 7. *Pseudogoera singularis* larva. Photo by BIO Photography Group, through Creative Commons.



Figure 8. *Goera calcarata* larva showing large rock fragments on sides of case. Photo by Bob Henricks, with permission.



*Goerita* is a small genus with only three species and is restricted to the Appalachian Mountains and Allegheny Plateau in eastern North America (Parker 1998). The larvae are **bryobionts**, in this case living on rocks covered with mosses and liverworts where the rocks can be dry or covered by a film of water. The larvae do not eat the bryophytes, but instead feed on detritus and diatoms growing there.

*Goerita semata* lives on the undersides of rocks (Flint 1960), but in western North Carolina, Huryn and Wallace (1985) found the larvae among liverworts and mosses on vertical rock faces; fewer than 2% were found on other substrata. *Goerita betteni* lives in a similar habitat (Wiggins 1973). Huryn and Wallace (1985) suggested that the bryophytes may offer the larvae some protection from desiccation. Pupae typically occur on these same rocks with mosses and a thin film of water. Ultimately, females lay their eggs away from water on bare rock, mosses, and liverworts. Food of the larvae consists primarily of fine amorphous detritus (65%), and diatoms (32%), but diatom composition increases to an average of 64% in spring. Bryophyte clumps are typically good sources of both. Although the mechanisms of desiccation resistance are unknown in larvae of this species, it is likely that they are adapted behaviorally by living among the bryophytes.

In the River Rajcianka in Slovakia, *Lithax niger* (Figure 9) is a bryophyte dweller, living under water, but not in the wet emergent bryophytes (Krno 1990). This is a mountain species, occurring in the Alps and Balkans.



Figure 9. *Lithax niger* adult, a species whose larvae live among mosses in the River Rajcianka. Photo by Paul Frandsen, through public domain.

The larvae of *Archithremma ulachensis* move to a layer of *Sphagnum* (Figure 10) on the bank of a spring to pupate (Levanidova & Vshivkova 1984). These pupae are morphologically reduced, lacking long **setae** (hairs) and projections used to clean the silk disks that close the case. They also lack swimming legs. The larvae live in streams that have low water temperatures (3-5°C) in summer.

In a cool mountain stream of central Japan Tada and Satake (1994) found that *Pseudostenophylax ondakensis* (Figure 12) was significantly more abundant on mats of the moss *Platyhypnidium riparioides* (Figure 13) than in bare rock areas. Décamps (1967, 1968) found *Rhadicoleptus spinifer* (see Figure 14) to be abundant among mosses in the Pyrénées; at one station it comprised ~15% of the moss **Trichoptera** fauna (Décamps 1967).



Figure 10. *Sphagnum cuspidatum*, a pupation site for *Limnephilus peltus* and *Archithremma ulachensis*. Photo by Bernd Haynold, through Creative Commons.

### Limnephilidae – Northern Caddisflies

The **Limnephilidae** encompasses a wide variety of case-making caddisflies in a wide range of habitats. Their ingenuity in making these homes could challenge some of our most creative artists. This is one of the largest caddisfly families, with recent segregate families diminishing its numbers. Although it occurs worldwide, its records are concentrated in Europe and North America (Limnephilidae 2015). In North America it is often the dominant group in higher elevation streams. But these are mostly large caddisflies (15-35 mm) (Houghton 2012), making navigation difficult among bryophytes. *Fontinalis* (Figure 11), on the other hand, is a large enough moss with a streamer habit that permits these larger larvae to navigate (Glime 1968, 1994). Their dependence on terrestrial litter makes the larvae vulnerable to deforestation (Houghton 2012).



Figure 11. *Fontinalis antipyretica*, home to many kinds of insects. Photo by Kristian Peters, with permission.





Figure 12. *Pseudostenophylax ondakensis* larva, a species that is significantly more abundant on the moss *Platyhypnidium riparioides* than on bare rock. Photo by Takao Nozaki, with permission.



Figure 13. *Platyhypnidium riparioides*, home to *Pseudostenophylax ondakensis* in Japan. Photo by J. C. Schou, with permission.



Figure 14. *Rhadicleptus alpestris* adult. *Rhadicleptus spinifer* larvae are abundant among mosses in the Pyrénées. Photo by Niels Sloth, with permission.

The larvae of *Chaetopterygopsis maclachlani* (Figure 15) typically occur among clumps of *Fontinalis* (Figure 11) in the Vosges Mountains, eastern France, mostly in areas with slower or laminar flow (Lehrian *et al.* 2010). The mosses constitute ~65% of their diet, with the remainder being coarse leaf detritus (Dangles 2002). Dangles warned that some species, including this one, are

able to shift their diet based on availability, causing misinterpretations based on the general feeding guild classification of these insects. Dangles (2002) considered *Chaetopterygopsis maclachlani* (Figure 15) to be a specialist on bryophytes; they furthermore build their cases from *Fontinalis* (Figure 62) (Malicky 1994). As adults they typically crawl, not fly, among the **riparian** (streambank) vegetation.

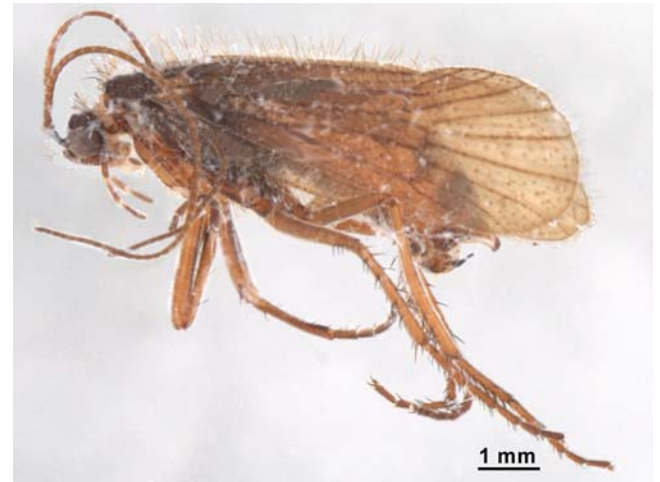


Figure 15. *Chaetopterygopsis maclachlani* adult, a species whose larvae live among *Fontinalis* and eat mosses as 65% of their diet. Photo from Biodiversity Institute of Ontario, through Creative Commons.

*Chaetopterygopsis machlachlani* is widespread in the Pyrenees to Baikal, specializing in *Fontinalis* and other streambed mosses (Báilint *et al.* 2011).

In the mid-Appalachian Mountain, USA, streams, the **Limnephilidae** are poorly represented among bryophytes (Glime 1968). Furthermore, those few that are present differ from any of the species I found in the literature as moss dwellers. Two species of *Pycnopsyche* [*P. luculenta*, *P. cf. scabripennis* (Figure 16)] were the most common, appearing in clumps of *Fontinalis* (Figure 62) (Glime 1968). This restriction is most likely due to the large size of the **Limnephilidae** larvae, especially when their bulky case is considered. They would have real difficulty moving about in *Hygroamblystegium fluviatile* (Figure 4-Figure 5) or *Platyhypnidium riparioides* (Figure 13).



Figure 16. *Pycnopsyche scabripennis* larva, a *Fontinalis* dweller. Photo by Tom Murray, through Creative Commons.



In an experimental study on *Limnephilus rhombicus* (Figure 17), Higler (1975) was able to keep the larvae alive on a diet of *Fontinalis antipyretica* (Figure 11) with dead birch and oak leaves. However, it appears that its natural diet is mostly living plants (Slack 1936), dead leaves (Slack 1936; Lepneva 1966) and sometimes Naididae (aquatic segmented worms). It is not typically a moss dweller, so the moss diet was most likely unnatural. But Slack (1936) did find that it ate *Fontinalis* in the field. On the other hand, when *Potamophylax rotundipennis* (Figure 18-Figure 19) was provided choices of birch, oak, and beech leaves and *Fontinalis antipyretica*, it avoided the moss and beech leaves.



Figure 17. *Limnephilus rhombicus* larva, showing yet a third very different case, one using snail shells. Photo by Dragiša Savić, with permission.



Figure 18. *Potamophylax* larva and case. *Potamophylax rotundipennis* rejects *Fontinalis antipyretica* as a food choice. Photo by Michael Wiesner <[www.waldzeit.ch](http://www.waldzeit.ch)>, with permission.

Although most of the *Limnephilidae* make large cases with large components of twigs and leaf fragments, some use bryophytes. *Limnephilus externus* (Figure 20-Figure 21) larvae are known to use the moss *Leptodictyum riparium* (Figure 22) to construct their barrel-shaped cases (Pritchard & Berté 1987). In experiments, this species was able to use wheat flakes, but not alder leaves, to make its case. In the same experiment, *Nemotaulius hostilis* (Figure 23) used alder, willow, and burreed but did not use wheat flakes or mosses. These same two insects are shredders that consume tracheophyte detritus, but the proportion of mosses in the diet increases as the larvae become older.



Figure 19. *Potamophylax* adult. Photo through Creative Commons.



Figure 20. Two *Limnephilus externus* larvae with the second grabbing the rear of the first. The two cases appear to be made of bits of grass and this camouflage most likely fools their predators because it confused my non-biologist reviewer! Photo by Wendy Brown <[www.gunnisoninsects.org](http://www.gunnisoninsects.org)>, with permission.



Figure 21. *Limnephilus externus* larva. Photo by Wendy Brown <[www.gunnisoninsects.org](http://www.gunnisoninsects.org)>, with permission.

*Limnephilus peltus* (Figure 24) doesn't spend much time among mosses as a larva, but when it is time to pupate, it burrows into mosses along fen streams where it spends its pupal life (Erman 1984). Unfortunately, if the stream dries out, the pupa is likely to die.





Figure 22. *Leptodictyum riparium*, home of larvae of *Limnephilus externus*. Photo by Jan-Peter Frahm, with permission.



Figure 23. *Nemotaulius hostilis* larva showing case made of leaf litter. Photo by Donald S. Chandler, with permission.



Figure 24. *Limnephilus* sp. larva, a genus that sometimes pupates in mosses of fens. Photo by Jason Neuswanger, with permission.

The habitat of larvae of the high altitude *Drusus discolor* (Figure 25) in the Pyrénées consisted of filamentous algae and the moss *Bryum* (Figure 26) (Décamps 1968). This caddisfly is one of the two most abundant caddisflies among mosses (Décamps 1967). In the River Rajcianka in Slovakia, *Drusus annulatus* (Figure 27) occurs not only among submerged bryophytes but also moving about among the wet bryophytes that emerge above the water level (Krnó 1990).



Figure 25. *Drusus discolor* adult, a species that lives among the moss *Bryum* in the Pyrénées. Photo from Biodiversity Institute of Ontario, through Creative Commons.

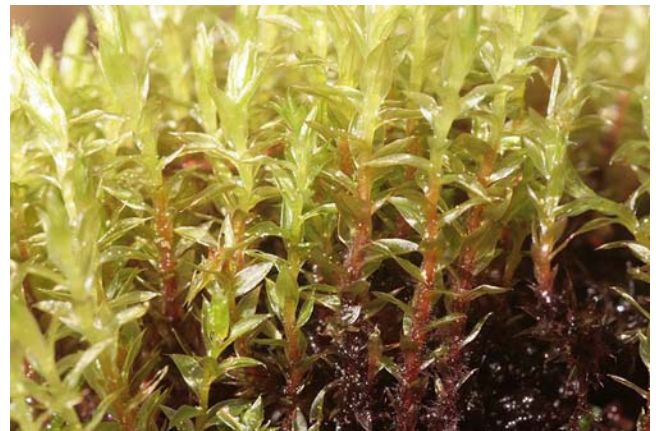


Figure 26. *Bryum pseudotriquetrum*, home to several species of *Drusus* in Europe. Photo by Hermann Schachner, through Creative Commons.



Figure 27. *Drusus annulatus* adult, a species whose larvae can live above or below the water surface among bryophytes. Photo by James K. Lindsey, with permission.

*Frenesia difficilis* (Figure 28) lays its eggs out of the water, sometimes on mosses that overhang the water (Flint 1956). In this terrestrial location the eggs may freeze in winter. In the Massachusetts, USA, fish hatchery, Flint found no other relationship with mosses during the life cycle.



Figure 28. *Fresnia difficilis* male, a species that sometimes lays its eggs on mosses that overhang the water. Photo by Tom Murray, through Creative Commons.

The Arctic caddisfly *Sphagnophylax meiops* lives in Arctic pools in the tundra in the Northwest Territories of Canada (Wiggins & Winchester 1984) where the larvae take advantage of the surface water in the pool (Winchester *et al.* 1993). When the water recedes the larvae move to the organic materials accumulated above the permafrost to feed, grow, and metamorphose into pupae and adults. This caddisfly is flightless and has long bristles on its short wings.

Most **Trichoptera** spend their larval life in the water, but in the genus *Enoicyla* (**Limnephilidae**; Figure 29), the larvae are terrestrial and the adult female has only vestigial wings, limiting her travel and agility. Males, however, are capable fliers. Larvae may live far from water among the mosses around tree roots (Watson & Dallwitz 2003). Green (2012) noted at least 50 of these larvae climbing up logs, with several browsing a black slime mold. One can observe many larvae together on the surface of mosses and liverworts growing on a stream bank following rain.

*Enoicyla pusilla* (Figure 29) uses fine sand grains and other vegetable matter to make cases where it lives among the mosses (Watson & Dallwitz 2003). The larvae of *Enoicyla*, despite being terrestrial, require 100% humidity (Green 2012). But when they become saturated, they climb upwards to dry, then drop back down when they need to get wet again (at 7% relative humidity). Their respiration is through the cuticle; they lack gills.



Figure 29. *Enoicyla pusilla* larvae, a terrestrial species that requires 100% humidity – a condition often found among mosses. Photo by Ernest van Asseldonk, through Creative Commons.

In his arguments to support that the **Trichoptera** (with hairs on wings) and **Lepidoptera** (with scales on wings) were closely related, Crampton (1920) used the common ability to use mosses in the caddisfly *Enoicyla* (**Limnephilidae**; Figure 29) and the larvae of moths in **Micropterygidae**.

The caddisflies living in peatlands are typically generalist taxa with wide habitat requirements (Flannagan & Macdonald 1987). But a few are **tyrphobionts** (living only in peat bogs and mires). The larvae of *Phanocelia canadensis* (Figure 30-Figure 31) are elusive. The second report of the larvae by Colburn and Clapp in 2006 was from kettle hole wetlands in Massachusetts, USA. Colburn and Clapp attribute the limited reports of larvae of this species to its limited habitat requirements. It lives in *Sphagnum* (Figure 10) habitats with low pH and makes its case from *Sphagnum* (Figure 30) [The picture below (Figure 31) indicates other mosses are used as well.] Larvae remain closely associated with the moss during development. They become dormant in summer, remaining in unsealed cases that are firmly attached to the moss. In autumn they seal the ends of the case and develop into pupae. Even fossil records support their preference for *Sphagnum* (Figure 10) bogs. The larva was originally described from floating *Sphagnum* at the edge of acidic ponds in a spruce-*Sphagnum* bog in New Brunswick, Canada (Fairchild & Wiggins 1989). It appears that adult habitats are much broader, perhaps misleading its collectors (Colburn & Clapp 2006).



Figure 30. *Phanocelia canadensis* larva showing its case made with *Sphagnum*. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Figure 31. *Phanocelia canadensis* larva showing case made with at least some non-*Sphagnum* mosses. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Leberfinger and Bohman (2010) gave larvae of *Limnephilus bipunctatus* (Figure 32) choices of food that included grasses, mosses, algae, and leaves. The larvae preferred leaves of the shrubby cinquefoil. Although they ate little of the mosses, grass was the least preferred food.

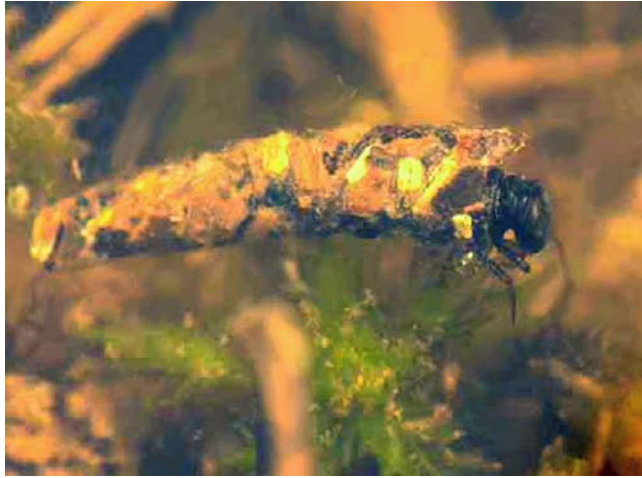


Figure 32. *Limnephilus bipunctatus* larva in case, a species that includes mosses in its diet. Photo by James K. Lindsey, with permission.

*Philocasca* is not a genus one often reads about in moss habitats. Nevertheless, mosses appear to be suitable sites for pupation. In describing the new species *Philocasca rivularis* (see Figure 33) Wiggins and Anderson (1968) state that pupae attach to the undersides of moss clumps along stream banks. Mutch and Pritchard (1984) found that instar V larvae of *P. alba* (Figure 34) in a Rocky Mountain stream had mostly moss (*Hygrohypnum luridum* – Figure 35) in the gut in spring and summer, but had leaf fragments in the gut in autumn. Furthermore, when fed detritus supplemented with moss these larvae grew significantly better than when fed detritus alone, suggesting that the moss was an important nutrient source.



Figure 33. *Philocasca thor* adult. *Philocasca rivularis* pupates on undersides of moss clumps on streambanks. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Figure 34. *Philocasca alba* adult, a species whose larvae feed on the moss *Hygrohypnum luridum* in a Rocky Mountain, USA, stream in spring and summer. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Figure 35. *Hygrohypnum luridum*, a species that typically occurs both in the water and above it. Photo by Dale Vitt, with permission.

*Onocosmoecus unicolor* (Figure 36-Figure 37) is a large shredder that includes mosses in its varied diet (National Park Service 2014).



Figure 36. *Onocosmoecus unicolor* larva, a moss consumer. Photo by Jason Neuswanger, with permission.



Figure 37. *Onocosmoecus unicolor* adult. Photo by Bob Newell, with permission.



*Chyranda centralis* (Figure 38) is a caddisfly of small spring streams among leaf accumulations. Its food includes leaves, bark, and may even include mosses (National Park Service 2014).



Figure 38 *Chyranda* larva of small spring streams; it may sometimes eat mosses. Photo from California Department of Fish and Wildlife, through public domain.

Mosses provide vertical zonation possibilities for the caddisflies. Krno (1990) addressed these vertical zones in the River Rajcianka in Slovakia. There, the limnephilids *Allogamus auricollis* (Figure 39-Figure 40) (a shredder), *A. uncatus*, and *Drusus annulatus* (Figure 41) occurred among the submerged mosses, but above water only *Allogamus auricollis* and *Drusus annulatus* occurred among emergent wet mosses. On the other hand *Parachiona picicornis* (Figure 42) was only found above water among the wet mosses.



Figure 39. *Allogamus auricollis* larva, a species that traverses among mosses both below and above the water surface. The larva is seen here breaking the surface tension. Photo through Creative Commons.



Figure 40. *Allogamus auricollis* larvae. Photo by Wolfram Graf, with permission.



Figure 41. *Drusus annulatus* adult, a species whose larvae live among submerged mosses and will venture above the water among wet mosses. Photo by James K. Lindsey, with permission.



Figure 42. *Parachiona picicornis* adult, a species whose larvae live among submerged mosses but will not venture above the water among wet mosses. Photo by James K. Lindsey, with permission.

*Chaetopterygopsis maclachlani* larvae in the Carpathians are "specialized" on the aquatic moss *Fontinalis* (Figure 62) in mountain streams (Bálint *et al.* 2011).



Figure 43. *Chaetopterygopsis machlachlani* larva, a *Fontinalis* dweller. Photo by Michael Balke, through Creative Commons.



### Lepidostomatidae – Bizarre Caddisflies

This family is widespread in the Northern Hemisphere, extending southward to Panama, New Guinea, and the Afrotropical region (Holzenthal *et al.* 2010a). Hilsenhoff (1975), in reporting on Wisconsin, USA, **Lepidostomatidae**, considered the larvae of this family to inhabit a wide range of clean streams. The larvae live among rocks, debris, and mosses on rocks and eat mostly detritus (BugGuide 2005). In North America the larvae inhabit springs, streams, and large slow-moving rivers where they eat detritus. They build a log cabin style of case from stem and leaf pieces or sand grains.

I did find *Lepidostoma americana* in clumps of *Hygroamblystegium fluviatile* (Figure 4-Figure 5) in the Appalachian Mountain streams (Glime 1968). Some older cases of *Lepidostoma* sp. contained fragments of the liverwort *Scapania undulata* (Figure 74) in them near the opening. *Lepidostoma hirtum* (Figure 44-Figure 45) is common among mosses at both Ballysmuttan and Straffan in the UK (Frost 1942). Its diet consists of algae, mosses, and tracheophytes (Rousseau *et al.* (1921). The moss not only provides a suitable location to find its food, but provides it protection from trout and other fish that are its predators.



Figure 44. *Lepidostoma hirtum* larva, an inhabitant of bryophytes that also eats them. Photo by Urmas Kruus, with permission.



Figure 45. *Lepidostoma hirtum* larva head. Photo by Urmas Kruus, with permission.

*Crunoecia irrorata* (Figure 46) prefers moss cushions and fallen leaves (Köcherfliegen 2015). In UK streams, this species had mosses in the gut (Percival & Whitehead 1929).

### Oeconesidae

This is a small family from Tasmania (1 species) and New Zealand (Holzenthal *et al.* 2007), but of a relatively large size (adults 30-38 mm) (Oeconesidae 2013). Larvae live in small, forested streams, make cases from plant and

rock material, and feed on plant debris (Holzenthal *et al.* 2007).



Figure 46. *Crunoecia irrorata* larva, a moss consumer. Photo by Niels Sloth, with permission.

In New Zealand, both *Oeconesus maori* (see Figure 47) and *Zelandopsycha ingens* (Figure 48) occasionally ingest bryophytes (Suren 1988). Suren and Winterbourn (1991) determined that of the 14 taxa that had bryophyte fragments in their guts, only *Zelandopsycha ingens* and *Oeconesus similis* consumed them regularly.



Figure 47. *Oeconesus* larva, a bryophyte dweller and bryophyte consumer in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 48. *Zelandopsycha* larva and case, a bryophyte dweller and regular bryophyte consumer. Photo by Stephen Moore, Landcare Research, NZ, with permission.

## Uenoidae

This family lives mostly in cool, fast-flowing headwaters and is distributed in North America, southern Europe, and eastern Asia (Holzenthal *et al.* 2007). Their cases may be constructed either of coarse pebbles, as in *Neophylax* (Figure 53-Figure 55), or of fine sand, flattened, and shaped like the shell of a limpet, as in *Thremma* (Figure 49). Larvae eat diatoms and fine particulate matter that they scrape from rocks. These larvae are among the smaller caddisflies, being up to 15 mm (Wiggins 2004), although for moss dwellers they would be in the medium to large category.



Figure 49. *Thremma gallicum* larva showing limpet type of case. Photo from Guillaume Doucet, with permission.

*Thremma* sp. (Figure 49) in the trout streams of Yellowstone National Park, USA, occurs among mosses and the alga *Cladophora* in strong rapids (Muttkowski & Smith 1929). Each of these caddisflies collected from the mosses had mosses in the gut, averaging 70% of the contents. The alga *Epithemia* (Figure 50), most likely living among the mosses, comprised the remaining 30%. Brown (2007) found significant numbers of *Neothremma alicia* (Figure 51-Figure 52) in small, mossy streams in the headwaters of the East River, Colorado, USA.



Figure 50. *Epithemia*, a diatom genus that is a common food source for the caddisfly *Thremma*. Photo by Kristian Peters, with permission.



Figure 51. *Neothremma alicia* larva with case, a moss dweller in small, headwater streams. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Figure 52. *Neothremma alicia* larva outside its case. Photo from Biodiversity Institute of Ontario, through Creative Commons.

In the Appalachian Mountain stream bryophytes, the **Uenoidae** were represented by a completely different genus from the ones I found in publications, the only one being *Neophylax* (Figure 53-Figure 55), a genus that sometimes reached large numbers among the **Trichoptera**, but usually was absent (Glime 1968). Nevertheless, three species were represented: *N. concinnus* (Figure 53), *N. consimilis* (Figure 54), *N. oligius* (Figure 55). These were usually in the mat-forming bryophytes, a location permitted by their smaller size.



Figure 53. *Neophylax concinnus* larva, a moss dweller in mid-Appalachian Mountain streams. Photo by Bob Henricks, with permission.





Figure 54. *Neophylax consimilis* larva, a moss dweller in mid-Appalachian Mountain streams. Photo by Bob Henricks, with permission.



Figure 55. *Neophylax oligius* larva, a moss dweller in mid-Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.



Figure 56. *Brachycentrus numerosus* larva, a species like one that is common among *Hygroamblystegium fluviatile* in the Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.



Figure 57. *Brachycentrus montanus* adult, a species that lives among stream mosses. Photo by James K. Lindsey, with permission.

## Phryganeioidea

### Brachycentridae – Humpless Casemaker Caddisflies

The **Brachycentridae** are a Northern Hemisphere family (Holzenthal *et al.* 2010b). They eat algae and plankton (Neuswanger 2015b), but some also ingest bryophytes (Muttkowski & Smith 1929). These caddisflies build cases that resemble log cabins or cylinders made of tiny plant fragments (Holzenthal *et al.* 2010b), including bryophytes in some genera (Glime 1968). Often they are found among mosses (Bouchard 2004). When they emerge, they do so on the surface, which sometimes subjects them to 3-7 m of drifting (Neuswanger 2015b). Females may dive to lay eggs or land with spread wings on the surface to accomplish the task.

#### *Brachycentrus*

Larvae of *Brachycentrus* (Figure 56-Figure 59) species actually attach to the mosses (Armitage 1961; Glime 1968). *Brachycentrus* was one of only two genera of caddisflies that Muttkowski and Smith (1929) found among mosses in the trout streams of Yellowstone National Park, USA. Needham and Christenson (1927) reported *Brachycentrus* from mosses in streams of northern Utah, USA. In Europe, Krno (1990) found *Brachycentrus montanus* (Figure 56) among mosses in the River Rajcianka, Slovakia. In the Appalachian Mountains, *B. cf. numerosus* (Figure 56) occurred in clumps of the moss *Hygroamblystegium fluviatile* (Figure 4-Figure 5) (Glime 1968).



Figure 58. *Brachycentrus americanus* larva, a moss consumer. Photo by Donald S. Chandler, with permission.



Figure 59. *Brachycentrus occidentalis* larvae, a moss consumer species. Photo by Arlen Thomason, with permission.

Gallepp (1977) found that two species of *Brachycentrus* were more responsive to temperature and food availability than to the flow rate. Although case-building decreased with increasing temperature over the range of 4-17°C, *B. occidentalis* (Figure 59) grew faster as the temperature increased in the range of 4-27°C.

### *Micrasema*

The larvae of the grazer genus *Micrasema* (Figure 60) (Gallepp 1977) are common among mosses (Glime 1968, 1994; Tada & Satake 1994). In the mid-Appalachian Mountain streams I was able to distinguish three different morphotypes (species?) among the bryophytes (Glime 1968). In fact, this genus seems to be almost restricted to that habitat (Hilsenhoff 1975). Tada and Satake (1994) found a species in this genus to be the most abundant insect taxon on mats of *Platyhypnidium riparioides* (Figure 13) in a cool mountain stream in central Japan. Among the bryophyte mats its density exceeded 100,000 individuals per square meter in November, an abundance that was 2.8-16.3 times as high as that on the bare rock bottom. At least one species of *Micrasema* (Figure 60) constructs a "log cabin" out of moss stems and leaves (Glime 1968).



Figure 60. *Micrasema charonis* larva, a common moss-dweller that often makes its case from mosses. Photo by Bob Henricks, with permission.

Chapman and Demory (1963) found that in two streams in Oregon, USA, this genus occurred only among mosses and liverworts where there was little detritus. They graze on periphytic algae during the first instar, but in later instars they are likely to be herbivore-chewers (shredders) on mosses and other small photosynthetic material (Chapman & Demory 1963; Aquatic Insects). In fact, Chapman and Demory (1963) found that *Platyhypnidium*

*riparioides* (Figure 13) was the most frequent food, but both mosses and liverworts were eaten. Diatoms were also present in the gut, but they might have been eaten inadvertently along with the bryophytes. And in the Pyrénées *Micrasema morosum* behaves as a shredder and eats mosses (and periphyton) as well (Décamps & Lafont 1974).

In the Pyrénées Décamps (1968) found that *Micrasema morosum* was abundant in the mosses *Cratoneuron commutatum* (Figure 61) and *Bryum* (Figure 26) and was the most abundant bryophyte-inhabiting caddisfly. At one station *M. morosum* comprised 56% of the Trichoptera fauna among mosses and at another it comprised 87.8% (Décamps 1967). *Micrasema vestitum* was abundant in *Fontinalis squamosa* (Figure 62) and in one location it comprised 69% of the Trichoptera fauna among the mosses.



Figure 61. *Cratoneuron commutatum*, home to several species of *Micrasema*. Photo through Creative Commons.



Figure 62. *Fontinalis squamosa*, home to several species of *Micrasema* larvae. Photo by David T. Holyoak, with permission.

Décamps and Lafont (1974) demonstrated the change in moss substrate for *Micrasema morosum* as altitude changes in the Pyrénées. At 1940 m asl the dominant bryophytes were *Brachythecium rivulare* (Figure 63), *Cratoneuron commutatum* (Figure 61), and *Hygrohypnum molle* (Figure 64). At 1590 m asl dominance shifted to *Fontinalis squamosa* (Figure 62), *Fissidens polyphyllus* (Figure 65), and *Platyhypnidium riparioides* (Figure 13). At 1360 m asl *Fissidens grandifrons* (Figure 66) appeared and *Platyhypnidium riparioides* (Figure 13) remained in the stream flora. At



550 m asl the dominant mosses were *Brachythecium rivulare*, *Fissidens grandifrons*, *Platyhypnidium riparioides*, and *Chiloscyphus polyanthos* (Figure 67), with a change in the *Micrasema* species to *M. morosum*, *M. longulum*, *M. moestum*, *M. difficile*, and *M. minimum*. At the lowest location of 430 m, asl *Brachythecium rivulare*, *Cinclidotus fontinaloides* (Figure 68), *Fontinalis antipyretica* (Figure 11), *Platyhypnidium riparioides*, and *Cratoneuron filicinum* (Figure 69) with *Micrasema morosum* once again the predominant species. The food of these *Micrasema* species consisted of fragments of mosses and periphytic algae, with some food unidentifiable.



Figure 63. *Brachythecium rivulare*, home to several species of *Micrasema* larvae. Photo by David T. Holyoak, with permission.



Figure 64. *Hygrohypnum molle*, home to several species of *Micrasema* larvae. Photo by Jan-Peter Frahm, with permission.



Figure 65. *Fissidens polyphyllus*, home for several species of *Micrasema*. Photo by David T. Holyoak, with permission.



Figure 66. *Fissidens grandifrons*, home to larvae of several *Micrasema* species. Photo by Scot Loring, through Creative Commons.



Figure 67. *Chiloscyphus polyanthos*, home to lower elevation species of *Micrasema* larvae in the Pyrénées. Photo by Barry Stewart., with permission



Figure 68. *Cinclidotus fontinaloides*, home to lower elevation species of *Micrasema* larvae in the Pyrénées. Photo by David T. Holyoak, with permission.



Figure 69. *Cratoneuron filicinum* in Europe, home for many immature insects. Photo by Michael Lüth, with permission.



In Japan, *Micrasema uenoi* (Figure 70) feeds on the leaves of *Platyhypnidium riparioides* (Figure 13) and the first instar larvae make their cases of its leaves (Kato 1995). The first two instars live in greater numbers among mosses than on cobble, but by third to fifth instars the numbers are about equal. When artificial mosses (glass wool) and cleaned mosses were introduced, these larvae reached normal densities in 15-30 days. Surprisingly, the density on the glass wool was 2-3 times that among the mosses, but it subsequently decreased quickly. Gut contents of those third to fifth instars on bryophytes was 80% moss; those on the glass wool contained litter and detritus instead. The larvae move about a lot between the pebbles and the mosses. Eggs were apparently absent on the mosses, suggesting that the hatchlings move there.



Figure 70. *Micrasema uenoi* adult, a species whose larvae feed on leaves of *Platyhypnidium riparioides* in Japan. Photo by Takao Nozaki, with permission.

D. N. Bennett (pers. comm. 6 August 2013, 12 August 2014) observed *Micrasema wataga* (Figure 71-Figure 72) larvae eating moss (possibly *Hygrohypnum montanum*) leaves (Figure 71) in the Blue Ridge Mountains of Virginia, USA. They made their cases of the same moss, starting with a tiny cone of minute sand grains. The mosses closest to this cone part, hence the oldest, were no longer green, but those near the opening were still green. This can be a possible source of dispersal of fragments that break away from the unfinished cases. But a later observation showed that the mosses in the case actually sprouted there (Figure 72)! This case was apparently occupied by a pupa, ceasing the activity that could break off these sprouts before they attained sufficient size to exist on their own.



Figure 71. *Micrasema wataga* eating moss (*Hygrohypnum montanum*?). Photo by D. N. Bennett, with permission.



Figure 72. *Micrasema wataga* case with moss sprouts. A pupa is hiding inside. Photo by D. N. Bennett, with permission.

### ***Adicrophleps hitchcockii***

This interesting larva makes its case from bryophytes. It was relatively common among *Hygroamblystegium fluviatile* (Figure 4-Figure 5) in Appalachian Mountain streams (Glime 1968). It appeared to have used costae from this moss in the construction of its cases.

D. N. Bennett likewise collected larvae of the somewhat rare *Adicrophleps hitchcockii* (Figure 1, Figure 73) in several cold, rapid streams (1-10 m wide) from the aquatic leafy liverwort *Scapania* (Figure 74) growing in riffle areas (Henricks 2013; D. N. Bennett, pers. comm. September 2014). But the case is not made of liverworts, but rather it displays mosses. Wiggins (1977) described these as "4-sided, tapered, and constructed of pieces of moss arranged transversely; trailing ends frequently left attached to the moss pieces give the case a furry appearance."



Figure 73. *Adicrophleps hitchcockii*, a species that lives among bryophytes and makes its case from mosses. Photo by D. N. Bennett, with permission.





Figure 74. *Scapania undulata*, home for *Adicropheps hitchcocki* but not used for case building. Photo by Hermann Schachner, through Creative Commons.

### Phryganeidae – Giant Casemakers

This family with relatively large larvae lives mostly in lakes and rivers (Neuswanger 2015a). The pupae crawl from their watery location to shore to emerge. Females run across the water surface to lay their eggs. The larvae are most common among aquatic plants in ponds and marshes, but some occur in streams and others in temporary pools and deep in lakes (Holzenthal *et al.* 2007). Larvae are typically either predators or herbivores.

This family is not common among the bryophytes. But, *Yphria californica* (Figure 75), a species restricted to the west coast states of USA, lays its eggs (Figure 76) underwater among mosses that dangle over the stream in the Sierra Nevada, North America (Erman 1984). To do that, the adult must swim underwater.



Figure 75. *Yphria californica* adult, a USA west coast species that lays its eggs among mosses. Biodiversity Institute of Ontario, through Creative Commons.



Figure 76. *Trichoptera* eggs, often laid on bryophytes. Photo by Bob Armstrong, with permission.

The larvae of *Eubasilissa regina* (Figure 77) in Japan begin their construction days by making cases of liverworts, but as they develop they change to terrestrial leaf litter and move their abode from the liverworts to pools (Ito 1988).



Figure 77. *Eubasilissa regina* adult, a large Japanese caddisfly for which the larvae begin their case construction using liverworts. Photo through Creative Commons.

*Oligostomis ocelligera* (Figure 78) lives in moist places such as under mosses where it is protected (Redell *et al.* 2009). It usually occupies positions with a mean distance of 6.1 cm below the surface.



Figure 78. *Oligostomis ocelligera* larva, a species that lives under mosses. Photo by Tom Murray, through Creative Commons.

*Hagenella clathrata* is a rare caddisfly in Europe, inhabiting the disappearing bog habitat (Buczyńska *et al.* 2012). In particular, the species often occurs in bog pools that occur only in rapidly disappearing floating bogs, hence being dependent on the particular habitat created by *Sphagnum* (Figure 10) (Kleef *et al.* 2012).

## Sericostomatoidea

### Beraeidae

This family is scattered about the globe, being concentrated in the western **Palearctic Region** (Eurasia from western Europe to the Bering Sea), but also occurs in Tanzania, Japan, and eastern North America (Hamilton 1985; Holzenthal *et al.* 2007). Adults have forewings that are only 4-6 mm long (Watson & Dallwitz 2003). Larvae live in springs, seeps, and small streams where they utilize a variety of substrates, including bryophytes (Hamilton 1985; Holzenthal *et al.* 2007). They eat plant and fungal material, but there seem to be no records of eating bryophytes.

*Beraea maura* (Figure 79) represents this family in the River Rajcianka, Slovakia, where it inhabits the submerged bryophytes (Krno 1990). Unlike several members of the **Limnephilidae** and **Rhyacophilidae**, this species is not found above the water level in the wet mosses there. In the Pyrénées, Décamps (1968) found larvae of this family among mosses, but this family had a wide range of habitats in addition to the mosses.



Figure 79. *Beraea maura* adult, a species that lives among submerged bryophytes as larvae. Photo from Biodiversity Institute of Ontario, through Creative Commons.

### Conoesucidae

Among the unfamiliar **Trichoptera** names (to those of us in the northern hemisphere), the **Conoesucidae** (Figure 80) is another of bryophyte-dwelling families from down under (Winterbourn & Gregson 1981). The family is endemic to Australia, New Zealand, and Tasmania (Johanson *et al.* 2009). Among the bryophyte dwellers is *Confluens hamiltoni*, an endemic on the North Island, New Zealand, where it is associated with mosses, liverworts, and algae in rapid-flow streams (Winterbourn & Gregson 1981). On the South Island, this species is replaced by *C. olingoides*, occupying conditions like those of *C. hamiltoni*.



Figure 80. *Pycnocentroides aureolus* adult, member of a family (**Conoesucidae**) with bryophyte dwellers in the Australian region. Photo by Maurice, through Creative Commons.

### Helicophidae

This family of 6-14 mm length (Helicophidae 2015b) is mostly known from Australia, New Zealand, and New Caledonia, but also from southern South America and scattered locations in North America (Helicophidae 2015a). The larvae live in slow streams and are mostly detritivores (Helicophidae 2015b).

**Trichoptera** are not as common in New Zealand as in other parts of the planet, but the **Helicophidae** are represented there, sometimes associated with mosses (Winterbourn & Gregson 1981). *Zelolessica cheira* (Figure 81) occurs among *Fissidens rigidulus* (Figure 82) in the torrential waters near the middle of stream channels in the Southern Alps (Cowie & Winterbourn 1979). *Zelolessica cheira* is usually associated with mosses and liverworts in rapid streams with a stable, rocky substrate (Winterbourn & Gregson 1981; Eward *et al.* 1994). The cases are curved, comprised variously of sand grains, liverworts, and mosses.



Figure 81. *Zelolessica* larvae. Some members make their cases from bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.





Figure 82. *Fissidens rigidulus*, home for *Zelolessica cheira* in torrential New Zealand waters. Photo by Bill & Nancy Malcolm, with permission.

*Alloecentrella* (Figure 83) is known from China, Australia, New Zealand, and the Antarctic. In New Zealand, *Alloecentrella magnicornis* and an unnamed species occur among mosses and liverworts in rocky streams where they build their cases using bryophytes (Eward *et al.* 1994).



Figure 83. *Alloecentrella* sp. larva, a species that covers its case with mosses and liverworts. Photo by Stephen Moore, Landcare Research, NZ, with permission.

### Sericostomatidae – Bushtailed Caddisflies

These caddisflies are of moderate size, with wings 8–15 mm long (Watson & Dallwitz 2011). This family is cosmopolitan except for the Australian region (Sericostomatidae 2015). Nevertheless, many of the genera are endemic to small areas of their continents. At least some larval members of the family move little. For example, more than 120,000 larvae of *Gumaga nigricula* (Figure 84–Figure 85) were released in pools of a California mountain stream and 87–93% of them remained within 4 m of the pools (Jackson *et al.* 1999). In this clever experiment, the larvae were provided with bright gold or magenta sand grains to complete their cases so that they could easily be tracked.



Figure 84. *Gumaga* sp. larva, a relatively immobile caddisfly. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Figure 85. *Gumaga nigricula* adult, a relatively immobile caddisfly in the larval stage. Photo from Biodiversity Institute of Ontario, through Creative Commons.

The **Sericostomatidae** live in both streams and lakes and mostly feed on leaf litter (Family Sericostomatidae 2015). They build slightly to strongly curved tubular cases from sand grains or just silk. Because of their interesting designs and strength, the Tupi-Guarani Indians in Brazil used the cases of *Grumicha* as adornment.

Some of the moss dwellers are quite rare. Stern and Stern (1969) found the larvae of *Sericostoma* sp. (Figure 86) only among algae and mosses in a Tennessee, USA, springbrook.

*Sericostoma pedemontanum* (Figure 86), a caddisfly of fast-running streams, refused *Fontinalis antipyretica* (Figure 11) when provided a diet of birch, beech, and oak leaves with it (Higler 1975). Birch was the preferred food.



Figure 86. *Sericostoma pedemontanum* larva, a species that refused *Fontinalis* and chose various species of leaf litter in a feeding experiment. Photo by Massimo Del Guasta, with permission.



## SUBORDER SPICIPALPIA

### Glossosomatoidea

#### Glossosomatidae – Tortoise or Saddle-case Makers

This worldwide family makes its larval cases from pebbles in the shape of a turtle shell (Glossosomatidae 2014). It is probably this structure that forces them to build a new case in each new instar, rather than adding to the old one as most caddisfly families do. These small to medium-sized larvae usually occur in cool mountain streams where they scrape algae from the rocks as their food. The female adults lay their eggs in gelatinous masses under rocks at the water surface or on floating objects, probably including mosses. The gelatinous material protects the eggs from desiccation.

From Ceylon, Schmid (1958) reported *Agapetus rawana* (see Figure 87-Figure 90) from large, mossy rocks in the torrent. In the Appalachian Mountains, *Glossosoma* (Figure 91) larvae and pupae were often present among the bryophytes (Glime 1968).



Figure 87. *Agapetus fuscipes* larva and case, a genus known from large, mossy rocks of torrents in Ceylon. Photo by J. C. Schou, with permission.



Figure 88. *Agapetus fuscipes* larvae showing the unusual shape of the case. Photo by Dragiša Savić, with permission.



Figure 89. *Agapetus* prepupa in larval case. Photo by Mark Melton, with permission.



Figure 90. *Agapetus* pupa removed from case. Photo by Mark Melton, with permission.



Figure 91. *Glossosoma* sp. larvae, showing its "turtle shell" case. Photo by Jason Neuswanger, with permission.

### Hydroptiloidea

#### Hydroptilidae – Microcaddisflies, Purse-case Caddisflies

This is a worldwide family, less than 5 mm long, that builds flattened cases often resembling an eyeglass case (Hydroptilidae 2015). The members of the family solve the problem of locating food by depositing their eggs near a suitable food source (Leader 1970). They typically feed on algae by sucking out the cell contents or by feeding on diatoms.



In the Appalachian Mountain streams where I worked, this tiny caddisfly is usually not very common, but Percival and Whitehead (1929) found them more commonly among mosses on stones than on other substrates in the UK. Hughes (1966) found them to be more abundant in open areas than in shaded ones, a factor that usually contrasts with bryophyte preferences. Percival and Whitehead (1929) found that the hydroptilids from mosses feed on algae and diatoms. The larvae of this family have mouthparts that are able to pierce and suck, enabling them to suck the contents from filamentous algae or to scoop up diatoms (Nielsen 1948).

It is perhaps telling that at least in Denmark, the genera *Agraylea* (Figure 92), *Hydroptila* (Figure 93), *Oxyethira* (Figure 94-Figure 95), and *Orthotrichia* (Figure 96) are very common in eutrophic lakes (Nielsen 1948). This suggests that in streams we should look for the bryophyte dwellers deep within the mat where there is reduced flow. But even in the lakes these genera occupy vegetation near the surface. *Agraylea* and *Orthotrichia* occur in slowly flowing water, and this is where mosses can add possible niches. *Orthotrichia* often becomes coated in detritus and will pass one of its hind legs down the dorsal side of its abdomen to clean the tracheal gills there.



Figure 92. *Agraylea sexmaculata* larva, a genus that lives among bryophytes in slowly flowing water. Photo by Massimo Del Guasta, with permission.



Figure 93. *Hydroptila sparsa* larvae, member of a genus that occurs among bryophytes in lakes and streams. Photo by Massimo Del Guasta, with permission.



Figure 94. *Oxyethira* larva, a moss dweller in Danish lakes. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 95. *Oxyethira* pupa. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 96. *Orthotrichia* sp larva and case, a species that lives among mosses in lakes. Photo by Urmas Kruus, with permission.

*Hydroptila* (Figure 93) can build a case of detrital matter and sand grains in about four hours (Nielsen 1948). To increase the size of the case, the larva splits it open along the ventral edge, adding sand grains to the edge. The completed case, as in most members of the family, looks like a case for eye glasses (Figure 93) – the one with an

open end – which is where the head protrudes in the caddisfly version. Some cases are built with algal filaments, especially in *Agraylea* (Figure 92), and I have observed cases made almost entirely of diatoms. In both *Hydroptila* and *Agraylea* the outer coating of sand or algae will wear off as the larva nears maturity, leaving only the smooth inner wall made of silk spun by the larva as it cements the case together. *Orthotrichia* (Figure 96) and *Ithytrichia* (Figure 97) species use only silk in the construction of their cases. These genera feed by sucking the contents out of algal cells.



Figure 97. *Ithytrichia lamellaris* larva & case, a genus that uses only silk in its case. Photo by Urmas Kruus, with permission.

When these four genera (*Agraylea*, *Hydroptila*, *Orthotrichia*, *Ithytrichia*) emerge, they split the pupal case, then move about until they find a protruding object to climb up and out of the water (Nielsen 1948). Once out they can flit about on the water surface and in the air.

The moss-dwelling genus *Oxyethira* (Figure 94-Figure 95), including more than one species, comprised 44.5% of the Trichoptera fauna at the acid site in Frost's (1942) moss fauna study of the River Liffey, Ireland. It was absent at the alkaline site. *Oxyethira frici* lives in the angle between the leaf and the stem of the moss and pupates among the mosses, a behavior that is uncommon among caddisflies. By contrast, *Ithytrichia lamellaris* (Figure 97), a species almost restricted to mosses, was common at the alkaline site and absent from the acid site. It likewise lives in the angle between the leaf and the stem of the moss and pupates among the mosses. Both of these genera were present, but rarely, among the bryophytes of Appalachian Mountain mostly acid streams, USA (Glime 1968). They were more common on *Fontinalis*, where larvae of *Oxyethira* and *Hydroptila* sometimes decorated the branches of *Fontinalis dalecarlica* (Figure 98).

From Ceylon, Schmid (1958) reported *Chrysotrichia hapitigola*, and *Hydroptila kirilawela* from large, mossy rocks in the torrent.

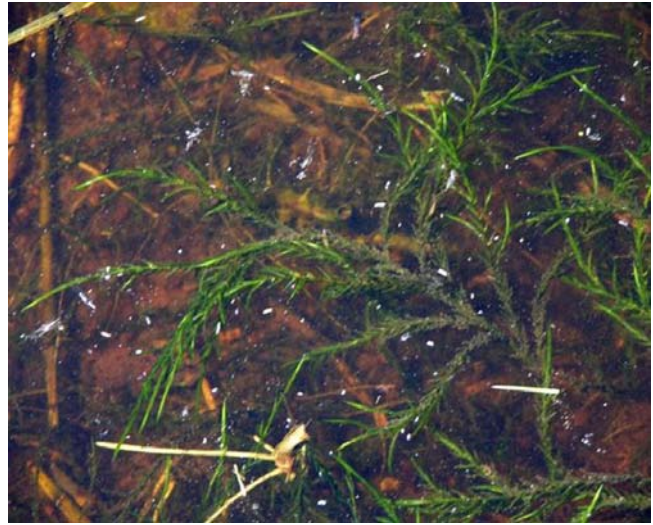


Figure 98. *Fontinalis dalecarlica*, home to many insects. Photo by J. C. Schou, with permission.

Woodall and Wallace (1972) found *Ochrotrichia* sp (Figure 99) on moss-covered granite outcrops in the Appalachian, USA, streams that they studied. They considered the moss-covered rock outcrops to be the central factor influencing the distribution of this species in the area. In my own studies of the mid-Appalachian Mountain streams, this genus was not present, but I did occasionally find *Mayatrichia*, *Neotrichia*, and *Stactobiella* in addition to the more common ones discussed above under this family (Glime 1968).



Figure 99. *Ochrotrichia eliaga* larva and case, a genus found on moss-covered granite outcrops in Appalachian streams. Photo by Trevor Bringloe, Biodiversity Institute of Ontario, through Creative Commons.

In a Tennessee, USA, springbrook, *Ochrotrichia unio* (see Figure 100) live among algae and mosses as larvae, then move to bare rocks to pupate (Stern & Stern 1969). In Great Britain, the larvae of this species feed on diatoms and other algae (Percival & Whitehead 1929).





Figure 100. *Ochrotrichia* larva, a genus in which some larvae live among mosses, then migrate to bare rocks to pupate. Photo from California Department of Wildlife, through public domain.

### *Ptilocolepus*

*Ptilocolepus granulatus* is **crenophilic** (describing organism preferring spring environments but may also occupy similar habitats), living in montane to subalpine regions of central Europe (Waringer & Graf 2002). Wesenberg-Lund (1943) reported that *Ptilocolepus granulatus* lives in moss cushions and makes its case from moss fragments. Similarly, González *et al.* (2000) reported that *P. extensus*, an endemic on the Iberian Peninsula and a close relative, uses leaf pieces of several moss and liverwort species to make its final instar case. Unlike most of the **Hydroptilidae**, this case is flattened dorsiventrally, but still has the typical elongate-oval shape.

In the Pyrénées, Thienemann (1950) and Décamps (1968) found *Ptilocolepus granulatus* among mosses and liverworts. These bryophytes also formed a significant portion of their food as well as construction material for their cases. Ito (1998) reported that this genus lives among, eats, and builds its cases from the leafy liverworts *Chiloscyphus polyanthos* (Figure 67) and *Scapania undulata* (Figure 74). Depisch (1999) and Ito and Higler (1993) all found that the species commonly lives among and feeds on the liverwort *Scapania undulata*. In Belgium *Ptilocolepus granulatus* uses *Jungermannia riparia* for food, but surprisingly, it also sometimes builds its case from the moss *Fontinalis* (Figure 11) (Ito & Higler 1993). Thus it is not surprising that Dittmar (1955) found it associated with *Fontinalis*. Ito and Higler found that it does not seem to feed on the moss, but later Ito (1998) states that it is the only species in the subfamily **Ptilocolepinae** that is able to feed on *Fontinalis* (and other mosses), attributing this ability to its large mandibles.

### *Palaeagapetus*

Microcaddisflies such as *Hydroptila* (Figure 93) often attach their tiny homes to the moss leaves and stems, but *Palaeagapetus* in the same family constructs its home strictly out of leafy liverworts (Flint 1962; Glime 1978; Ito & Hattori 1986; Ito 1991), even when these are growing

side by side with mosses such as *Fontinalis* (Figure 11). The species of liverwort depends on availability, with cases of *Palaeagapetus celsus* from the eastern USA known from *Scapania nemorea* (Flint 1962; Glime 1978) (Figure 101), *S. undulata* (Glime 1978) (Figure 74), *Plagiochila porelloides* (Glime 1978) (Figure 102), *Frullania* sp. (Glime 1978) (Figure 103). In those I observed, the pieces of liverwort were cut into nearly circular pieces and cemented together along their margins, forming a case typical of many hydroptilids – the shape of an eyeglass case. Ito and Vshivkova (1999) described the pieces of liverworts comprising the cases of *Palaeagapetus finisorientis* from the Russian Far East similarly as being roughly rounded fragments.



Figure 101. *Scapania nemorea*, one of the species used for making cases of *Palaeagapetus celsus*. Photo by Bernd Haynold, through Creative Commons.



Figure 102. *Plagiochila porelloides*, a species used by *Palaeagapetus celsus* for making its case. Photo by Hermann Schachner, through Creative Commons.

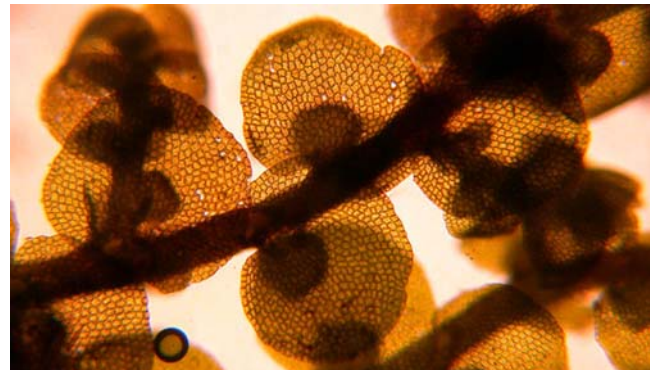


Figure 103. *Frullania eboraensis*, a terrestrial epiphytic species that may fall into the water and be used in the case of *Palaeagapetus celsus*. Photo by Bob Klips, with permission.



Not only do members of this genus use liverworts in the construction of their cases, but the liverworts are also a primary food source (Botosaneanu & Levanidova 1987). In his review of four species of *Palaeagapetus*, Ito (1998) found that all of them used the liverworts *Chiloscyphus polyanthos* (Figure 67) and *Scapania undulata* (Figure 74) for food, housing, and case construction. It appears that all known members of the genus have this same strong dependence on leafy liverworts, including those in the eastern part of the former Soviet Union (Botosaneanu & Levanidova 1987), Japan (Ito & Hattori 1986; Ito 1988, 1991), and North America (Flint 1962; Glime 1978). In the western USA, *Palaeagapetus nearcticus* uses *Scapania uliginosa* for its case and food (Ito *et al.* 2014). The larvae pierce the cells and consume the liverwort one cell at a time. Ito and Vshivkova (1999) found that in the *Palaeagapetus* species they observed, the early instars fed on the contents of the liverwort cells, whereas the final instar cut off the leaves and apparently ingested them, reminiscent of human babies who also shift from sucking to chewing. Ito (1991) found that *Palaeagapetus rotundatus* feeds on the leaves of leafy liverworts *Chiloscyphus polyanthos* and *Scapania undulata* (Figure 74), but will not feed on the moss *Platyhypnidium riparioides* (Figure 13).

Ito (1988) followed the life history of *Palaeagapetus ovatus* in a spring stream in Japan. He found that the density changed with season, reaching the highest in winter and being low in summer. Living with it was a predatory Trichoptera, *Eubasilissa regina* (Phryganeidae; Figure 77), that preyed upon it among the liverworts.

We know more about this genus and its liverwort relationship through the description of a new species, *Palaeagapetus ovatus*, in Japan (Ito & Hattori 1986). This liverwort dweller fed exclusively on the leaves of the leafy liverwort *Chiloscyphus polyanthos* (Figure 67). Its fifth and final instar made the typical oval case from the leaves of this liverwort. And the females, within two days of emergence, laid 50-85 eggs on the leaves of this liverwort. The eggs do not form a mass and at 10.5-12°C they hatch in 21-23 days. *Palaeagapetus nearcticus* also deposits its orange eggs on liverwort leaves (Ito *et al.* 2014).

More recently, Woods (2002) was surprised to find the thallose liverwort *Riccardia chamedryfolia* (Figure 104) moving in a slow, jerky motion on the sandy bottom of a pool in Wales. Investigation revealed that two matching pieces of the thallus had been cemented together by a caddisfly larva that was using it for a home (case). The larva was not identified but could have been a member of Hydroptilidae.

### *Scelotrichia*

My email makes Christmas come all year-round. One of these nice surprises came when Andi Cairns sent me pictures of a caddisfly that was a bryological surprise. This new species, actually in a genus new to Australia, was *Scelotrichia willcairnsi* (Figure 105) living among the mosses in a waterfall (Figure 106). It was feeding on *Rhynchostegium brevnerve* (Figure 107), a new species previously thought to be *Platyhypnidium muelleri* and renamed by Huttunen and Ignatov (2010), in north-eastern Queensland, Australia. This microcosm was full of surprises!

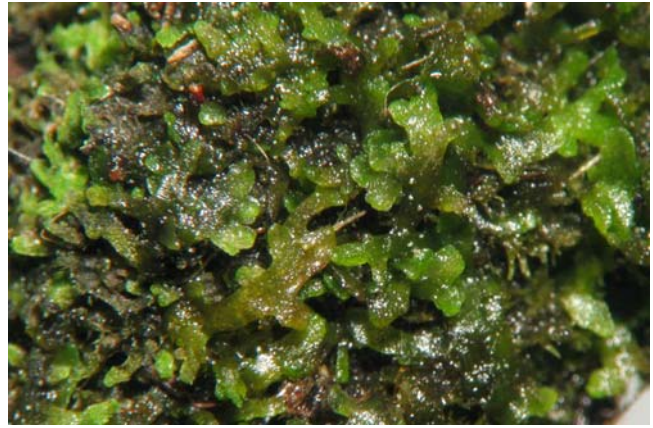


Figure 104. *Riccardia chamedryfolia*, a liverwort that some caddisflies use to make a case. Photo by Kristian Peters, with permission.



Figure 105. The caddisfly *Scelotrichia willcairnsi* (Hydroptilidae) with a case made of pieces of the moss *Rhynchostegium brevnerve*. Note the way pieces fit together as parallel rings. Photo courtesy of Andi Cairns.



Figure 106. *Rhynchostegium brevnerve* in Fishery Falls, Australia, home to *Scelotrichia willcairnsi*. Photo courtesy of Andi Cairns.





Figure 107. *Rhynchosetegium brevinerve*, home to the caddisfly *Scelotrichia willcairnsi*. Photo courtesy of Andi Cairns.

The *Scelotrichia willcairnsi* larva had a case (Figure 105) it had built by cementing moss leaf fragments together (Figure 108) – the same species of moss it was eating (Cairns & Wells 2008). It remained in this case to pupate, cementing it to the moss stems (Figure 109). When making a case, the larvae cut the leaves longitudinally, in parallel with the long axis of the leaf and its cells, giving them long pieces (Figure 108). Cairns and Wells described these: "neatly, the fragments fitted together, almost in rings." Ohkawa and Ito (2002) had already distinguished the types of cuts for leaves and for food in *Scelotrichia ishiharai*. This microcaddis uses the moss *Rhynchosetegium* sp. (Figure 107-Figure 109) for food (Figure 110-Figure 111) and case building (Figure 105-Figure 109), likewise using different orientations for the two kinds of cuts.

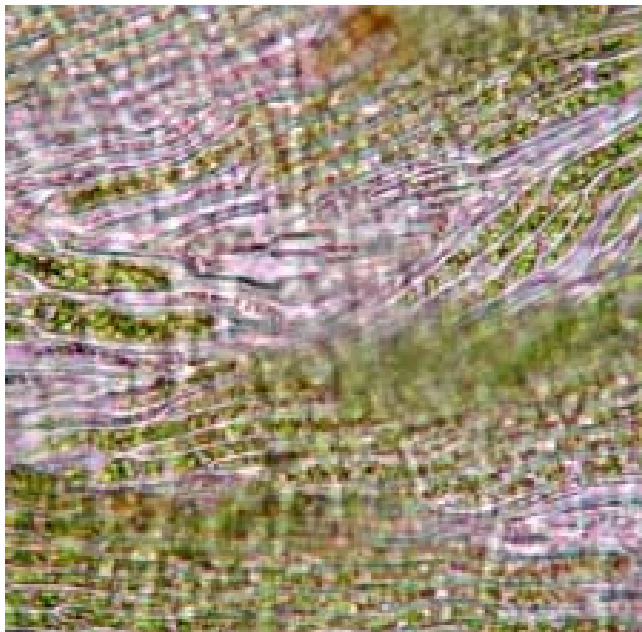


Figure 108. Pieces of the moss *Rhynchosetegium brevinerve* from the case of the caddisfly *Scelotrichia willcairnsi* (Hydroptilidae). Photo courtesy of Andi Cairns.



Figure 109. Pieces of the moss *Rhynchosetegium brevinerve* with numerous cases of the caddisfly *Scelotrichia willcairnsi* (Trichoptera: Hydroptilidae). Photo courtesy of Andi Cairns.

When Cairns and Wells (2008) examined the gut contents, they discovered that these tiny caddisfly engineers cut the pieces of moss very differently for food than they did for cases. For food, they cut the leaves perpendicular to the long axis and across the cells (Figure 110-Figure 111). Such a cut would give the gut enzymes more access to the contents of the cells.

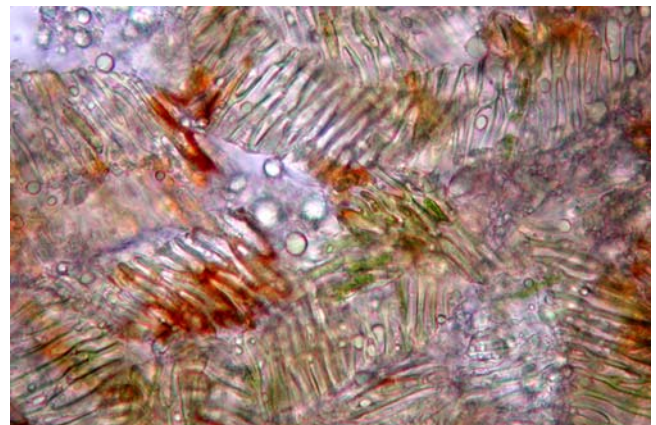


Figure 110. Pieces of the moss *Rhynchosetegium brevinerve* from the gut of the caddisfly *Scelotrichia willcairnsi* (Hydroptilidae). Photo courtesy of Andi Cairns.

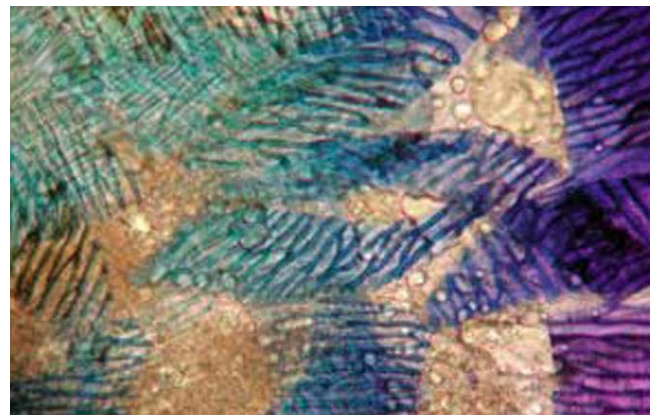


Figure 111. Pieces of the moss *Rhynchosetegium brevinerve* from the gut of *Scelotrichia willcairnsi*. The moss fragments are stained with Toluidine blue to make cell walls more evident. Note that cell contents appear to be gone in nearly all fragments, suggesting digestion. Photo courtesy of Andi Cairns.

Elsewhere, in Papua New Guinea, *Scelotrichia* was similarly collected from mosses in the strong currents at the crest of a short waterfall (Wells 1990). They likewise made their cases of the moss leaves and later attached their pupal cases to the stems of the same species of moss. Wells found adults of two other species of *Scelotrichia* near waterfalls or soaked mosses. As in *S. willcairnsi* (Figure 105), the caddisfly larvae from Papua New Guinea had cut slivers of the moss down the long axis of the leaf, making the cells parallel to the length of the fragment. These differed from the pieces cut by *Paleagapetus* and *Ptilocolepus*, which were cut from leafy liverworts and glued together to resemble a patchwork quilt (Ito 1998; Ito & Higler 1993). It appears that cutting behavior can determine the type of bryophyte that is suitable for making the case.

## Rhyacophiloidea

### Rhyacophilidae – Free-living Caddisflies

This is a Northern Hemisphere family from the temperate parts of North America, Europe, and Asia, extending into India and the tropical areas of southeastern Asia (Kjer 2010). The larvae are 9-16 mm long and are green or brown, blending easily with the bryophytes (Bumble.org 2013). Don't be misled by the pink color they assume in preservative.

Larvae of this family do not build cases (Figure 112), so they do not attach themselves to the substrate by gluing their cases like some caddisflies do. Their life cycle is one year, with two generations overlapping. The larvae prefer rapid, cold streams where they are able to stay themselves in the current by clinging to mosses or debris (Hilsenhoff 1975). Most are carnivorous, but a few are herbivorous. And some can live above the water level among wet emergent mosses: *Rhyacophila nubila* (Figure 113), *R. polonica*, and *R. tristis*, whereas in the same River Rajcianka, Slavakia, these three species plus *R. obliterate* (Figure 117), *R. philopotamoides*, and *R. vulgaris* occur among the mosses under water (Krnó 1990).

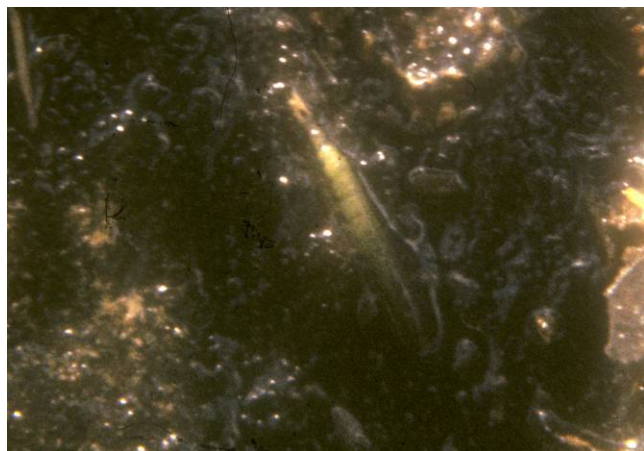


Figure 112. The free-living caddisfly, *Rhyacophila*, is a common member of the stream moss community. Its color is typically green, and it has large hooks that permit it to cling to mosses and other substrata to avoid being washed away by the fast-flowing water it inhabits. Its lack of a case permits it to traverse the internal chambers of the moss without getting caught by the branches. Photo by Janice Glime.



Figure 113. *Rhyacophila nubila* larva, a species that can live among mosses above or below the water surface. Photo by Niels Sloth, with permission.

In my studies of Appalachian Mountain stream mosses in Maryland and Pennsylvania, USA, the genus *Rhyacophila* was among the most common and constant of the caddisfly larvae among the bryophytes. Décamps (1967, 1968) found *Rhyacophila laevis* to be abundant among mosses in the Pyrénées. In a cool mountain stream of central Japan, Tada and Satake (1994) found that *R. towadensis* was significantly more abundant among the moss *Platyhypnidium riparioides* (Figure 13) than in bare rock areas.

Many members of *Rhyacophilidae* most likely benefit both from the protection afforded by the bryophytes, but also from the resident fauna that serves as food, especially the numerous *Chironomidae*. In their study of four small Appalachian, USA, streams, Woodall and Wallace (1972) found larvae of *Rhyacophila torva* (Figure 124) (see also Roback 1975), *R. nigrita* (Figure 114), *R. carolina* (Figure 121), *R. minora* (Figure 115) (see also Glime 1968), *R. glaberrima* (Figure 116), and *R. fuscula* (Figure 122-Figure 123) among mats of mosses on rock outcrops. They fed on the *Chironomidae* larvae (Ross 1944) that shared the bryophyte habitat. In one of my collections from the mid-Appalachian Mountains I caught *R. carolina* in the act – it was preserved with a chironomid larva in its mouth. Although *R. minora* in a wooded Ontario, Canada, stream is typically carnivorous, early instars feed on plant material (Singh *et al.* 1984). This strategy works well until they gain the size and skill to be predators.



Figure 114. *Rhyacophila nigrita* larva, a moss dweller in Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.





Figure 115. *Rhyacophila minora* larva, an Appalachian Mountain stream bryophyte dweller. Photo from Biodiversity Institute of Ontario, through Creative Commons.



Figure 116. *Rhyacophila glaberrima* larva, a common species among mosses in the Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.



Figure 117. *Rhyacophila obliterata* adult, a species whose larvae are common among bryophytes. Photo by James K Lindsey, with permission.

## Food

Most *Rhyacophila* species are carnivores that do not make cases, but the *Verrula* group eat photosynthetic organisms with their **hypognathous** heads (oriented downwards), feeding on algae, diatoms, and particularly bryophytes (Smith 1968; Thut 1969). Cummins (1973) likewise reported that *R. verrula* in western North America is a herbivore and especially eats aquatic mosses (Slack 1936; Gerson 1982; Smith 1968). In his study of diets of the *Rhyacophila* species in constructed streams in western USA, Thut (1969) found that *R. verrula* feeds predominantly on aquatic mosses. This effect is intensified in winter when several mosses are dominant and diatoms are abundant. Interestingly, diatoms become more important in the fourth and fifth instars than they are in earlier instars.

In a Tennessee cold springbrook, *Rhyacophila lobifera* larvae fed among the moss and algae, eating smaller caddisfly larvae, midge larvae, naiads of mayflies and stoneflies, detritus, and diatoms (Stern & Stern 1969). Slack (1936) also reported that one out of nine *Rhyacophila dorsalis* (Figure 118) had leaves of *Fontinalis antipyretica* (Figure 11) in the gut, but that it is primarily carnivorous. Nevertheless, one specimen contained only diatoms in the gut and the one with *Fontinalis* had only plant material. In a study in the English Lake District, Elliott (2005) found that early instars ate primarily diatoms (mostly *Achnanthes* spp., Figure 119), with bryophyte fragments also present in nearly all gut samples, but the bryophytes appeared to be undigested, displaying their chlorophyll. These bryophytes may have been eaten to obtain adhering diatoms. Both second and third instars would disappear into the bryophyte clumps to search for prey, but they returned to the surface of those clumps to consume their finds. Fourth and fifth instars fed only at night and used an ambush strategy to capture prey, which includes *Baetis* and *Gammarus*.



Figure 118. *Rhyacophila dorsalis* larva, a carnivorous species that sometimes has leaves of *Fontinalis antipyretica* in its gut. Photo by Walter Pfliegler, with permission.

Larvae of most of the predominantly carnivorous *Rhyacophila dorsalis* (Figure 118) occur among bryophytes [leafy liverwort *Scapania* sp. (Figure 74) and mosses *Platyhypnidium riparioides* (Figure 13) and *Fontinalis antipyretica* (Figure 11)] (Slack 1936). For less active prey they use a searching strategy (**Chironomidae**, **Simuliidae**). The percentage of larvae with bryophytes in the gut was much smaller than that of prey. It appears that this species changes its diet as it grows, but it may also be

an opportunist regarding its diet. But if one considers that both the diatoms and bryophytes still had chlorophyll in their cells, it appears that even the first and second instar larvae may have been carnivores, eating these photosynthetic organisms by chance while attempting to capture prey. Instead, the first and second instar larvae eat copepods, rotifers, and tardigrades, common bryophyte inhabitants, but these require special preservation techniques in order to recognize them in gut samples. Instead of a shift from apparent herbivore to carnivore, Elliott (2005) demonstrated a shift in size of prey.



Figure 119. *Achnanthes longipes*. Photo by Victor Chepurinov, through non-commercial license.

The caddis larvae of *Rhyacophila dorsalis* (Figure 118) begin their early instars by feeding equally day and night, but by the 4th to 5th instar they shift to feeding almost totally at night (Elliott 2005). They can feed on other insects inhabiting their moss habitat, such as **Ephemeroptera** (mayflies), **Simuliidae** (blackflies), and **Chironomidae** (midges). As they grow older, instars 4 and 5, they adopt an ambush strategy at dusk and dawn, catching such active prey as the mayfly *Baetis* and the scud *Gammarus*. During the night they used a searching strategy to capture the more sedentary prey, for example **Chironomidae** (midges) and **Simuliidae** (blackflies).

Thut (1969) suggested that the high proportion of moss fragments in the diets of the herbivorous *Rhyacophila* was at least in part the result of seasonal changes in the available primary producers in streams. Bryophytes are available in winter when most of the algae are dormant in a resting stage.

### Substrate Preference

*Rhyacophila* species typically make their larval homes under rocks or among mosses (Bouchard 2004). They are able to use their claws (Figure 120) to anchor themselves or cling to the mosses, but also use them as they creep along in the stony stream bed (Badcock 1949). Percival and Whitehead (1929) found that *Rhyacophila dorsalis* (Figure 118) preferred thick mosses and *Potamogeton* on stones. Elliott (2005) found some larvae found under large stones, but most were among bryophytes growing on the upper surfaces of large stones [*Scapania* (Figure 74), *Platyhypnidium riparioides* (Figure 13), *Fontinalis antipyretica* (Figure 11)].



Figure 120. *Rhyacophila fuscula* larva showing anal hooks that cling to its substrate. Photo by Jason Neuswanger, with permission.

In the Great Smoky Mountains National Park, *R. montana* lives in the films of water that flow over vertical rock faces, crevices, or among wet mosses (Parker *et al.* 2007). *Rhyacophila evoluta* and *R. intermedia* are characteristic of mosses in torrents in the Pyrénées (Décamps 1967). *Rhyacophila evoluta* has the ability to go into a cold-induced diapause at any stage in its development. This permits it to complete its development in one, two, or three years, depending on the temperatures.

Some species seem to prefer liverworts and some to prefer mosses for their homes (locations, not cases). In the mid-Appalachian Mountain streams I found *Rhyacophila* cf. *carolina* (Figure 121) primarily among liverworts (*Scapania undulata*; Figure 74), whereas *R. fuscula* (Figure 120, Figure 122-Figure 123) predominated in *Fontinalis dalecarlica* (Figure 98) and *R. torva* (Figure 124) in *Hygroamblystegium fluviatile* (Figure 4-Figure 5) and *Platyhypnidium riparioides* (Figure 13). *Rhyacophila invaria* (Figure 125) occurred frequently among clumps of the moss *Platyhypnidium riparioides* (36% frequency) but was absent among *Hygroamblystegium fluviatile* clumps despite the frequent intermingling of these two mosses. It reached its greatest numbers in *Scapania undulata*.



Figure 121. *Rhyacophila carolina* larva, species that is common among clumps of the leafy liverwort *Scapania undulata* in Appalachian Mountain, USA, streams. Photo by Bob Henricks, with permission.





Figure 122. *Rhyacophila fuscula* larva, a moss dweller on boulders in the Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.



Figure 123. *Rhyacophila fuscula* pupa. Photo by Bob Henricks, with permission.



Figure 124. *Rhyacophila torva* larva, a moss dweller in Appalachian Mountain streams. Photo by Trevor Bringloe, Biodiversity Institute of Ontario, through Creative Commons.



Figure 125. *Rhyacophila invaria* larva, a species that occupies both mosses and liverworts in Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

## Unknown Caddisfly Cases

One caddisfly larva included moss leaves, liverwort leaves, and even hornwort thallus, all in one case (Chris Cargill, pers. comm. 30 March 2016). And all these pieces were still alive! (Figure 126-Figure 129).



Figure 126. *Megaceros flagellaris* fragments used in caddisfly case. Photo courtesy of Andi Cairns.

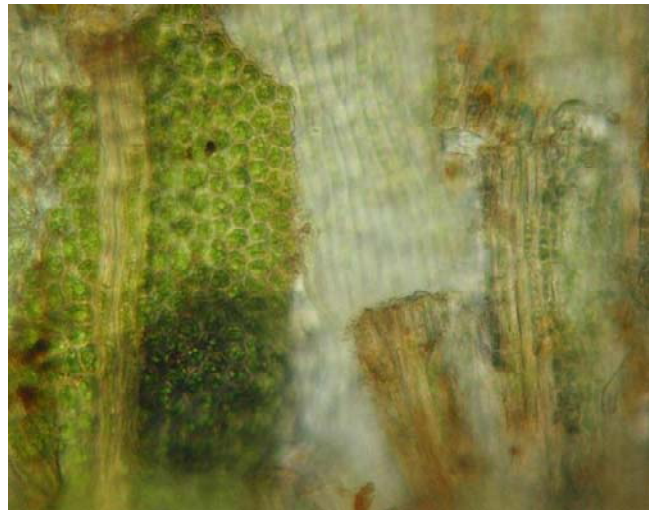


Figure 127. *Megaceros flagellaris* fragments used in caddisfly case. Photo courtesy of Andi Cairns.



Figure 128. *Megaceros flagellaris* fragments used in caddisfly case. Photo courtesy of Andi Cairns.

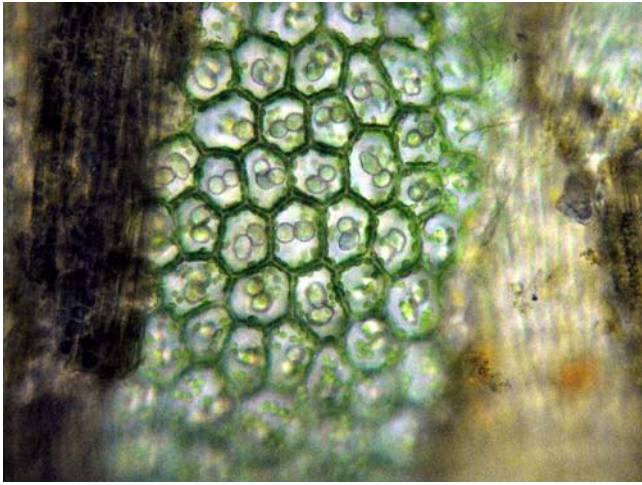


Figure 129. *Megaceros flagellaris* fragment used in caddisfly case. Photo courtesy of Andi Cairns.

Chris Cargill told me she later found discarded cases made of thalli from liverworts or hornworts and new thalli had started to grow from the case (Figure 130). I think we have just added a new means of bryophyte dispersal!



Figure 130. Caddisfly case with old thalli and new growth of living liverworts. Photo courtesy of Chris Cargill.

### Helicophidae

Andi Cairns brings me many interesting interactions of animals with bryophytes. This one is a member of the **Helicophidae** (Figure 131Figure 132) that has made a case from *Solenostoma* sp. (Figure 133) leaves where it lives in a stream in Australia.



Figure 131. **Helicophidae** sp with *Solenostoma* sp case, Cloudy Ck, Australia. Photo courtesy of Andi Cairns.



Figure 132. **Helicophidae** larva. Photo courtesy of Andi Cairns.



Figure 133. *Hypnodendron vitiense* ssp *australe* (dark green) and *Solenostoma* sp (medium green) underwater at Cloudy Creek Paluma, Australia, home of **Helicophidae** larva that uses the liverwort leaves to make its case. Photo courtesy of Andi Cairns.



## Summary

The **Limnephilidae** are mostly large and therefore are usually absent from the smaller mosses. However, sometimes several may occur within a clump of *Fontinalis*.

The **Brachycentridae** are common among bryophytes. Some (*Micrasema*, *Adicrophleps hitchcockii*) use mosses in their cases and some also eat them.

The genera *Palaeagapetus* and *Scelotrichia*, both in the **Hydroptilidae**, use bryophytes (exclusively?) for food and case construction, the former using leafy liverworts and the latter using mosses. In the same family, *Ptilocolepus* uses both mosses and liverworts for food and in case construction.

The family **Rhyacophilidae** is a free-living caddisfly and is mostly carnivorous. However, some of the bryophyte dwellers eat bryophytes, whereas others use them as a place to capture prey.

Other families that can be found among bryophytes less commonly include **Odontoceridae**, **Goeridae**, **Limnephilidae**, **Lepidostomatidae**, **Oeconesidae** (especially in New Zealand), **Uenoidae**, **Phryganeidae**, **Beraeidae**, **Conoesucidae**, **Helicophidae**, **Sericostomatidae**, and **Glossosomatidae**. Among these, the **Limnephilidae** and **Phryganeidae** have mostly large larvae that are unable to move about in most of the bryophytes but that can live among the large branches of *Fontinalis* species. Unlike the **Coleoptera**, this order is poorly represented in bogs and fens, but they are common in streams and less so in lakes.

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# CHAPTER 11-13a

## AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER NEMATOCERA

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# CHAPTER 11-13a

## AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER NEMATOCERA



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).

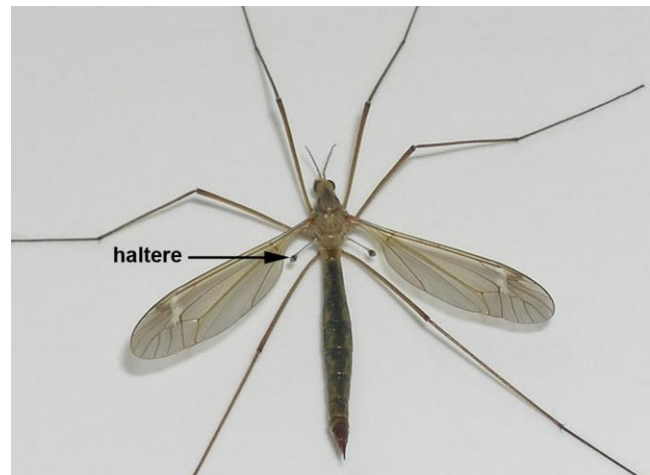


Figure 2. **Tipulidae** showing two wings and halteres. Photo by Pinza, through Creative Commons.



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.

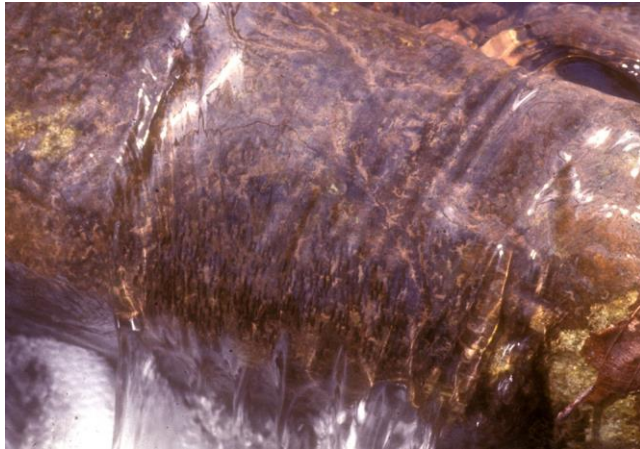


Figure 3. **Simuliidae** larvae in the rapid flow of a stream. Photo by Janice Glime.



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.

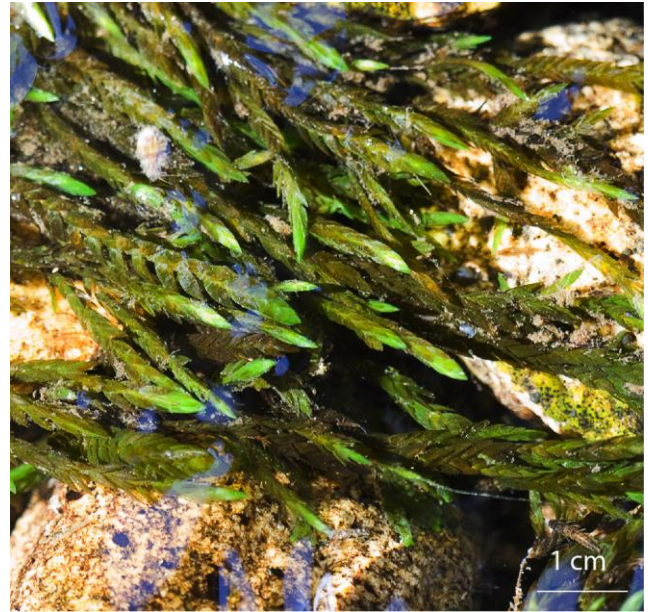


Figure 5. *Fontinalis antipyretica*, home for numerous aquatic insects and suitable for larger ones. Photo from Projecto Musgo, through Creative Commons.

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.].

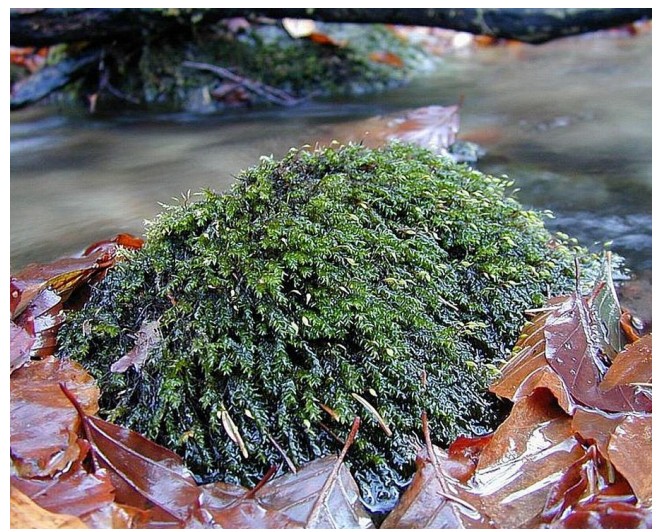


Figure 6. Emergent but wet *Platyhypnidium riparioides* in Europe, a common home for **Diptera**. Photo by Michael Lüth, with permission.





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 *Ricciocarpus natans* (Figure 10) and *Riccia fluitans* (Figure 11). In some cases, the **Diptera** associated with the thallose floating liverwort *Ricciocarpus 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](http://www.dfg.ca.gov)>, with permission.



Figure 10. *Ricciocarpus 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 Rajcianska 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 crane fly known to disperse bryophyte spores or protonemata. Photo by Paul Rhine <[www.discoverlife.org](http://www.discoverlife.org)>, through Creative Commons.

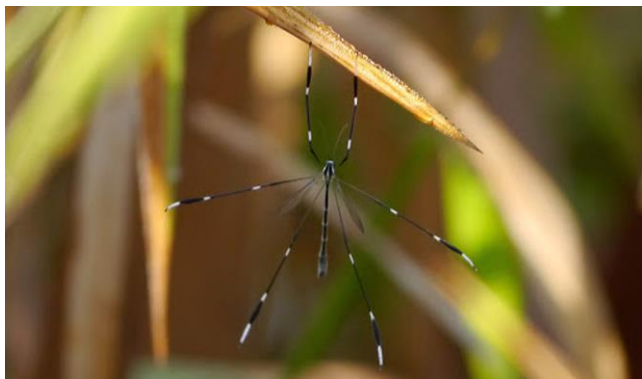


Figure 13. *Bittacomorpha clavipes* adult, a phantom crane fly that carries bryophyte spores or protonemata. Photo by Matt Muir, through Creative Commons.



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 crane flies, 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) (Gelhaus *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 *Phalacrocer 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. *Phalacrocer replicata* larva, an effective moss mimic that develops among mosses. Photo through Wikimedia Commons.

*Phalacrocer 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 *Phalacrocer replicata*. Photo by Michael Lüth, with permission.

Clymo and Hayward (1982) reported that *Phalacrocer 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 *Phalacrocer 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 allenii* (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.

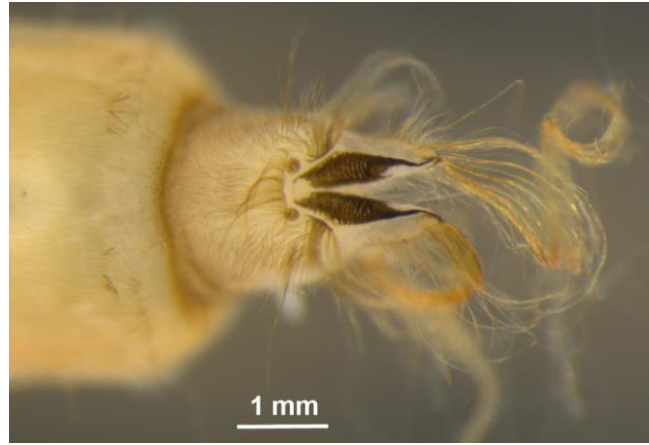


Figure 36. *Piliaria* sp. larva breathing apparatus, a genus that lives among Wisconsin mosses. Photo by Urmas Kruus, with permission.



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 crane fly *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. Crane fly 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 crane flies 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 crane fly 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 carinifrons* 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* (*Savtshenka*) (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.

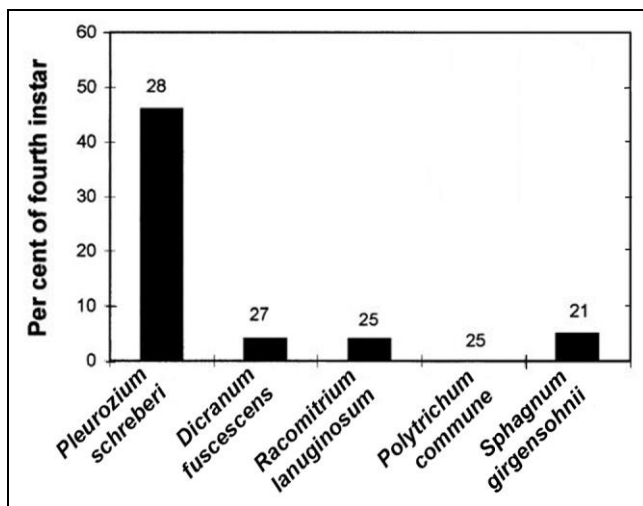


Figure 56. Survival percentages of *Tipula montana* larvae, starting with second-instar larvae, entering fourth instar after 52 days of feeding on diets of five moss species. Sample sizes appear above bars. Redrawn from Smith *et al.* 2001.

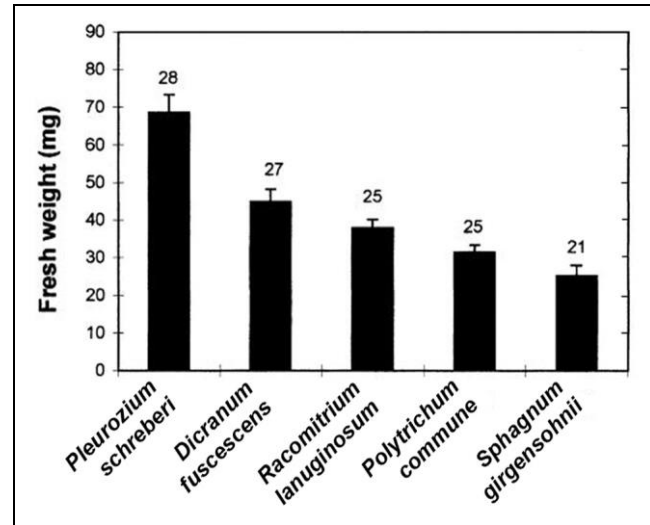


Figure 57. Mean fresh weight (+ standard error) of larvae of *Tipula montana*, starting with second-instars, after 52 days on each of five moss species. Sample sizes appear above bars. Redrawn from Smith *et al.* 2001.

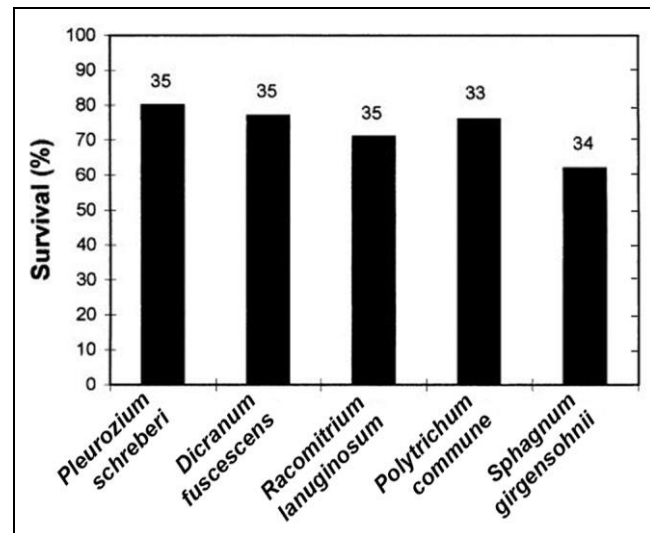


Figure 58. Percent survival of *Tipula montana* larvae fed on each of five moss species for 52 days. Sample sizes appear above bars. Redrawn from Smith *et al.* 2001.

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 crane fly 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](http://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](http://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 *pH* of the gut (Martin *et al.* 1980). Very high and very low *pH* levels seem to work best. But Barlocher and Porter (1986) found that the larvae of *Tipula caloptera* (Figure 73) have a gut *pH* 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 *pH* 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 *pH* near 11.5 in a narrow section where there is extremely high proteolytic activity (Martin *et al.* 1980). In addition to low *pH* 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 *pH* 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 crane fly 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. *Dolichozepe 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. *Sylvicola 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, *Kolenohalea 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.

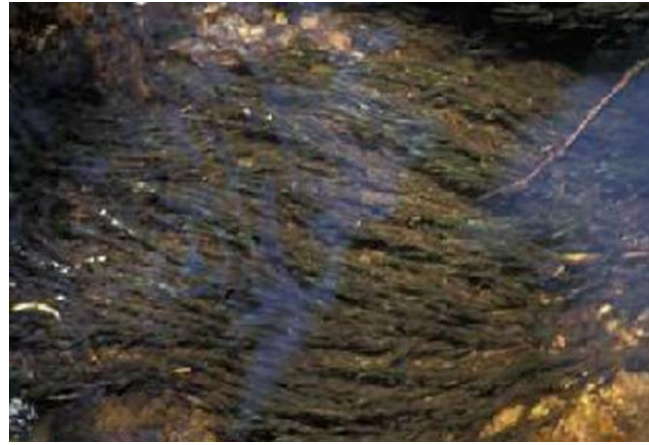


Figure 92. *Fontinalis dalecarlica*, home for a number of genera of *Ceratopogonidae*. Photo by Kristoffer Hylander, with permission.

## 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 *pH* 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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# CHAPTER 11-13b

## AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER NEMATOCERA

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# CHAPTER 11-13b

## AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER NEMATOCERA



Figure 1. **Chironomidae** larvae, the most common and abundant family of insects among mosses. Photo by Simon Carmichael, through Creative Commons.

### Suborder Nematocera, continued

#### Chironomidae – Midges

These small flies are 1-10 mm long and are everywhere (Cotinis 2004)! Only some areas of the desert seem to lack them. They are the flies that seem to follow you as clouds (swarms). The larvae are mostly aquatic and use filter feeding.

If you haven't met the **Chironomidae**, you haven't looked at the bases of aquatic moss leaves. Hynes (1961) considered the **Chironomidae** (Figure 1) to be the "key industry" organisms among mosses. Such a concept is supported by their role as food for fish. Johannsen (1969) contended that in some locales they may constitute almost the entire diet of brook trout (*Salvelinus fontinalis*). But

the mosses provide excellent hiding places for these larvae, so the bryophytes may be a detriment rather than a source of fish food.

Thienemann (1936) reported many **Chironomidae** from mosses in the alpine areas of Europe. These occurred in springs, waterfalls, bogs, and streams. The **Chironomidae** are by far the most numerous organisms in most stream bryophyte habitats (Arnold & Macan 1969; Gerson 1982; Maurer & Brusven 1983; Brusven *et al.* 1990; Glime 1994; Chantha *et al.* 2000; Linhart *et al.* 2002a), typically comprising more than 50% of the insects living there (Brusven *et al.* 1990). Needham and Christenson (1927) reported *Chironomus* (Figure 1) and



*Tanytarsus* (Figure 2) from moss-covered boulders in streams of northern Utah, USA. Frost (1942) found that among submerged mosses she studied in Ireland, about five-sixths of the almost 600,000 organisms in those streams were **Chironomidae**. Lindegaard *et al.* (1975) found that more than 40% of the invertebrates living among the moss *Cratoneuron* (Figure 3) were **Chironomidae**.



Figure 2. *Tanytarsus* larva and tube. Photo from Cobb County, GA, government, Cobb County Water System website, through public domain.



Figure 3. *Cratoneuron commutatum* var *falcatum* in Europe, a habitat where many **Chironomidae** live among the mosses. Photo by Michael Lüth, with permission.

**Chironomidae** (Figure 1) can reach 100,000 in a collection of *Cratoneuron* (Figure 3) (Gerson 1969). Frost (1942) found that in an acid stream the **Chironomidae** comprised 84% of the moss fauna; in the alkaline stream they comprised 83%. Haefner and Wallace (1981) found that this family had mean annual densities of 23,000 m<sup>2</sup> among the thick mosses of rockface habitats in a southern Appalachian, USA, stream. Brusven *et al.* (1990) reported that moss clumps had insect communities in which 50% of the organisms were **Chironomidae**. These did not seem to contribute to increased daytime drift.

Boerger *et al.* (1982) found that densities of **Chironomidae** (Figure 1) on mosses in a brown-water stream of Alberta, Canada, were high (978) compared to a

range of 32-466 on tracheophytes, sponge colonies, and algae. But diversity was only 3 species on mosses, compared to 13 for sediment, 2 for *Sparganium*, and 1 for the other tracheophytes, algae, wood, and none for sponges and leaf litter.

Nolte (1991) found that the **Chironomidae** (Figure 1) in the mosses of a small upland stream in central Germany were small, with 98% being <5 mm. There were more than 65 species in 26 genera! The greatest diversity was near the source and the species changed downward in the stream. The fully submersed mosses had approximately five times as many larvae as those that were semi-submersed. The highest density reached 830 larvae per 10 square cm. Nolte found that the location of the moss in the stream had the greatest effect on the diversity, but the biomass and abundance were most influenced by the constancy of flow and factors such as temperature and detritus deposition that related to flow.

In most locations, species of bryophyte doesn't seem to matter much. In the Appalachian Mountain streams of eastern USA, they were abundant in all three dominant species: *Fontinalis dalecarlica* (Figure 4), *Hygroamblystegium fluviatile* (Figure 5) – *Platyhypnidium riparioides* (Figure 6), and *Scapania undulata* (Figure 7).

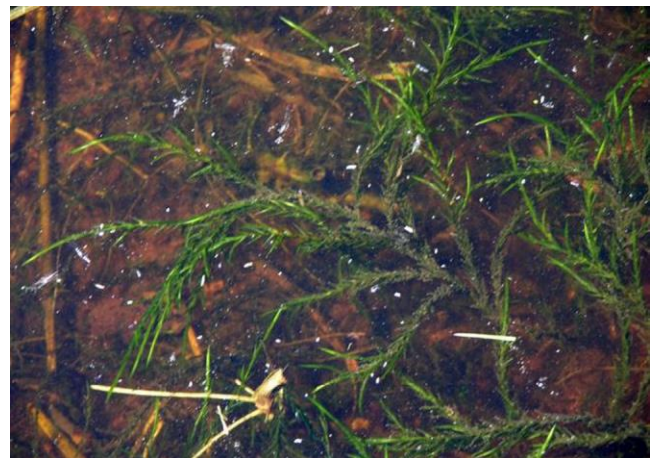


Figure 4. *Fontinalis dalecarlica*, moss that is home to large numbers of **Chironomidae**. Photo by J. C. Schou, with permission.



Figure 5. *Hygroamblystegium fluviatile*, a moss that is home to large numbers of **Chironomidae**. Photo by Hermann Schachner, through Creative Commons.





Figure 6. *Platyhypnidium riparioides*, home to many **Chironomidae**. Photo by Michael Lüth, with permission.



Figure 7. *Scapania undulata*, a leafy liverwort that is home to large numbers of **Chironomidae**. Photo by Hermann Schachner, through Creative Commons.

### Emergence

Some **Chironomidae** (Figure 1) use the mosses for emergence. Adults of *Microtendipes pedellus* (Figure 8) emerged from both mossy and muddy substrates in a Quebec highland stream (Harper & Cloutier 1979). The researchers suggested that some typically lentic (non-moving water) chironomid species were able to live in the protection of mosses in streams. The huge numbers found there and in other habitats result in clouds of adults during emergence time (Figure 9).



Figure 8. *Microtendipes pedellus* adult, a midge that often uses mosses for emergence. Photo through Wikimedia Commons.



Figure 9. **Chironomidae** adult swarm. Photo by Robert Janke, with permission.

Unger (1974) reared *Boreochlus* sp. (Figure 10) from mosses in a bog near Washington, D.C., USA. Becker and Wagner (2004) compared the emergence of **Chironomidae** (Figure 1) from sand and moss-covered rocks in a stream in Germany. They recorded 99 species from the sand traps and 85 from the traps over the moss-covered stones! The **Tanytarsini** (Figure 2) dominated in the traps on the moss-covered stones, whereas the **Prodiamesinae** and **Chironomini** predominated in traps above sand. They suggested that the smaller number of species above the moss-covered rocks may have been due to escapes from the nets on the irregular surfaces with lower flow rates trapping more pupae over the sand.

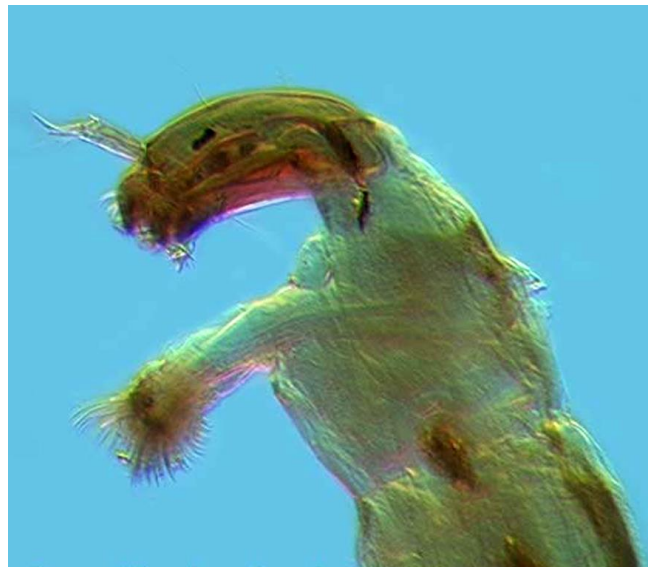


Figure 10. *Boreochlus sinuaticornis* larva, member of a genus that lives among bryophytes in bogs. Photo by Pete Cranston, with permission.

In Appalachian Mountain, USA, streams, the **Chironomidae** make thin cases for their pupae between the upper and lower leaves of the leafy liverwort *Scapania undulata* (Figure 7) (Glime 1968). One larva even crawled into an empty case of the caddisfly *Paleagapetus celsus* to pupate, a case made from *Scapania undulata*. The leaves of this liverwort also provide a location where one can find larvae and eggs of the midges.



## Seasons

The **Chironomidae** (Figure 1) are present year-round, but the taxa change. For example, among bryophytes in an Atlantic Forest stream (biome along the Atlantic coast of Brazil from Rio Grande do Norte in the north to Rio Grande do Sul in the south), Rosa *et al.* (2011) found that **Chironomidae** were dominant in both periods of study (3 months each of dry season and rainy season). In the dry season, the **Naididae** (annelid worms) were second in number.

*Pseudodiamesa branickii* (Figure 11) demonstrates the variability in life cycles of some **Chironomidae**. This species produces three generations in one year in a German stream, but the generation time varies based on photoperiod effects on eggs and larvae (Nolte & Hoffmann 1992). In this stream there are two strains, one that is **bivoltine** (producing two broods per season) and one that is **trivoltine** (producing three broods per season).



Figure 11. *Pseudodiamesa branickii* larva, a species with at least two strains that differ in the length of the life cycle. Photo by Erik Bostrom, NTNU Museum of Natural History and Archaeology, through Creative Commons.

Temperature differences can cause differences in emergence times. For example, in the high Arctic, **Chironomidae** (Figure 1) from deeper water emerge as much as three weeks later than those in warmer shallow water (Danks & Oliver 1972). Among the 112 species of **Chironomidae** in a muskeg stream in Alberta, Canada, emergence extends over 140 days. In New South Wales, emergence (Figure 12) is governed by flooding, with *Chironomus tepperi* (Figure 13) emerging first and *Procladius paludicola* (see Figure 14) emerging as the former declines (Stevens 1994).



Figure 12. *Chironomus dorsalis* emerging to an adult. Photo by James K. Lindsey, with permission.



Figure 13. *Chironomus tepperi* adult male, an earlier emerger than *Procladius paludicola*, thus separating their niches. Photo through Creative Commons.



Figure 14. *Procladius lugens* adult. *Procladius paludicola* is a later emerger than *Chironomus tepperi*, thus separating their niches. Photo by James K. Lindsey, with permission.

Differences in emergence times can maintain the isolating mechanism that keeps species distinct, as in two sibling species of **Chironomus** (Figure 15) in Arctic ponds (Butler 1982). Although the two species are morphologically indistinct as larvae, they maintain strict, but different, emergence times, despite 7-year developmental periods.



Figure 15. *Chironomus*, a genus known from among bryophytes. Photo by Gerard Visser, with permission.

### Cold-water Species

Cold temperatures seem to favor some of the **Chironomidae** (Figure 1). Welch (1976) found that *Orthocladius* (Figure 16), *Pseudodiamesa arctica* (see Figure 11), *Paracladius quadrinodosus* (see Figure 17), and *Micropsectra*(?) sp. (Figure 18) occur primarily in the rocky and moss zones. They are able to withstand temperatures down to 0°C, which is important for their life cycle of 2-3 years. The genus *Diamesa* (Figure 19-Figure 20) is common among mosses of European glacier-fed streams where the temperature is constantly less than 2°C (Lods-Crozet *et al.* 2001). Elgmork and Sæther (1970) found it among mosses in creeks and springs in the Colorado Rocky Mountains, USA. It is able to overwinter under the snow (Anderson *et al.* 2013).



Figure 16. *Orthocladius rubicundus*, a genus with larvae among bryophytes in cold water. Photo by J. K. Lindsey, with permission.



Figure 17. *Paracladius conversus* female adult. Some members of this genus live among mosses in rocky zones of cold streams. Photo by James K. Lindsey, with permission.



Figure 18. *Micropsectra* larva, member of a genus with moss-dwelling species. Photo by NTNU University Museum, Department of Natural History, through Creative Commons.



Figure 19. *Diamesa mendotae* larvae, member of a genus that is common among mosses in cold-water streams. Permission to reproduce given by Leonard Ferrington on behalf of the Chironomidae Research Group at the University of Minnesota.



Figure 20. *Diamesa mendotae* female on snow. Permission to reproduce given by Leonard Ferrington on behalf of the Chironomidae Research Group at the University of Minnesota.

*Macropelopia notata* (Figure 21) and *M. adauca* are cold-water species that are **crenobionts** (living in springs) (Fittkau 1962). They prefer mosses in soft water. *Macropelopia notata* occurs in **rheo-hygropetric** springs (flowing film of water on rocks in springs) and **helocrenes** (springs originating from marshes or bogs) with abundant mosses (Lencioni *et al.* 2011). In the Danish spring



Ravnskilde, Lindegaard *et al.* (1975) found large numbers of *Macropelopia notata* in the moss carpets. These carpets exhibit both vertical and horizontal zonation patterns that do not seem to be influenced by the fauna of the neighboring stone. Rather, horizontal distribution seems to result from differences in current velocity and detritus capture.



Figure 21. *Macropelopia notata* adult, a species whose larvae live among mosses in springs. Photo by James K. Lindsey, with permission.

In the Antarctic, mosses often play a role in protecting invertebrates from the harsh and changeable environment. The **Chironomidae** (Figure 1) are no exception, living among bryophytes in a first-order stream of the Atlantic Forest (Tilbrook 1967; Rosa *et al.* 2013). The mosses are able to provide protection from the rushing waters during periods of higher rainfall, and the high retention of food particles support both species richness and density during the high rainfall periods.

*Parochlus steinenii* (Figure 22) is a chironomid of lakes in the central plateau of the Byers Peninsula, Antarctica (Rico & Quesada 2013). It lives among the mosses on the bottoms of lakes and streams. The second of the two chironomids in that part of Antarctica is *Belgica antarctica* (Figure 23) that lives in streams that run through moss beds. Both species feed on a variety of foods associated with the biofilm and microbial material among the mosses.



Figure 22. *Parochlus steinenii* adults, a chironomid that lives among mosses in the Antarctic. Photo by Roger S. Key, with permission.



Figure 23. *Belgica antarctica* larvae, a chironomid that is common in streams running through moss beds of Antarctica. Photo by Juanita Constible, through Creative Commons.

### Overwintering

Some **Chironomidae** larvae become encased in ice in winter, yet survive, an ability that is rare among the insects (Moore & Lee 1991). Although this seems only to be known where they can live in sediments of pools and ponds, it is possible that they likewise do this among sediments collected by bryophytes. Irons *et al.* (1993) found that **Chironomidae** (Figure 1) in Alaska, USA, are able to overwinter in a frozen habitat.

Frost (1942) found that the chironomid larvae in her River Liffey, Ireland, survey reached their peak in winter in the moss samples.

### Current Velocity

Many of the **Chironomidae** (Figure 1) live in areas of high water velocity, but are protected from it by the bryophytes. They are able to nestle at leaf bases where they benefit not only through protection from the current, but also from the collection of detritus there. Oliver and Bode (1985) described a new species of *Cardiocladius* (Figure 24) that resembles *Cardiocladius albiplumus* among bryophytes where the current velocities are 20-100 cm s<sup>-1</sup>.



Figure 24. *Cardiocladius* adult, a genus that has larvae that sometimes live among bryophytes. Photo by M. J. Hatfield, through Creative Commons.



### Diversity

The **Chironomidae** do not lack species diversity among bryophytes (see Table 1). In a mountain river in the Western Tatra Mountains, Ertlova (1984) found 56 species. The most varied species composition occurred among mosses on large stones. The dominant species was *Orthocladius rivicola* (Figure 25).



Figure 25. *Orthocladius rivicola* larva, a moss inhabitant. Photo from Stroud Water Research Center, through Creative Commons.

The **Chironomidae** is a large family and its species are difficult to identify. Few people attempt the identification of larvae (Figure 1). Most ecologists simply indicate **Chironomidae**. This results from the difficulty of finding distinguishing characters between related species and the need to rear them before a name can be applied and the larva described. For example, *Krenosmittia* (Figure 26) larvae are known in Europe from springs and moss-filled seeps (Ferrington 1984). The habitat of North American larvae is unknown, although adults are known, but the habitat is likely to be similar, or they might occur in the **hyporheic** zone (area or ecosystem beneath bed of river or stream, saturated with water and supporting invertebrate fauna) of streams. Creating a list of bryophyte taxa is further complicated by changing views of the classification. For many of the taxa in Table 1 I was unable to verify the name or find the name currently in use.

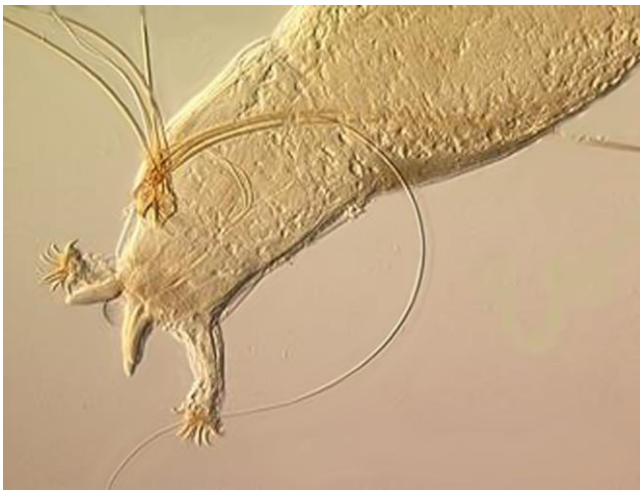


Figure 26. *Krenosmittia* larva posterior, an inhabitant of moss-filled seeps in Europe. Photo by Peter Cranston, with permission.

A few brave souls have done the tedious work to provide species lists of **Chironomidae**. In their study of the Colorado Rocky Mountain, USA, streams, Elgmork and

Sæther (1970) identified a number of **Chironomidae** (Figure 1) species among mosses. These included *Pseudokiefferiella parva* (Figure 27) in creeks and springs, and occasionally *Orthocladius* (Figure 16). Among the mosses of high mountain brooks they found *Metriocnemus* (Figure 28), *Parakiefferiella*, and *Rheocricotopus effusus* (see Figure 29). *Paraphaenocladius* (Figure 30), a primarily terrestrial genus, can also occur in bogs and among mosses of mountain creeks, particularly cold springs. They found species of *Nanocladius* (Figure 31) in their streams, but did not mention mosses; *Nanocladius bicolor* lives among mosses in high mountain creeks in Europe (Thienemann 1954; Freeman 1956). Likewise, *Thienemannia* cf. *gracilis* (see Figure 32), present in their study, is known among mosses in mountain creeks (Thienemann 1954; Brundin 1956a, b) and among perennial mosses in a river in Romania (Gardenfors 2001). Frost (1942) was also among the brave who identified the **Chironomidae** among the mosses in the River Liffey, Ireland. Including both an acid and an alkaline area, she found 24 genera, many different from those of Elgmork and Sæther (1970) in the Rocky Mountain, USA, streams, as seen in Table 1.



Figure 27. *Pseudokiefferiella parva* larva, an inhabitant of mosses in the Rocky Mountains, USA, streams and springs. Photo from <Benthos.narod.ru>.



Figure 28. *Metriocnemus edwardsii* from *Darlingtonia californica* (western pitcher plant). Photo by Barry Rice, through Creative Commons.





Figure 29. *Rheocricotopus atripes* female adult, member of a genus known from mosses in high mountain brooks in the Colorado Rocky Mountains. Photo by James K. Lindsey, with permission.



Figure 31. *Nanocladius* larva amid the legs of a larger invertebrate. *Nanocladius bicolor* lives among mosses in high mountain creeks of Europe. Photo by Pete Cranston, with permission.



Figure 30. *Paraphaenocladus* sp. adult; larvae of this genus can occur in bogs and among mosses of mountain creeks. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.



Figure 32. *Thienemannia gracei* adult, member of a genus whose larvae often live among mosses in mountain streams and rivers. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.

Table 1. Chironomidae known to include bryophytes among their choices of shelter in streams. Taxa preceded by \* indicate taxa I was unable to verify on current nomenclature lists. Available images follow the table.

Taxon	Habitat	References
* <i>Ablabesmyia costalis</i>	River Liffey, Ireland European alpine	Humphries & Frost 1937; Frost 1942; Thienemann 1936
<i>Ablabesmyia mallochii</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
* <i>Ablabesmyia minima</i>	European alpine streams; River Liffey, Ireland	Thienemann 1936; Humphries & Frost 1937; Frost 1942
<i>Ablabesmyia nigropunctata</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Ablabesmyia sexannulata</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Belgica antarctica</i>	Antarctic streams in moss beds	Rico & Quesada 2013
* <i>Brillia alulata</i>	European alpine springs	Thienemann 1936
<i>Brillia modesta</i>	European alpine	Thienemann 1936
<i>Camptocladus</i> sp.	River Liffey, Ireland	Frost 1942
<i>Cardiocladus albiplumus</i>	fast water	Oliver & Bode 1985
<i>Chaetocladus perennis</i>	pupae in European alpine	Thienemann 1936
* <i>Chironomus genuines</i>	River Liffey, Ireland	Frost 1942

<i>Cladotanytarsus</i>	River Liffey, Ireland	Frost 1942
<i>Conchapelopia flavifrons</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Conchapelopia puncticollis</i>	European alpine	Thienemann 1936
<i>Corynoneura</i> sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942;
	larvae & pupae in European alpine	Thienemann 1936
<i>Corynoneura lobata</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Cricotopus</i> sp.	<i>Drepanocladus revolvens</i> , Alberta, Canada;	Boerger <i>et al.</i> 1982
	<i>Fontinalis</i> & <i>Hygrohypnum</i> in Russian lake outlets	Vuori <i>et al.</i> 1999
<i>Cricotopus bicinctus</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Cricotopus miricornis</i>	European alpine	Thienemann 1936
<i>Cricotopus prolongatus</i>	European alpine	Thienemann 1936
<i>Cricotopus trifasciatus</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Cryptochironomus</i> sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Culicoides rivicola</i>	European alpine	Thienemann 1936
<i>Culicoides neglectus</i> (nom dub)	European alpine	Thienemann 1936
<i>Diamesa</i> sp.	River Liffey, Ireland	Humphries & Frost 1937
<i>Diamesa fissipes</i> gr.	European alpine	Thienemann 1936
<i>Diamesa prolongata</i>	pupae in European alpine	Thienemann 1936
<i>Diamesa steinboeckii</i>	European alpine	Thienemann 1936
<i>Diamesa tonsa</i>	pupae among mosses in European alpine	Thienemann 1936
<i>Diplocadius cultriger</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Endochironomus</i> sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
* <i>Eukiefferiella alpestris</i>	European alpine streams	Thienemann 1936
<i>Eukiefferiella brevicar</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Eukiefferiella caerulea</i>	larvae among <i>Fontinalis</i> ; pupae among mosses	Thienemann 1936
<i>Eukiefferiella endobryonia</i>	larvae & pupae in tubes made of <i>Fontinalis</i> spp.	Imada 2020
* <i>Eukiefferiella longicalcar</i> (nomen dubium)	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Eukiefferiella lobifera</i>	European alpine	Thienemann 1936
<i>Eukiefferiella minor</i>	European alpine streams	Thienemann 1936
<i>Eukiefferiella subalpina</i>	European alpine streams	Thienemann 1936
* <i>Eutanytarsus inermepes</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Heterotrissocladius</i> sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Heterotrissocladius changi</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Krenosmittia</i>	European springs & seeps	Ferrington 1984
* <i>Labrudinia pilosella</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Limnophyes borealis</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Limnophyes globifer</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Limnophyes prolongatus</i>	European alpine	Thienemann 1936
<i>Macropelopia</i> sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Macropelopia adaucta</i>	mosses in coldwater springs	Fittkau 1962; Lindegaard <i>et al.</i> 1975
<i>Macropelopia notata</i>	mosses in coldwater springs	Fittkau 1962; Lindegaard <i>et al.</i> 1975
<i>Metriocnemus</i>	in high mosses of high mountain brooks of Europe	Thienemann 1954
	Colorado Rocky Mountain, USA, streams	Elgmork & Sæther 1970
* <i>Metriocnemus cuneatus</i>	European alpine springs	Thienemann 1936
<i>Metriocnemus fuscipes</i>	European alpine springs	Thienemann 1936
<i>Metriocnemus hygroetricus</i>	European alpine	Thienemann 1936
<i>Micropsectra</i> sp.	European alpine streams	Thienemann 1936
<i>Microtendipes</i> sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Microtendipes pedellus</i>	emergences in mossy areas, Quebec, Canada	Harper & Cloutier 1979
<i>Nanocladius</i> sp.	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Nanocladius bicolor</i>	high mountain streams in Europe	Thienemann 1954; Freeman 1956
<i>Neostempellina thienemanni</i>	exclusively alkaline springs & streams	Reiss 1984
<i>Orthocladus luteus</i>	European alpine streams	Thienemann 1936
<i>Orthocladus oblidens</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Orthocladus rivicola</i>	European alpine streams	Thienemann 1936
<i>Orthocladus rivulorum</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Orthocladus saxicola</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Orthocladus thienemanni</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Paraboreochlus minutissimus</i>	European alpine springs	Thienemann 1936
<i>Paracladius quadrimodulus</i>	moss & rock zones	Welch 1976
<i>Paracricotopus</i> sp.	larvae & pupae in alpine streams & waterfalls	Thienemann 1936
<i>Parakiefferiella</i> sp.	Holarctic mountain brooks	Thienemann 1944; Oliver 1963; Elgmork & Sæther 1970; Boerger <i>et al.</i> 1982
	<i>Drepanocladus revolvens</i> , Alberta, Canada;	Frost 1942
<i>Parakiefferiella bathophila</i>	River Liffey, Ireland	Boerger <i>et al.</i> 1982
<i>Paramerina fragilis</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Elgmork & Sæther 1970
<i>Paraphaenocladus</i>	bog mosses, mountain streams, cold springs	Epele <i>et al.</i> 2012
<i>Parapsectrocladius</i>	mountain streams, Argentina	Humphries & Frost 1937; Frost 1942
<i>Paratanytarsus</i> sp.	River Liffey, Ireland	Rico & Quesada 2013
<i>Parochlus steinenii</i>	mosses on Antarctic lake bottoms	



<i>Polypedilum</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Polypedilum scalaenum</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Psectrocladius dilatatus</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Psectrocladius psilopterus</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Psectrocladius simulans</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Pseudodiamesa arctica</i>	moss & rock zones	Welch 1976
<i>Pseudodiamesa branickii</i>	mid-mtn creeks, Colorado Rocky Mountain, USA	Elgmork & Sæther 1970
<i>Pseudodiamesa nivosa?</i>	European alpine	Thienemann 1936
<i>Pseudokiefferiella parva</i>	Colorado Rocky Mountain, USA, creeks and springs	Elgmork & Sæther 1970
<i>Rheocricotopus effusus</i>	pupae in alpine areas	Thienemann 1936;
	larvae in streams in high mountain areas	Elgmork & Sæther 1970
<i>Rheocricotopus fuscipes</i>	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
	European alpine	Thienemann 1936
<i>Rheotanytarsus</i> sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Rheotanytarsus distinctissimus</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Stempellina bausei</i>	European alpine streams	Thienemann 1936
* <i>Syndiamesa macronyx</i>	European alpine	Thienemann 1936
<i>Synorthocladus semivirens</i>	European alpine	Thienemann 1936
* <i>Synorthocladus tipulatus</i>	River Liffey, Ireland, European alpine springs	Thienemann 1936; Humphries & Frost 1937; Frost 1942
		Boerger <i>et al.</i> 1982
<i>Tanytarsus curticornis</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Tanytarsus dispar</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Humphries & Frost 1937; Frost 1942
<i>Tanytarsus gregarius</i>	River Liffey, Ireland	Thienemann 1936, 1954; Brundin 1956a, b; Elgmork & Sæther 1970
<i>Thienemannia gracilis</i>	mountain streams in Europe & Iceland	Thienemann 1936
	streams, Colorado Rocky Mountain, USA	Vuori <i>et al.</i> 1999
<i>Thienemanniella fusca</i>	European alpine	Humphries & Frost 1937; Frost 1942
<i>Thienemannimyia</i>	Russian streams	Thienemann 1936
* <i>Trichocladus</i> sp. (invalid genus)	River Liffey, Ireland	Boerger <i>et al.</i> 1982
<i>Trissopelopia longimana</i>	European alpine streams	Thienemann 1936
<i>Trissopelopia ogemawi</i>	<i>Drepanocladus revolvens</i> , Alberta, Canada	Boerger <i>et al.</i> 1982
<i>Tvetenia bavarica</i>	European alpine waterfalls	Thienemann 1936
<i>Tvetenia calvescens</i>	semiterrestrial mosses in springs, Europe	Stur <i>et al.</i> 2005; Thienemann 1936;
	European alpine streams; River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Tvetenia discoloripes</i>	European streams	Thienemann 1936, 1954
	Colorado Rocky Mountain, USA, streams	Elgmork & Sæther 1970
	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
<i>Xenochironomus xenolabis</i>	Quebec highland stream	Harper & Cloutier 1979



Figure 33. *Ablabesmyia* larva, a common genus among bryophytes in Europe. Photo by Walter Pfliegler, with permission.



Figure 34. *Ablabesmyia* egg sack, a common genus among bryophytes in Europe. Photo by Walter Pfliegler, with permission.



Figure 35. *Brillia bifida* adult, member of a genus that inhabits aquatic mosses in Europe. Photo by James K. Lindsey, with permission.



Figure 36. *Chaetocladius perennis* adult, a species whose larvae are known from bryophytes. Photo by James K. Lindsey, with permission.

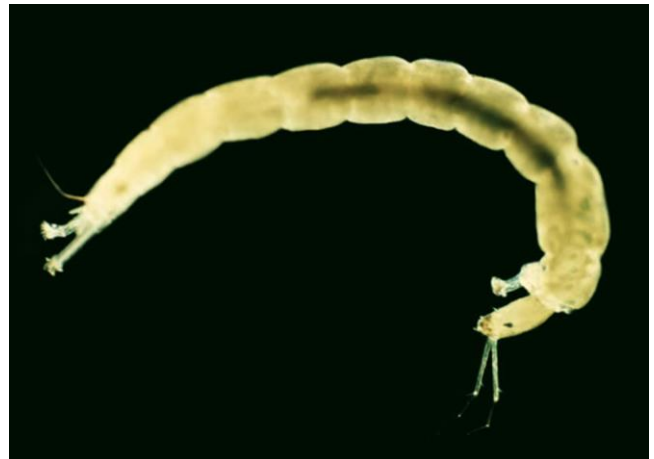


Figure 37. *Corynoneura taranaki* larva, member of a genus with bryophyte dwellers. Photo by Stephen Moore, Landcare Research, NZ, with permission.





Figure 38. *Cricotopus lebetis* larva, member of a genus known from the mosses *Fontinalis* and *Hygrohypnum* in Russia. Photo by Jerry F. Butler, with permission.



Figure 39. *Cryptochironomus obreptans* female adult, member of a genus with larvae that can inhabit stream mosses. Photo by James K. Lindsey, with permission.



Figure 40. *Culicoides imicola* adult, member of a genus whose larvae can live among bryophytes. Photo by Alan R. Walker, through Creative Commons.



Figure 41. *Diplocladius cultriger*, a species whose larvae sometimes live among mosses. Photo by Tom Murray, through Creative Commons.



Figure 42. *Endochironomus* larva, a genus whose larvae sometimes live among mosses. Photo by J. C. Schou, with permission.



Figure 43. *Endochironomus* male adult, genus with larvae that sometimes live among bryophytes. Photo by Don Loarie, through Creative Commons.



Figure 44. *Eukiefferiella* (arrow) on *Nesameletus ebopohaupapa*. Several species of *Eukiefferiella* live among stream bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 45. *Limnophyes habilis* adult, member of a genus with several species that live among bryophytes. Photo by James K. Lindsey, with permission.



Figure 46. *Macropelopia nebulosa* pupa, member of a genus with larvae of some species occurring among aquatic mosses. Photo by J. C. Schou, with permission.



Figure 47. *Macropelopia nebulosa* adult, member of a genus that sometimes lives among mosses as larvae. Photo by James K. Lindsey, with permission.





Figure 48. *Metriocnemus fusipes* male adult, a species whose larvae can occur among stream bryophytes. Photo by James K. Lindsey, with permission.



Figure 51. *Paratanytarsus tenuis* male adult, member of a genus whose larvae inhabit stream bryophytes. Photo by James K. Lindsey, with permission.



Figure 49. *Paracladius conversus* female adult, member of a genus that is represented among the bryophyte fauna of streams in Europe. Photo by James K. Lindsey, with permission.



Figure 52. *Polypedilum* larva in plant litter. *Polypedilum scalaenum* occurs among *Drepanocladus revolvens*. Photo by Stephen Moore, Landcare Research NZ, with permission.



Figure 50. *Paramerina fragilis* adult, a species whose larvae occur with the moss *Drepanocladus revolvens* in Canada. Photo by Ilona L, through Creative Commons.



Figure 53. *Psectrocladius sordidellus* emerging female adult, member of a genus that sometimes occurs among stream bryophytes. Photo by James K. Lindsey, with permission.



Figure 54. *Stempellina bausei* adult, a species whose larvae live among bryophytes in European alpine streams. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.



Figure 55. *Trissopelopia longimana* adults mating, a species whose larvae live in European alpine streams. Photo by James K. Lindsey, with permission.

Suren (1993) considered that the dominance of **Chironomidae** (Figure 1) among New Zealand mosses may reflect the absence in New Zealand of some of the important moss families of **Ephemeroptera**, **Plecoptera**, and **Trichoptera** in other parts of the world.

### Bryophyte Preferences?

Like the **Chironomidae** (Figure 1), the mosses are difficult for non-bryologists to identify and few studies actually name both the mosses and the **Chironomidae** associated with them. In the pristine streams of the Russian Karelia, Vuori *et al.* (1999) found that algae-eating **Chironomidae** larvae dominated the insect fauna in stable lake outlets where mosses formed abundant vegetation. The mosses were predominantly *Fontinalis* (Figure 4) and *Hygrohypnum* (Figure 56). *Cricotopus* sp. (Figure 38) and *Thienemannimyia* sp. (Figure 57) were the dominant **Chironomidae**.



Figure 56. *Hygrohypnum ochraceum*, home of **Chironomidae**. Photo by Michael Lüth, with permission.



Figure 57. *Thienemannimyia* larva posterior, a moss dweller. Photo by Pete Cranston, with permission.

In their study of an Arctic stream (Alaska, USA), Lee and Hershey (2000) found that **Chironomidae** increased in density when the mosses (*Hygrohypnum*, Figure 56) increased to dense growths. They suggested that it was the increase in habitat complexity that caused the increase in the **Chironomidae**.

In New Zealand, the **Chironomidae** (Figure 1) were most abundant in *Fissidens rigidulus* (Figure 58) in the midstream torrential water, whereas other taxa dominated in mosses of the spray zones (Cowie & Winterbourn 1979).

### What's for Dinner?

Aside from nematodes and rotifers, the **Chironomidae** were the dominant fauna in beds of *Fontinalis antipyretica* (Figure 59) in the Czech Republic, making them the most abundant insect group (Linhart *et al.* 2000, 2002a,c). Those among mosses had a positive density correlation with organic particles of 30-100  $\mu\text{m}$ . Some **Chironomidae** larvae build tubes to trap detritus (Figure 60). In one rip-rapped channel (used to stabilize the stream banks) in the Czech Republic, Linhart *et al.* (2002b) found the fine particulate matter trapped by the moss provided a food source for the moss dwellers. Unlike those in many mossy habitats, the **Chironomidae** comprised only 4.08% of the fauna, outnumbered by rotifers and nematodes. They concluded that the rip-rap rocks, covered with mosses, increased both stability and diversity of the streams.





Figure 58. *Fissidens rigidulus*, a moss that houses abundant **Chironomidae** midstream in New Zealand. Photo by Bill & Nancy Malcolm, with permission.



Figure 59. *Fontinalis antipyretica*, a moss where **Chironomidae** are dominant in the Czech Republic. Photo by Michael Lüth, with permission.

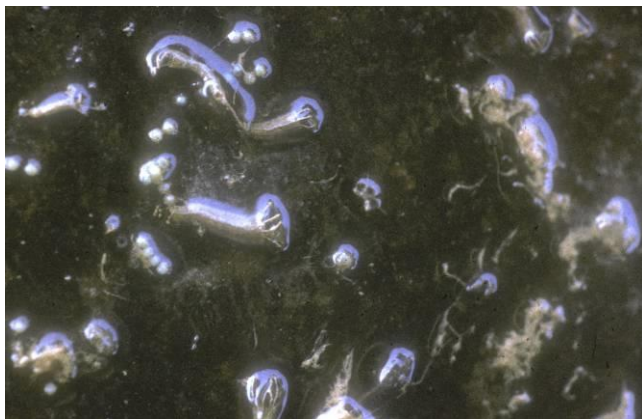


Figure 60. These tubes of **Chironomidae** are often present among mosses. The larvae live near the bottom of the moss clump and trap detritus in the net or use the moss as a trap, using the detrital matter for food. Photo by Janice Glime.

Smirnov (1961) concluded that no abundant insects fed on mosses in bogs, but *Psectrocladius psilopterus* (Figure 61) – a chironomid larva, ate the *Sphagnum* (Figure 62). There is some evidence that bryophytes may serve insects as emergency foods or provide an important part of the diet, albeit in small proportions.



Figure 61. *Psectrocladius sordidellus* emerging female adult. Larvae of *Psectrocladius psilopterus* eat *Sphagnum*. Photo by James K. Lindsey, with permission.



Figure 62. *Sphagnum capillifolium*, member of a genus that is eaten by *Psectrocladius psilopterus* in bogs. Photo by Blanka Shaw, with permission.

Although **Chironomidae** (Figure 1) feed predominately on the detritus among the mosses, they consume mosses as well (Kalachova *et al.* 2011). This consumption may actually be moss components of the detritus. Using acetylenic acids as biomarkers from the moss *Fontinalis antipyretica* (Figure 59), Kalachova *et al.* (2011) demonstrated this chemical group in the **Chironomidae**, especially in winter when other food sources, especially zoobenthos and biofilms, become scarce.

### Parasite Protection?

Mosses might offer an advantage unknown in most habitats. They protect their guests from parasitic mites. In Luxembourg, two species of *Chaetocladius* (Figure 63) were free of water mite parasites (Stur *et al.* 2005). Stur *et al.* suggested that the semiterrestrial lifestyle of these insects among the mosses made them less available to the



mite larvae. On the other hand, moss dwellers like *Tvetenia calvescens* and *T. bavarica* (see Figure 64-Figure 65) did have mite parasites in the springs where they lived. Of the **Chironomidae** species examined, those free of mites lived in bryophyte habitats where the numerous generalist parasitic mites *Sperchon thienemanni* (see Figure 66) and *Atractides fonticolus* were not likely to occur.



Figure 63. *Chaetocladius piger*, a member of a chironomid genus that seems to be protected from mites when it lives in wet, semiterrestrial mosses. Photo by J. K. Lindsey, with permission.



Figure 64. *Tvetenia discoloripes* larva, a bryophyte inhabitant. Photo by Walter Pfliegler, with permission.



Figure 65. *Tvetenia discoloripes* larva, a bryophyte inhabitant. Photo by Walter Pfliegler, with permission.



Figure 66. *Sperchon* cf. *setiger*, member of a genus with parasites on **Chironomidae**. Photo by Yann, through Creative Commons.

### Refuge in Bryophytes

Not only do the bryophytes provide a refuge among their leaves, but some Chironomidae use bryophytes to make a case and others **pupate** (Figure 67) among the leaves (Suren 1988). But Humphries and Frost (1937) found few pupae of **Chironomidae** (Figure 1) among the mosses in the River Liffey in any season, despite the huge numbers of larvae. Rather, most pupae are free-living in the open water (Armitage *et al.* 1995).



Figure 67. **Chironomidae** pupa, a rare find among bryophytes. Photo by Jason Neuswanger, with permission.

### Tube Makers

It is not unusual for **Chironomidae** larvae to make tubes. However, *Eukiefferiella endobryonia* (Figure 68) is unusual (Imada 2020). It lives in streams among the leaves of *Fontinalis dalecarlica* (Figure 69) and *Fontinalis novae-angliae* (Figure 70) and feeds on the leaves (Figure 71). It makes its "tubes" (more like a case) for pupation by



binding together a case from the leaves of *Fontinalis* (Figure 72), a truly aquatic moss. The third instar larva may use feces of mature larvae to build its case (Figure 73), but the fourth instar larva uses *Fontinalis* spp. leaves exclusively and it remains attached to the apical shoot of the moss (Figure 74-Figure 75). The larvae pupate in this moss case. Debris and other materials are deposited at one end of the case as the larva changes into a pupa (Figure 76-Figure 77). There are few other chironomids that make tubes exclusively of plant materials.



Figure 68. *Eukiefferiella endobryonia* 4th instar larva. Photo by Yume Imada, with permission.



Figure 69. *Eukiefferiella endobryonia* habitat in a colony of *Fontinalis dalecarlica* growing on the sides of pebbles in a gently flowing inlet. Photo by Yume Imada, with permission.



Figure 70. *Eukiefferiella endobryonia* habitat among *Fontinalis novae-angliae* occurring in a rapidly flowing stream at Sparks Lane, Tennessee, USA. Photo by Yume Imada, with permission.



Figure 71. *Eukiefferiella endobryonia* fourth-instar larva feeding on leaf margin of *Fontinalis dalecarlica*. Photo by Yume Imada, with permission.



Figure 72. *Eukiefferiella endobryonia* early fourth instar larva with undulating body in tube. Photo by Yume Amada, with permission.



Figure 73. *Eukiefferiella endobryonia* tube of third-instar larva, mostly built from feces of mature larvae. Photo by Yume Imada, with permission.





Figure 74. *Eukiefferiella endobryonia* case of *Fontinalis dalecarlica*. Photo courtesy of Yume Imada.



Figure 75. *Eukiefferiella endobryonia* pupa in its case. Photo by Yuma Imada, with permission.



Figure 76. *Eukiefferiella endobryonia* dissected leaf-rolling cases. Photo by Yume Imada, with permission.

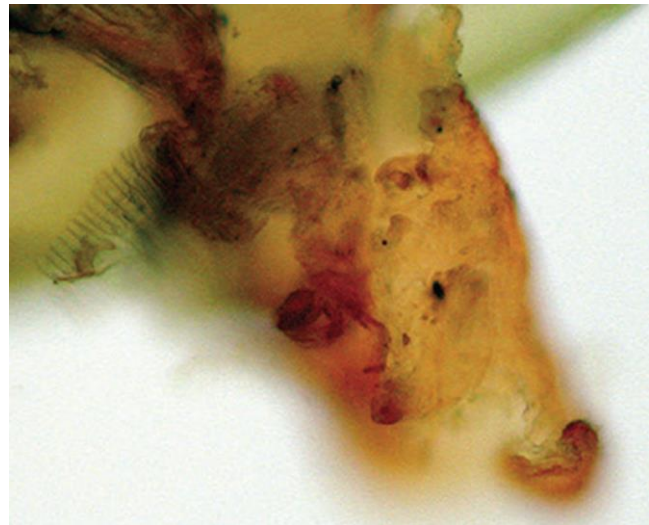


Figure 77. *Eukiefferiella endobryonia* amorphous, jelly-like silk mass spotted with detritus and diatoms, ripped off inner wall of end of pupal case. Photo by Yume Imada, with permission

### Culicidae – Mosquitoes

Although most mosquitoes are small, they can range 3-15 mm long (Bartlett 2004a). They are distributed worldwide and the larvae live almost anywhere there is quiet water. These larvae are able to feed on algae, Protozoa, and organic debris that is filtered from the water. Only a few are predaceous.

Bryophytes are not typical habitats for the mosquitoes. Nevertheless, Elgmork and Sæther (1970) found that *Aedes excrucians* (Figure 78; a woodland mosquito that bites humans) occurred in bog pools and occasionally among *Sphagnum* mosses (Figure 79).





Figure 78. *Aedes excrucians* larvae, inhabitants among *Sphagnum* and bog pools. Note the posterior breathing tube that often hangs from the water surface. Photo by Donald S. Chandler, through Discover Life.



Figure 79. *Sphagnum cuspidatum* and bog pool, suitable habitat for larvae of *Aedes excrucians*. Photo by Michael Lüth, with permission.

### Simuliidae – Blackflies

These are small flies, 1-5.5 mm (Kits 2005). They are best known for their nasty bite that leaves the wound bleeding due to an injection of an anticoagulant, although most species get their blood meal from birds. Although they are more abundant at higher latitudes, their distribution is worldwide in rapid, cold water. They are filter feeders and must therefore live on the surface of the substrate.

In the right habitat, blackfly larvae occur in large numbers (Figure 80). Blackfly larvae require fast flowing water where they can get sufficient oxygen and trap their food with their large head fans. Carlson (1967) suggested that at depths within 10 cm of the surface, the bryophytes offer a preferred habitat for the **Simuliidae**. In suitable sites, they can be quite dense; *e.g.*, one blade of grass 1 cm wide and 15 cm long can hold 300-800 *Simulium vittatum* (Figure 81) larvae (Anderson & Dicke 1960).

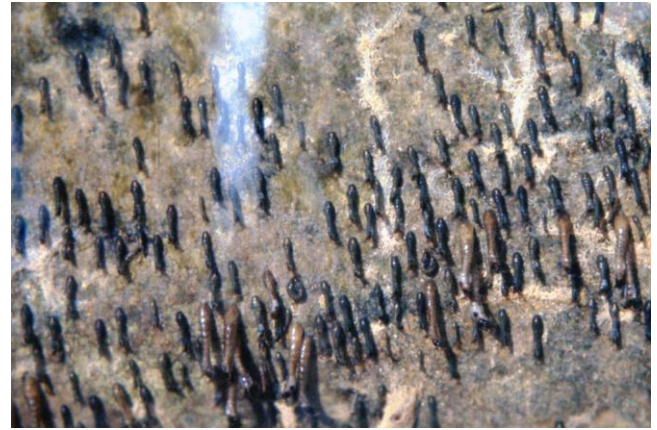


Figure 80. **Simuliidae** larvae on rock, showing how dense they can be. Photo by Janice Glime.



Figure 81. *Simulium vittatum tribulatum* complex larva, an abundant species on some bryophytes. Photo by D. S. Chandler <[www.discoverlife.org](http://www.discoverlife.org)>, through Creative Commons.

They are adapted to such sites by a circle of hooks on the abdominal posterior and on the prolegs, facilitating their anchorage (Arnold & Macan 1969). They furthermore produce silken threads that serve as anchors and that they use to cover the surfaces of stones to make a small mat to anchor themselves (Arnold & Macan 1969; Tarshis & Neil 1970). When water flow is stopped in a stream, larvae form both single silken threads and cables. The latter, supporting the greatest numbers of blackflies, reveal 25-50 threads with the larvae attached in concentric rings around the threads and cables (Tarshis & Neil 1970). The threads can be more than 1 m long and facilitate regaining the original position when falling from it or travelling to a new one (Rubtsov 1962). Tarshis and Neil (1970) observed a spectacular display of threads ranging 1-8 m long!

Many blackflies overwinter in the egg stage (*e.g.* *Simulium venustum* (Figure 82), *S. vittatum* (Figure 81) , but others hatch as early as December. Hatching of the eggs is apparently dependent on temperature, as noted in this family in Wisconsin, USA (Anderson & Dicke 1960). Larval development takes several weeks, 4-5 at temperatures of ~15-20°C, but the pupal stage is brief, lasting only 5-7 days. Wolfe and Peterson (1959) reported a unique use of stems of dead mosses to form the stalk on the pupal cocoon of *Ectemnia invenusta* (Figure 83). Depending on the local species, late summer and autumn often lack blackflies in bryophyte collections; at this time

some species are either in egg or adult stages (Anderson & Dicke 1960).



Figure 82. *Simulium venustum verecundum* complex, blackflies that overwinter as eggs. Photo by David S. Chandler, with permission.



Figure 83. *Ectemnia invenusta* larva, a blackfly that uses dead mosses to form its pupal stalk. Photo by Tom Murray, through Creative Commons.

Needham and Christenson (1927) reported **Simuliidae** from mosses in streams in northern Utah. In the Plitvice Lakes National Park in the Dinaric **karst** (landscape underlain by limestone eroded by dissolution, producing ridges, towers, fissures, sinkholes, *etc.*) region of Croatia, the **Simuliidae** showed a statistically significant preference for moss on **tufa** [porous limestone formed from calcium carbonate ( $\text{CaCO}_3$ ) deposited by springs *etc.*] and pebbles (Čmrlec 2013). This family is known from every continent but Antarctica (Clifford 2014).

In their experiments on the effects of phosphorus on Arctic streams, Lee and Hershey (2000) found that the moss *Hygrohypnum* (Figure 56) increased, forming dense growths. As one might expect, this changed the structure of the insect communities. Whereas some may have benefitted from an increase in periphyton abundance as a food source, the **Simuliidae** were apparently not affected by these changes. Since these larvae live at the surface and collect food from the passing water, the increased habitat complexity of the mosses did not change the available habitat for them.

In a Polish river, blackflies were in greater numbers on the tracheophyte *Potamogeton* than on the brook moss *Fontinalis* (Figure 59) (Niesiołowski 1980). Niesiołowski attributed this to the differences in leaf size and position that permitted the blackflies to live both at the water surface and on any of the lower leaves of *Potamogeton*. Blackflies are restricted to the surface region of the substrate where they can use their head fans to filter algae from the passing water, and in mosses this prevents them from living in the interior of the moss clumps.

Crosskey (1990) describes larvae in this family, stating that they use mosses as larval food as well as a substrate. As adults they use the mosses for mating.

The blackflies do not seem to be able to sort the food flowing by them. Anderson and Dicke (1960) found that all the food available in the flowing water was also present in the gut. In addition to these, the guts contained the diatoms *Rhoicosphenia* spp. (Figure 84) and *Cocconeis* spp. (Figure 85). The latter is a common diatom adhering to moss leaves (*pers. obs.*).

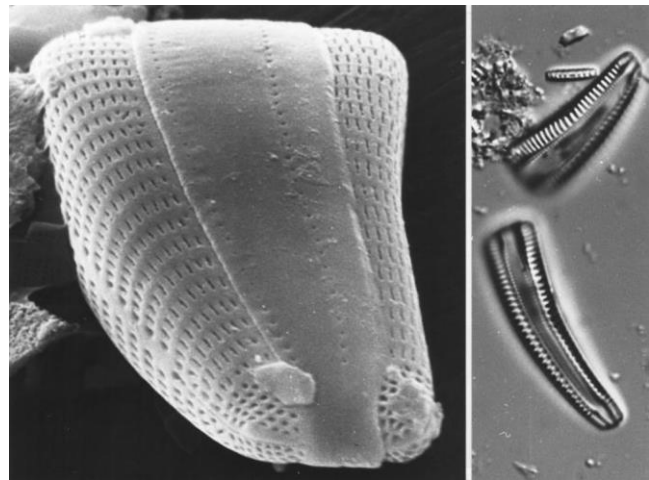


Figure 84. *Rhoicosphenia abbreviata*, member of a genus that is food for moss-dwelling blackflies. Photo by Pauli Snoeijs, through Creative Commons <[www.nordicmicroalgae.org](http://www.nordicmicroalgae.org)>.

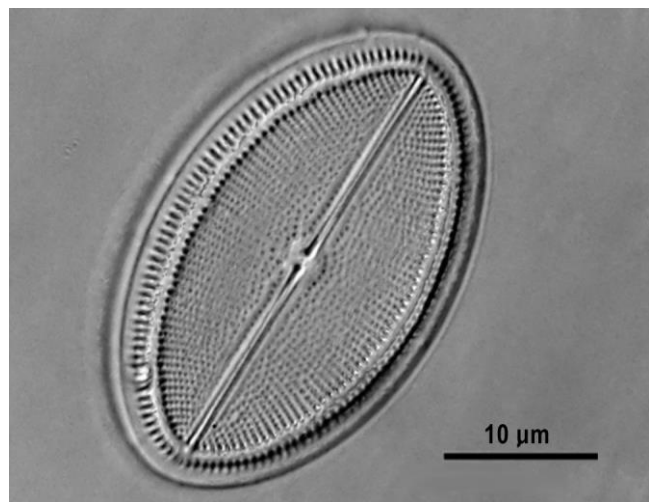


Figure 85. *Cocconeis placentula*, a diatom that embeds itself in the surface of bryophyte leaves and also serves as food for blackflies in streams. Photo by Ralf Wagner at <<http://www.dr-ralf-wagner.de/>> (Mikroskopie).



### *Simulium*

These larvae can be quite dense on their substrate. For example, *Simulium pictipes* is common in the eastern USA where larvae attach to bedrock of swift-flowing streams, especially below waterfalls (Kurtak 1974) where the water is well oxygenated. These larvae congregate, forming dense patches with as many as 50 individuals per cm<sup>2</sup>. Members of this species, and most blackflies, overwinter as larvae and are among the most abundant insects in winter. Reisen and Prins (1972) found that *Simulium* increased in the drift as the temperature increased. This genus has a low tolerance for temperatures above 16°C.

Butcher *et al.* (1937) suggested that *Simulium equinum* (Figure 86) apparently does not occur among mosses because it was absent in the River Tees above Croft. But Frost (1942) found it among mosses in the River Liffey, Ireland, in alkaline waters, along with *S. ornatum* (Figure 87). In acid waters of the same river she found *S. venustum* (Figure 82) and *S. latipes* (Figure 88) on bryophytes. Pentelow (1935) likewise found *S. equinum* in alkaline waters. But in a different river he found *S. ornatum*, likewise in alkaline water.



Figure 86. *Simulium equinum* s.l. adult, a blackfly whose larvae occur on mosses in some streams and not others in the same area. Photo by Malcolm Storey, Discover Life through Creative Commons.



Figure 87. *Simulium ornatum* / *intermedium* / *trifasciatum* adult, a blackfly complex whose larvae are common on bryophytes. Photo by Malcolm Storey through Discover Life.



Figure 88. *Simulium latipes* adult, a blackfly of mosses in acid waters. Photo by James K. Lindsey, with permission.

*Simulium cataractarum* (Figure 89), as its name implies, lives in waterfalls. It seems to play it safe, living primarily on the wet mosses on the rock wall beside the main waterfall Schroeder 1988).



Figure 89. *Simulium cataractarum* devouring an *Ephydriidae* larva. Photo by Simon Pollard, Department of Biological Sciences, University of Alberta, Canada.

In studying blackflies in Utah, USA, Peterson (1956) found that *Simuliidae* avoid algae-covered rocks and sticks. Rather, the dominant *Simulium* species occur primarily on rocks that are covered with mosses and the alga *Vaucheria*. Peterson found that these larvae would scrape algae and other food items from the surrounding substrate. But when only slimy algal films cover the rock, they are unable to attach. In his study of New York, USA, blackflies, Jamnback and Stone (1955) found several bryological associates. *Simulium fibrinflatum* (Figure 90) occurred on mosses at several locations, but also occurred on twigs and other types of vegetation.



Figure 90. *Simulium fibrinflatum* larva, a moss-dweller in streams in New York, USA. Photo by Donald S. Chandler, with permission.

In the Appalachian Mountain streams this family is common among the bryophytes, repeating many of the species reported by other studies in North America and Europe. These include *Simulium* cf. *gouldingi*, *S. impar*, *S. parnassum*, *S. tuberosum* (Figure 91), *S. venustum*-*S. verecundum* complex (Figure 82), and *S. vittatum* (Figure 81). The most widespread of these is *S. tuberosum*, appearing among all the common bryophytes: *Fontinalis dalecarlica* (Figure 4), *Hygroamblystegium fluviatile* (Figure 5) – *Platyhypnidium riparioides* (Figure 6), and *Scapania undulata* (Figure 7).



Figure 91. *Simulium tuberosum*, the most common blackfly on mosses and liverworts in Appalachian Mountain, USA, streams. Photo by Tom Murray, through Creative Commons.

The **Simuliidae** require a relatively rapid flow rate. For *Simulium ornatum* (Figure 87) this is a rate of at least 20 cm/sec in order to filter enough food items from the water using their head fans (Figure 92) (Harrod 1965). For *Simulium*, these head fans catch algal cells, especially diatoms, but also trap fragments of mosses and leaves [Puri 1925; Percival & Whitehead 1929 (*S. reptans*); Jones 1949, 1950]. Fredeen (1960, 1964) fed several members of *Simulium* [*S. venustum* (Figure 82), *S. verecundum* (Figure 82), *S. vittatum* (Figure 81), *S. arcticum*] on three species of bacteria as food and concluded that bacteria form an important food base for these blackflies in some streams. In these experiments, *Simulium arcticum* did not develop past the last larval instar, but all the others reached the adult stage. *Simulium venustum*, *S. verecundum*, and *S. vittatum* are widespread and commonly abundant species (O'Kane 1926; Anderson & Dicke 1960); bryophytes are not a unique habitat for them.

Hynes (1970) noted that members of the genus *Simulium* are able to coexist due to developmental timing. *Simulium reptans* and *S. variegatum* exemplify such timing differences with large larvae of one coexisting with small larvae of the other. In this way they don't compete for the same food sizes.

Peterson (1956) observed the emergence of *Simulium vittatum* (Figure 81). These newly emerged adults took flight almost immediately when they broke through the surface tension of the water, but they soon alighted to dry their wings. Others [*S. vittatum*, *S. decorum* (Figure 93- Figure 94)] crawled out of the water onto various substrata to dry their wings before their first flight.



Figure 92. **Simuliidae** larva head showing head fans that are used to trap food. Photo by Bob Henricks, with permission.



Figure 93. *Simulium decorum* larvae, blackflies that crawl out of the water to dry their wings before flight. Photo by Whitney Cranshaw, through Creative Commons.



Figure 94. *Simulium decorum* pupa with thin cocoon. Photo by Whitney Cranshaw, through Creative Commons.

As one might expect for a fly whose larvae live on mosses, the adults use them for egg-laying sites (Baba &



Takaoka 1989). *Simulium japonicum* and *S. rufibasis* both laid eggs on bryophytes on a water-splashed boulder. These were laid individually in the upper 5 cm of water.

Females seem to have some difficulty in laying their eggs where there is sufficient oxygen because these locations have high water velocity. Peterson (1956) observed several that dived into the water and reappeared 70 cm downstream. Several were washed downstream. Some of these flies seem to have two options – dropping eggs into the water while in flight and letting them settle to the bottom or climbing/diving into the water and depositing the eggs on a substrate. Surely these flies fare better when they choose bryophytes for their egg-laying.

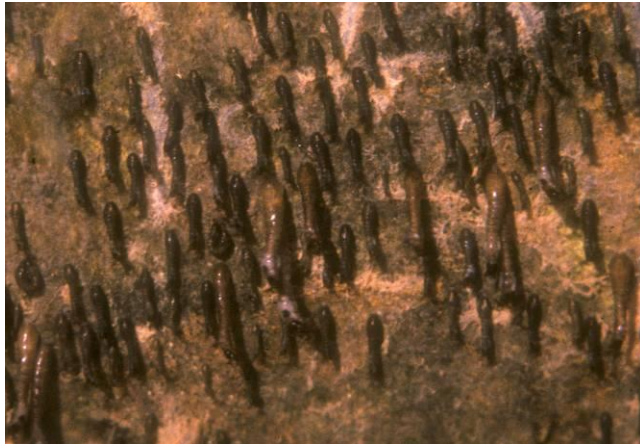


Figure 95. Blackfly (*Simuliidae*) larvae attach by tiny posterior hooks in fast current. Their heads with head fans point downstream and trap small particles of detritus, bacteria, algae, and even mosses for food. Photo by Janice Glime.

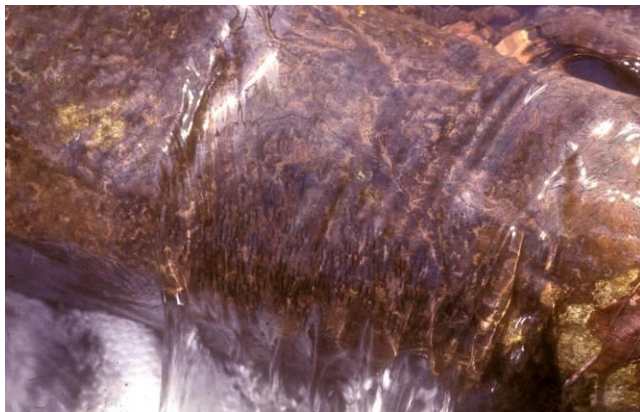


Figure 96. These blackfly larvae (*Simuliidae*) are just as common on these mosses as they often are on rocks in fast water. Larvae of the blackflies, *Simuliidae*, can use leaves of *Fontinalis* (Figure 59) in place of the usual net-like cocoon used to house the pupa. Photo by Janice Glime.

### *Prosimulium*

*Prosimulium* was a common genus among the bryophytes in my Appalachian Mountain stream study. Krno (1990) likewise found it among bryophytes in the River Rajčianka in Slovakia.

*Prosimulium fontanum* lives in forest and bog-fed streams (Davies & Syme 1958) where *Sphagnum* (Figure 62) influences the pH in the latter and may be an important

determinant of habitat suitability. This species commonly pupates in *Fontinalis* (Figure 59). Its cocoon is the least developed of all the *Prosimulium* species in three Ontario, Canada, streams.

It appears that this genus builds its cocoons based on flow rate and abrasive potential (Davies & Syme 1958). *Prosimulium fuscum* (Figure 97) lives in the fastest, most abrasive water of the three species studied and builds the strongest cocoon. The second in line is that of *P. mixtum* (Figure 98), an inhabitant of slower streams, that builds a somewhat weaker cocoon. Of these three, *P. fontanum* makes the weakest cocoon.



Figure 97. *Prosimulium fuscum*, a species that lives on bryophytes in very fast water. Photo by Donald S. Chandler, with permission.



Figure 98. *Prosimulium mixtum* larva lives on bryophytes in slower streams than those of *Prosimulium fuscum*. Photo by Donald S. Chandler, with permission.

The genus *Prosimulium* was common among bryophytes in Appalachian Mountain, USA, streams (Glime 1968). The most common was *Prosimulium hirtipes* (Figure 99-Figure 100, appearing among all the common mosses: *Fontinalis dalecarlica* (Figure 4), *Hygroamblystegium fluviatile* (Figure 5) – *Platyhypnidium riparioides* (Figure 6), and *Scapania undulata* (Figure 7). Others included *P. magnum* (mostly on *Hygroamblystegium fluviatile*), *P. mixtum* (Figure 98), and *P. rhizophorum*.





Figure 99. *Prosimulium hirtipes* among leafy liverworts. Photos by Janice Glime.



Figure 100. *Prosimulium hirtipes* is a common blackfly on stream mosses. Photos by Janice Glime.

*Prosimulium hirtipes* (Figure 99-Figure 100) avoids rocks with algal layers in a Utah, USA, stream, instead occupying those with mosses or the filamentous alga *Vaucheria*. In the mid-Appalachian Mountain streams, this species reaches its greatest abundance on the leafy liverwort *Scapania undulata* (Figure 7) (Glime 1968). In May one could find numerous pupae attached to the curled tips of the liverwort on both upper and lower surfaces. In June it was *Simulium tuberosum* that pupated there. This is a highly seasonal family, disappearing from June until the eggs hatch again in the cold water of late autumn (Davies *et al.* 1962).

Although some insects empty the gut rapidly, *Prosimulium hirtipes* (Figure 99-Figure 100) requires more than a week to empty its gut at 49-50°C (Davies 1949). Peterson (1956) found that at a lower temperature (4.4-10°C) it likewise takes more than a week for them to empty the gut. They can fill their guts in 20-26 hours (Davies 1949). This may permit them to digest intransigent materials that drift into their head fans.

*Prosimulium hirtipes* (Figure 99-Figure 100), *P. tomosvaryi*, and *P. subrufipes* use moist terrestrial mosses, mostly *Brachythecium rivulare* (Figure 101), for egg deposition, laying them about 20 cm above the streams (Davies 1949). Unlike those of many of the *Simuliidae*, the eggs are deposited in batches, sometimes quite large ones with as many as  $56 \times 10^6$  eggs. These eggs cannot survive complete desiccation, hence the need for mosses. Many eggs hatch in response to the diminishing temperatures and rainfall that saturates the mosses. But

others actually stay in the mosses and hatch in spring. The first instar larvae lack the distinctive head fans needed for filter feeding. Instead, the first instar feeds as a scraper in a stage that lasts 5-11 days at 10°C.



Figure 101. *Brachythecium rivulare* at the edge of a stream where some species of blackflies lay eggs. Photo by Janice Glime.

*Prosimulium kiotoense* in a stream on Kyushu Island, Japan, likewise oviposits among mosses on riverbank rock surfaces (Baba & Takaoka 1991). Although the eggs are laid singly, so many females select the same site that the eggs soon form large, irregular masses. These blackflies select dense bryophyte cover 0-15 cm above the water instead of depositing eggs in the water. Eggs are laid in late April when the air temperature rises to approximately 15°C. It appears that this above water position is sufficient to keep the eggs moist while they develop, permitting the larvae to take advantage of the June rainy season (and perhaps warmer temperatures for development).

### *Cnephia/Metacnephia*

I found larvae of *Cnephia mutata* (Figure 102) among mosses in my Appalachian stream study, but they were not as abundant as *Prosimulium* (Figure 97-Figure 100) or *Simulium* (Figure 86-Figure 95) (Glime 1968). Other aquatic bryophyte habitat studies I have found do not mention them.



Figure 102. *Cnephia* adult; larvae of *C. mutata* occasionally occur among mosses in mid-Appalachian, USA, streams. Photo by Sam Houston, with permission.



Meissner *et al.* (2009) conducted a fascinating experiment that explains the interesting relationship of the blackfly larvae of *Metacnephia pallipes* with the predator caddisfly *Rhyacophila nubila* (Figure 103) in Europe. In the absence of the predator, these blackflies show no preference between rocks and mosses. *Rhyacophila nubila* prefers stones only when the flow is slow. But, when *R. nubila* is present, the blackflies prefer mosses – the preferred habitat of the caddisfly! This seeming lapse in judgment by the blackflies must be examined in 3-d. The *M. pallipes* occupies the tips of branches, placing them at the surface of the moss clump, whereas *R. nubila* occupies the bases where they are protected from the rapid flow. When they attack the blackflies, the latter typically let go and enter the drift. If they are fast enough, they escape predation. They fully colonize artificial bryophytes (Finnturf) in only one day. The caddisflies are most successful in prey capture at intermediate velocities. For the blackflies to be safe from predation, they require velocities of 100 cm sec<sup>-1</sup>. The blackflies are a preferred food because they have high fat reserves (Wotton 1982; Crosskey 1990) and in this case seem to be the only food (Meissner *et al.* 2009).



Figure 103. *Rhyacophila nubila* larva, a predator that cohabits with the blackfly *Metacnephia pallipes* on mosses. Photo by Niels Sloth, with permission.

### **Stegopterna**

Pupae of the *Stegopterna mutata* complex (Figure 104-Figure 105) are often concealed among mosses in streams in Pennsylvania, USA (Adler & Kim 1986). Moving to mosses to pupate makes it easier for the adult to break through the surface tension to emerge.



Figure 104. *Stegopterna*, a genus that often moves to mosses to pupate. Photo courtesy of the State Hygienic Laboratory, University of Iowa, with permission.



Figure 105. *Stegopterna mutata-diplomutata* complex, with larvae that move to mosses to emerge from streams in Pennsylvania, USA. Photo by Donald S. Chandler, with permission.

In Slovakia, in the River Rajcianka, Krno (1990) found the genus *Odagnia*, a genus I have not found elsewhere in preparing for this chapter.

### **Thaumaleidae – Trickle Midges**

These are little fellows, 2-4.5 mm long (Carr 2013). They live mostly in the temperate areas of both hemispheres where their larval habitats are predominantly in vertical, thin water films alongside waterfalls and torrents where they are able to graze on diatoms.

Curran (1927) described *Thaumalea* adults (Figure 106) as occurring along streams, particularly those bordered by mosses. In the Appalachian Mountains, USA, I occasionally found larvae of this genus (Figure 107) among the stream mosses (Glime 1968). They may be more abundant among bryophytes elsewhere – typical stream sampling methods are likely to miss them in this habitat.



Figure 106. *Thaumalea* adult, an occupant along streams bordered by mosses. Photo by Kirk C. Tonkel, through Creative Commons.



Figure 107. *Thaumalea* larva, an occasional bryophyte dweller. Photo by J. C. Schou, with permission.

### **Psychodidae – Moth Flies and Sand Flies**

Larvae of this species are 3-10 mm long, but adults are smaller (1.5-4 mm) (Bartlett 2004b). They are worldwide,

but they are most common in the tropics. The larvae live mostly in organic sludge where they feed on algae, fungi, and bacteria, but a few wander into clean water where bryophytes may provide a habitat.

Usinger (1974) included mosses of quiet or slow-moving streams and splash areas among the typical habitats for members of this family in California, USA.

In Britain, the moss *Leptodictyum riparium* (Figure 108) has gotten the reputation of being a nuisance moss because of the **Psychodidae** and **Chironomidae** (Kelly & Huntley 1987). These insects breed in the organic and other particulate matter trapped by this moss in the brewery channels, causing swarms of insects.



Figure 108. *Leptodictyum riparium*, a stream and lake moss that is home for such nuisance **Diptera** as **Psychodidae** and **Chironomidae**. Photo by Michael Lüth, with permission.

Thorup (1963) found *Pericoma blandula* (Figure 109), a detritus feeder, living among mosses in a Danish springs. Satchell (1949) reported breeding of *Pericoma* among damp mosses. It, like other moss dwellers, has only one generation per year (**univoltine**) (Thorup 1963). The temperature among the mosses in the springs has almost no annual variation. Omelkova and Ježek (2012) likewise found this widespread European species among mosses in the Czech Republic in both shaded and unshaded habitats.



Figure 109. *Pericoma blandula* adult female; larvae live among mosses. Photo by Walter Pfliegler, with permission.

*Pericoma fallax* is a moss dweller that occurs in Europe and western Siberia where it is common in both shaded and unshaded habitats of ponds, swampy meadows, bottomlands of brooks, and reservoirs. In the streams of the Appalachian Mountains, USA, its larvae are fairly frequent among *Hygroamblystegium fluviatile* (Figure 5) and *Platyhypnidium riparioides* (Figure 6) colonies but not among those of the leafy liverwort *Scapania undulata* (Figure 7) or the large moss *Fontinalis dalecarlica* (Figure 4) (Glime 1968).

Both larvae and pupae of *Pericoma* (Figure 110) live in damp sites at the banks of streams in the UK, with mosses being a common habitat, sometimes with several species in a small (several meters) area (Satchell 1949; Roper 2001). *Pericoma albitarsis* lives among mosses in streams and among wet mosses near waterfalls (Johannsen 1969). In a Tennessee, USA, springbrook, this species lives among mosses and algae (Stern & Stern 1969; Stern & Stern 1969). The larvae of this genus are substrate feeders that eat the path in front of them (Vaillant 1959). They are able to do this even on a moss substrate. Vaillant found larvae of *Pericoma marginalis* and *Telmatoscopus* sp. (Figure 111) on a dripping rock cliff among mosses where diatoms were abundant. Egglshaw (1969) reported a species of *Pericoma* as being restricted to moss. In the southern Appalachian Mountains, Haefner and Wallace (1981) found that densities of *Pericoma* were five times as high in moss-covered outcrops compared to non-moss areas of a first-order stream.



Figure 110. *Pericoma* larva, a frequent bryophyte dweller. Photo from <www.dfg.ca.govpng> through public domain.



Figure 111. *Telmatoscopus* (*Clogmia*) larva. Some members live on dripping cliffs among mosses. Photo by Ashley Bradford, through Creative Commons.

In the Ghyll woodlands of Sussex, UK, several other members of this family are moss dwellers (Roper 2001). These include *Bazarella neglecta* larvae among mosses around mill races and waterfalls. *Bazarella subneglecta* is an uncommon Eurasian species from hygropetric (water on a vertical surface) ones with moss cushions, spring areas, and brooks (Omelkova & Ježek 2012). Ježek *et al.* (2012) reported *Peripsychoda fusca* from Czech Republic and Slovakia wetland habitats that have moss cushions and leaf packs.



Larvae of the moth fly *Sycorax silacea* (see Figure 112) live on wet stones and mosses near cascades, springs, and "trickles" (Jung 1958; Andersen 1992). Omelkova and Ježek (2012) reported this species from European spring areas and from mosses in running water habitats and their "neighborhoods." The ornate larvae in this genus are protected from would-be predators by mimicking mosses (Roper 2001).



Figure 112. **Psychodidae** larva, a family that occurs among bryophytes in small numbers. Photo by Erin Hayes-Pontius, through Creative Commons.

*Jungiella longicornis* is widely distributed in Europe and western Siberia, living in both unshaded and shaded stream banks among moss cushions, as well as in ponds and forest seepages (Omelkova & Ježek 2012). *Satchelliella crisp*i inhabits decaying organic matter in Europe, typically in leaf packs or moss cushions near springs and streams. *Satchelliella pilularia* is widespread in Europe, but is nevertheless relatively rare; its larvae live among mosses in running water of springs and streams from lowlands to mountains.

*Ulomyia fuliginosa* (Figure 113) is among the most common of European **Psychodidae** (Omelkova & Ježek 2012). It lives among mosses in running water where it associates with detritus and in springs, streambanks, marshes, swampy meadows, and forest pools.



Figure 113. *Ulomyia fuliginosa* adult, a species whose larvae live among mosses in running water. Photo by James K. Lindsey, with permission.

*Berdeniella* (Figure 114) larvae are also known to live among mosses (Troiano 1981) and are particularly abundant in alpine streams (Withers 2005). Wagner *et al.* (2011) contend that this genus lives exclusively among partly or totally inundated mosses at the shoreline of cold mountain streams in Central Europe, based on their study of the Breitenbach. In these habitats they found *B. illiesi*, *B. manicata*, and *B. unispinosa*.



Figure 114. *Berdeniella* sp., as genus whose larvae live among alpine stream bryophytes, showing the posterior of the larva. Photo by Urna S. Kruus, with permission.

## Summary

The two most common dipteran bryophyte dwellers are the **Chironomidae** and **Simuliidae**. The **Chironomidae** in particular can have many species within a single stream. **Chironomidae** have a wide range of habitats and temperatures and are tolerant of low oxygen and slow flow. **Simuliidae**, on the other hand, require cold temperatures and rapid flow with high oxygen content. **Chironomidae** eat mostly detritus that they can scavenge from that trapped by the bryophytes or available in the sediments, whereas the **Simuliidae** filter the detritus and microalgae from the water using their head fans.

Both families can overwinter among the bryophytes as larvae and emerge in spring or early summer. Both use the bryophytes for emergence, but the **Simuliidae** commonly pupate there whereas the **Chironomidae** are more common in open water as pupae.

Bryophytes can serve as a refuge from predators for both families. And in some cases, it appears that the bryophytes may protect the **Chironomidae** larvae from parasites, although the mechanism is unclear.

Other **Nematocera** of families of much less importance include the **Culicidae** (quiet water), **Thaumaleidae** (beside waterfalls), and **Psychodidae** (quiet or slow-moving water).

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# **CHAPTER 11-14**

## **AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER BRACHYCERA**

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# CHAPTER 11-14

## AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER BRACHYCERA



Figure 1. *Limnophora* sp. larva (**lower**) and pupa (**upper**) (*Muscidae*), occasional bryophyte inhabitants. Photo by Stephen Moore, Landcare Research, NZ, with permission.

### DIPTERA – FLIES

#### Suborder Brachycera

This suborder is less aquatic than the *Nematocera*. Furthermore, few of its members use aquatic bryophytes. Nevertheless, it is a convenient way to break up the chapter into shorter segments.

#### Athericidae/Rhagionidae – Watersnipe Flies

The larvae of these flies occur in pristine streams with the adults nearby (Kits 2005). They include predaceous members that eat other invertebrates, including caddisflies, and saprophagous members on wooden debris (Athericidae 2014). The larvae are distinguished by **crochets** on their abdominal prolegs (Figure 2), permitting them to live in rapid montane streams and torrents without being washed away.



Figure 2. *Atherix ibis* larva showing crochets in two rows in each proleg. Photo by Urmas Kruus, with permission.



This family is not well represented among bryophytes. *Atherix ibis* (Figure 3) includes bryophytes among its substrates in streams (Neveu 1976). The larvae eat small invertebrates (McLeod 2005), most likely finding the bryophytes to serve as an adequate dinner table. In Carpathian streams, this species is positively correlated with stream order and warmer water temperatures (Bulánková & Duricková 2009). Its eggs are laid on overhanging leaves and hatched larvae slide into the water; the larvae are henceforth very sensitive to desiccation. They are, however, quite tolerant of human activity and pollution.



Figure 3. *Atherix ibis* larva, a stream-dweller that can be found among bryophytes. Photo by Niels Sloth, with permission.

In the acid streams in the Appalachian Mountains, USA, *Atherix variegata* occurred in all of the common moss habitats [*Fontinalis dalecarlica* (Figure 4), *Hygroamblystegium fluviatile* (Figure 5), *Platyhypnidium riparioides* (Figure 6), and *Scapania undulata* (Figure 7)] (Glime 1968).



Figure 4. *Fontinalis dalecarlica* with capsules, home to *Atherix variegata* in Appalachian Mountain, USA, streams. Photo by Janice Glime.



Figure 5. *Hygroamblystegium fluviatile*, home to *Atherix variegata* in Appalachian Mountain streams. Photo by Janice Glime.



Figure 6. *Platyhypnidium riparioides*, home to *Atherix variegata* in Appalachian Mountain streams. Photo by Andrew Spink, with permission.



Figure 7. *Scapania undulata*, home to *Atherix variegata* in Appalachian Mountain streams. Photo by Michael Lüth, with permission.

In the Plitvice Lakes National Park in the Dinaric karst region of Croatia, the *Athericidae* preferred moss on tufa ( $P < 0.05$ ,  $n = 12$ ) (Čmrlec *et al.* 2013). These flies pupate on mosses, and that substrate is the preferred substrate for emergence of the adults (Thomas 1997; Čmrlec *et al.* 2013).

### Spaniidae/Rhagionidae

This family, well known from records in amber, exhibits only scattered records throughout the world today (Arillo *et al.* 2009). Roper (2001) reported the bryophyte dweller *Spania nigra* (Figure 8), a snipe fly, from ghyll (deep ravine) woodlands in Sussex, UK (Roper 2001).

### Dolichopodidae – Long-legged Flies

These are small (1-9 mm) flies with a worldwide distribution (Dolichopodidae 2015). The larvae are predominantly terrestrial, but there are also many semi-aquatic taxa that live in or near water margins. Some can even walk on the water surface. Larvae are typically predatory, although a few live in the stems of reeds and other monocots near water.





Figure 8. *Spania nigra* adult, a species with a larval bryophyte dweller in Sussex. Photo by Marko Mutanen through Creative Commons.

This family does not seem to be reported as a moss dweller, but it does occasionally live among mosses in the Appalachian Mountain, USA, streams (Glime 1968). I was able to identify *Hydrophorus* larvae (Figure 9-Figure 10) in these collections. But it is also possible that they fell in or got swept in by flooding.



Figure 9. *Hydrophorus oceanus* larvae, member of a genus that sometimes occurs among stream bryophytes. Photo by Hans Hillewaert, through Creative Commons.

### Empididae – Dance Flies

These are small flies with a worldwide distribution and that can be aquatic, but can also live in semiaquatic habitats, in dung, in bird nests, among roots, and associated with fungi (Cresswell 2004). Larvae mostly feed on decaying matter, but also can be predatory.



Figure 10. *Hydrophorus praecox* adult, member of a genus that can be found among Appalachian Mountain stream bryophytes. Photo by James K. Lindsey, with permission.

The **Empididae** (Figure 11) are little flies, so it is not any surprise to find them among mosses as larvae. In fact, larvae and pupae of many species occur among mosses in streams (Ivković *et al.* 2007).



Figure 11. **Empididae**, a frequent larva on bryophytes in streams. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Because of their small size and the tedious process of sorting through moss samples, this family is not well known among the mosses and more species are likely to be found on close observation. Pusch and Wagner (1993) found and described the new species *Bergenstammia aurinae* in the eastern Alps where it lived among wet mosses in two small brooks with a steep elevation gradient but no glacial melt water.

In the Plitvice Lakes National Park in the Dinaric karst region of Croatia, the **Empididae** preferred moss on tufa and macrovegetation where they have shelter and food (Watson & Rose 1985; Nolte 1991; Linhart *et al.* 1998, 2002a, b, c; Ivković *et al.* 2007). Emergence was almost equal above substrates of moss on tufa, pebbles, and tufa with detritus (Ivković *et al.* 2012).

Suren (1991) experimented with artificial bryophytes in two New Zealand alpine streams. He found that whereas most insects had densities similar to that on natural bryophytes, the **Empididae** had lower densities on the artificial ones, suggesting that the bryophytes themselves have an important role for these larvae.



### Fast-water Refuge

Those larvae that are truly aquatic stream-dwellers usually live among the mosses in fast water. Ivković *et al.* (2012) recorded the highest abundance of dance flies from Plitvice Lakes National Park, Croatia, in stream habitats that had moss, gravel, and particulate tufa with detritus and fast current. In Malaysia, larvae of *Hemerodromia* (Figure 12-Figure 13) live at least 10 cm beneath the water surface in the **hyporheic** zone (Grootaert 2004). They are sensitive to light and disappear from streams when the forest is gone. Light plays an important role in their mating – a behavior that earns them the name of dancing flies. Unlike many Diptera that rely on gills or spiracles, the aquatic larvae of *Hemerodromia* exchange oxygen directly from the water, whereas many other members of the family use spiracles positioned to be in direct contact with the air. Larvae are predacious and often feed on their cohabitants such as blackflies or **Chironomidae** (Vaillant 1951, 1967; Vaillant & Gagneur 1998; Grootaert 2004). The adults are small (3-5 mm) are mostly yellow or black and prefer boulders covered with moss or a splash zone where moisture loss is not a problem (Grootaert 2004). In Europe, *H. praecatoria* (syn. of *Chelifera praecatoria*?) live among mosses in nearly stagnant water (Bischoff 1924b; Johannsen 1969). In Belgium this species occurs in pools of *Sphagnum* bogs (DipteraInfo 2014). This same genus occurred among *Fontinalis dalecarlica* (Figure 4) in Appalachian Mountain, USA, streams (Glime 1968). The species resembled *H. rogatoris* and *H. seguyi*.



Figure 12. *Hemerodromia* larva, a frequent bryophyte inhabitant. Photo courtesy of the State Hygienic Laboratory, University of Iowa, with permission.

Bischoff (1924a) reported that the genus *Clinocera* occurred (Figure 14-Figure 15) among mosses in swift streams. In Malaysia, the larvae, like those of *Hemerodromia*, live at least 10 cm below the water surface in the hyporheic zone and exchange oxygen directly through the cuticle (Grootaert 2004). Sinclair (2000) described a new species, *Clinocera gressitti* (Figure 14), from mosses on submerged stones in New Zealand. Adrian Plant (pers. comm. 27 August 2014) observed that members of this genus often pupate (Figure 15) among the mosses.



Figure 13. *Hemerodromia superstitiosa* female adult, member of a genus with moss-dwelling larvae. Photo by Seth Burgess, through Creative Commons.



Figure 14. *Clinocera* larva, an inhabitant of mosses in swift streams. Photo from <www.dfg.ca.gov>, through public domain.



Figure 15. *Clinocera nigra* pupal exuvia. Photo by Adrian Plant, with permission.

In a springbrook in the Southern Alps of New Zealand, Cowie and Winterbourn (1979) found three zones of bryophytes. In the torrential waters near the middle of the channel, **Empididae** (Figure 11) were among the most abundant species living among *Fissidens rigidulus* (Figure 16). Not surprisingly, these were accompanied by several abundant species of **Chironomidae** (see Chapter 11-13b).



Figure 16. *Fissidens rigidulus*, home for **Empididae** in torrents. Photo by Bill and Nancy Malcolm, with permission.

In a German stream, larvae of *Wiedemannia bohemani* (see Figure 17) were abundant in the middle reach, with many occurring in partly submerged mosses on stones, both at and below the water level (Wagner & Gathmann 1996). Vaillant (1967) likewise found both larvae and pupae of *Wiedemannia* in streams and rivers of France, with adults remaining nearby on stones that were partially submerged. The larvae feast on the **Chironomidae** that are so abundant among mosses.



Figure 17. *Wiedemannia bistigma* emerging on stones. Photo by Adrian Plant, with permission.

Harper (1980) found that *Hemerodromia* (Figure 12-Figure 13), *Neoplasta* (Figure 18-Figure 19), and *Roederiodes* (Figure 20) in the Laurentian watershed, Quebec, Canada, typically inhabit the mainstream and the larger tributaries. These species usually prefer fast water with a substrate of moss and rubble.



Figure 18. *Neoplasta* larva, a bryophyte inhabitant. Photo from <dfg.ca.gov>, through public domain.



Figure 19. *Neoplasta* adult, a genus with larval bryophyte inhabitants. Photo by Adrian Plant, with permission.



Figure 20. *Roederiodes recurvatus* adult, a genus whose larvae are associated with mosses in fast water in the Laurentian watershed of Canada. Photo from Biodiversity Institute of Ontario, through Creative Commons.

*Hemerodromia* (Figure 12-Figure 13) larvae occur primarily in lotic habitats and among mosses on stream



cobble (Merritt & Cummins 1996), but also live in mosses at or just above the water level (Brammer *et al.* 2009). Larvae of *Hemerodromia* consume blackfly larvae that are living on the mosses (Vaillant 1953). Some of these **Empididae**, especially *Hemerodromia*, larvae have an interesting habitat choice, living in cases and nets of other insects. Larvae of the *Hemerodromia empiformis* complex have been found inside the tubes of the midge *Rheotanytarsus* (Figure 21-Figure 22) in southern California, USA. The last instar larvae and pupae of *H. brevifrons* have been found inside cocoons of **Simuliidae** (Figure 23) in a stream in Los Angeles County, California, USA. Pupae of a South American *Neoplasta* (Figure 18) can occur inside cocoons of caddisflies (Brammer *et al.* 2009). Thus their habitation of mosses may be indirect.



Figure 21. *Rheotanytarsus exiguus* larval tubes made by the moss inhabitant larvae, but these tubes also house the larvae of *Hemerodromia empiformis*. Photo by D. N. Bennett, with permission.



Figure 22. *Rheotanytarsus* sp. larva from the above tubes. This genus inhabits mosses and other sites. Photo by Jason Neuswanger, with permission.



Figure 23. *Simulium aureum* pupa with cocoon where the empidid *Hemerodromia brevifrons* sometimes lives. Photo by Malcolm Storey, Discover Life, through Creative Commons.

### Where Shall We Go for Dinner?

Some adult members of the family devour their food from invertebrates trapped by the surface film. *Wiedemannia bistigma* (Figure 24) adults climb about on floating algae for just this purpose (Laurence 1953). Like maggots on a road kill, the empidids gather in numbers on the carcass of a dead insect. This adult behavior may not be as effective for most larval bryophyte-dwellers because the bryophyte habitats are often in fast water.



Figure 24. *Wiedemannia bistigma* adult, a species whose larvae can live among stream mosses. Photo by Adrian Plant, with permission.

**Empididae** larvae include both predaceous and non-predaceous larvae (and adults) (Oldroyd 1964). Many species of the subfamily **Hemerodromiinae** live in streams where their predatory larvae live among mosses and on wet rocks (Gerson 1969; Roper 2001). Some members are predators on larval blackflies (Vaillant 1951, 1953; Sommerman 1962; Wirth 1983; Werner & Pont 2003).

### Empididae in the Cold

The **Empididae** are particularly adept at surviving cold conditions, whereas most insects lack cold resistance (Irons *et al.* 1993). Nevertheless, they cannot survive temperatures even 1°C below zero. In Alaska many insects survive by moving away from a freezing front or living in one that will not freeze. The **Empididae**, like the **Chironomidae**, will spend the winter in a frozen habitat. The **Empididae** have a high survival rate under freezing and thawing conditions. The ice serves as insulation

against sub-zero temperatures, with flowing water remaining typically at about 0.8°C.

### Oreogetonidae

The **Oreogetonidae** is a small family, a segregate from the **Empididae** (Bayless 2011). The larvae are freshwater carnivores (Cresswell 2004). The family is widespread, with a concentration in South America, but also occurring in North America, Europe (one species), Asia, Australia, and New Zealand (Oreogetonidae 2014).

The genus **Oreogeton** (Figure 25) associates with mosses, but they are sprawlers-burrowers that engulf their prey, including blackflies and caddisflies (Aquatic Insects 2008; National Park Service 2014). These prey insects may be the reasons they enter the moss realm.



Figure 25. *Oreogeton* sp. adult. Larvae in this genus are sprawler-burrowers among mosses, feeding on blackflies and caddisflies. Photo by Tom Murray, through Creative Commons.

### Syrphidae – Hoverflies

These worldwide flies are mostly 10-20 mm long, but can range up to 35 mm (Bartlett 2004). Many of the terrestrial larvae live in ant nests, but some occur in bogs. The larvae are mostly predators, although the family include a wide range of food sources. Some aquatic members have a long breathing tube, earning them the name of rat-tailed maggots. *Sericomyia borealis* (Figure 26) larvae occur in pools of peat bogs (Bloomfield 1897).



Figure 26. *Sericomyia silentis* adult, member of a genus in which some larvae live in bog pools. This one, like many syrphids, is a bee mimic. Photo by Richard Bartz, through Creative Commons.

### Ephydriidae – Shore-flies

The name **Ephydriidae** literally means "living on the water" (Moisset 2004). The larvae filter microorganisms, including bacteria, one-celled algae, and yeasts, but some are predators on **Chironomidae** larvae. They are small to medium in size (2.5-9 mm) and have a worldwide distribution.

This is not typically a bryophyte family. *Discocerina* (Figure 27) burrows into moss mats or lives among algae at the borders of streams, ponds, and lakes (Merritt *et al.* 1996). *Gymnoclasiopa plumosa* (see Figure 28) breeds in algae and mosses in the forest (Grünberg 1910).



Figure 27. *Discocerina obscurella* adult, a genus that burrows into moss mats at water's edge. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.



Figure 28. *Gymnoclasiopa taxoma* adult. *Gymnoclasiopa plumosa* breeds in forest mosses. Photo from USFWS, through public domain.

### Sciomyzidae – Marsh Flies

The **Sciomyzidae** family (Figure 29-Figure 30) has worldwide distribution. The adults are 5-10 mm long and



live around marshes, lakes, ponds, and wooded areas, but the larvae are aquatic (Leung 2004). These larvae feed on snails, either as predators or parasites. *Poecilographa decora* is the only American species in this genus (Usinger 1974). Its pupae are known from woodland mosses.



Figure 29. *Sciomyzidae* larva indicating spiracular disc. Photo by Stephen Moore, Landcare Research, NZ.



Figure 30. *Sciomyzidae* pupa; some species pupate among mosses. Photo by Stephen Moore, Landcare Research, NZ.

### Agromyzidae – Leaf-miner Flies

The *Agromyzidae* are 1-5 mm long and are leaf miners (Murray 2005). Although these are mostly miners on tracheophytes, the *Agromyzidae* are known from liverworts from scattered locations around the world in such distant locales as the West Indies, Mexico, Peru, the Juan Fernandez Islands, New Zealand, and France (Spencer 1990).

The leaf miner *Phytoliriomyza mesnili* (see Figure 31) develops successfully on the floating liverwort *Ricciocarpus natans* (Figure 32) (d'Aguilar 1945). It also occurs on *Riccia beyrichiana* (Figure 33) where the larva feeds within the thallus, then pupates there. This miner is known exclusively from liverwort and hornwort thalli.



Figure 31. *Phytoliriomyza melampyga* larva showing leaf mine trail in a tracheophyte leaf. Photo by Malcolm Storey.



Figure 32. *Ricciocarpus natans*, a suitable thallus for development of *Phytoliriomyza mesnili*. Photo by Jan-Peter Frahm.



Figure 33. *Riccia beyrichiana* with eggs deposited in a cavity made on the left thallus. This liverwort species serves as home for larvae of the agromyzid fly *Phytoliriomyza mesnili*. Photo by Malcolm Storey, DiscoverLife, Creative Commons.



## Muscidae – House Flies and Kin

This is a worldwide family whose larvae live in dung, carrion, soil, nests, decaying vegetation, and less commonly among bryophytes in running water (Balaban & Balaban 2004). Adults range 2-14 mm in length (Muscidae 2015).

Many species of *Limnophora* (Figure 1, Figure 34- Figure 35) carry out their larval development among mosses and liverworts in running water where they are able to prey on **oligochaetes** (segmented worms such as earthworms) and small insect larvae (Glime 1968; Skidmore 1985; Roper 2001). In the Appalachian Mountain, USA, streams these occur most abundantly among clumps of *Hygrohypnum luridum* (Figure 36), especially in small waterfalls (Glime 1968). Axelrod and Vorderwinkler (1983) found that the European muscid fly *Limnophora riparia* (Figure 35) prefers mosses as a substrate; it is a good place to eat chironomid, blackfly, and other larvae (Wotton & Merritt 1988). This species typically lives among bryophytes in waterfalls, splash zones, and lake outlets. When the larvae were placed under water in enamel trays, all of them drowned within 24 hours. They burrow into any possible substrate to avoid light.



Figure 34. *Limnophora* adult, a genus where some members use mosses for egg-laying, larvae, and pupae. Photo by Luis Miguel Bugallo Sánchez, through Wikipedia Commons.



Figure 35. *Limnophora riparia* larva, a species that lays its eggs, develops, and pupates in mosses as a preferred site. Photo by Niels Sloth, through Creative Commons.



Figure 36. *Hygrohypnum luridum*, home to *Limnophora* larvae in mid-Appalachian waterfalls. Photo by Hermann Schachner, through Creative Commons.

The larvae of *Limnophora riparia* (Figure 35) hatch from the egg as a third instar larva and are immediately ready to prey upon living invertebrates (Merritt & Wotton 1988). One of their peculiar adaptations is to attach the anterior of their prey and to remove and digest the contents of the head and body, leaving the cuticle and guts behind. The life cycle is synchronized with the main prey item, larvae of the blackfly *Simulium noelleri*, and other invertebrate prey items so that there is always plenty of food for the developing larva. When the larva matures, it continues to select mosses for its site to pupate.

Badcock (1949) found that the muscid *Calliophrys* only occurs in mosses on the vertical face of a waterfall in the Welsh Dee.

## Summary

The **Brachycera** are mostly terrestrial, but a few have associations with the aquatic bryophytes. Among these, the **Empididae** are probably the most common. Bryophytes seem to be important to them as they colonize bryophytes more readily than they colonize artificial bryophytes. Both larvae and pupae live among the bryophytes. And like the bryophytes, they are often in stream openings that don't freeze.

The most interesting family to a bryologist includes those few members of the leaf miners (**Agromyzidae**) that live exclusively in the tissues of thallose bryophytes – liverworts and hornworts. As such, the thalli provide both protection and food.

Some members of the **Ephydriidae** burrow into the mosses at the borders of streams and ponds. **Sciomyzidae** larvae live in the water, but the pupae occur among woodland mosses. Even some **Muscidae** complete their larval development among aquatic bryophytes. Other families with a few members living in association with aquatic or predominantly wet bryophytes are **Athericidae**, **Spaniidae**, **Dolichopodidae**, **Oreogetonidae**, **Syrphidae**, and **Sciomyzidae**.



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