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

TABLE OF CONTENTS

Suborder Nematocera............................................................................................................. 11-13b-2
Chironomidae – Midges ........................................................................................................ 11-13b-2
   Emergence ......................................................................................................................... 11-13b-4
   Seasons ............................................................................................................................. 11-13b-5
   Cold-water Species .......................................................................................................... 11-13b-6
   Overwintering .................................................................................................................. 11-13b-7
   Current Velocity ............................................................................................................ 11-13b-7
   Diversity .......................................................................................................................... 11-13b-8
   Bryophyte Preferences? ................................................................................................. 11-13b-15
   What's for Dinner? ........................................................................................................... 11-13b-16
   Parasite Protection? ......................................................................................................... 11-13b-17
   Refuge in Bryophytes .................................................................................................... 11-13b-18
Culicidae – Mosquitoes ........................................................................................................ 11-13b-18
Simuliidae – Blackflies ....................................................................................................... 11-13b-18
   Simulium ........................................................................................................................ 11-13b-20
   Prosimulium ................................................................................................................... 11-13b-22
   Cnephia/Metaenephia ...................................................................................................... 11-13b-24
   Stegopterina .................................................................................................................. 11-13b-24
Thaumaleidae – Trickle Midges ........................................................................................ 11-13b-25
Psychodidae – Moth Flies and Sand Flies ...................................................................... 11-13b-25
Summary .............................................................................................................................. 11-13b-27
Acknowledgments ............................................................................................................... 11-13b-27
Literature Cited .................................................................................................................. 11-13b-27
CHAPTER 11-13b
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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. Hyne (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; Chatha 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.](image)

**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 m² 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 submerged mosses had approximately five times as many larvae as those that were semi-submerged. 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.](image)

![Figure 5. Hygroamblystegium fluviatile, a moss that is home to large numbers of Chironomidae. Photo by Hermann Schachner.](image)
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).

Usinger (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.

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).

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).

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.
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 Saether (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.

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.

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. aducta are cold-water species that are crenobionts (living in springs) (Fittkau 1962). They prefer mosses in soft water. Macropelopia notata occurs in rheo-hygroptetic 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
Ravnkilde, 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.

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.

**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⁻¹.
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.

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, Thienemania cf. gracils (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.

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.

Figure 30. *Paraphaenocladius* 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.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Habitat</th>
<th>References</th>
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<tbody>
<tr>
<td><em>Ablabesmyia costalis</em></td>
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Available images follow the table.
Corynoneura sp. River Liffey, Ireland larvae & pupae in European alpine
Corynoneura lobata *Drepanocladus revolvens*, Alberta, Canada Humphries & Frost 1937; Frost 1942; Thienemann 1936
Cricotopus sp. *Drepanocladus revolvens*, Alberta, Canada Boerger et al. 1982
Cricotopus bicinctus Boerger et al. 1982
Cricotopus miricornis European alpine Thienemann 1936
Cricotopus longipennis European alpine Thienemann 1936
Cricotopus trifasciatus *Drepanocladus revolvens*, Alberta, Canada Boerger et al. 1982
Cryptochironomus sp. River Liffey, Ireland Humphries & Frost 1937; Frost 1942
Cryptochironomus atratus Thienemann 1936
Culicoides rivicola European alpine Thienemann 1936
Culicoides neglectus (nom dub) pupae in European alpine Thienemann 1936
Diamesa sp. River Liffey, Ireland Humphries & Frost 1937; Frost 1942
Diamesa fissipes gr. European alpine Thienemann 1936
Diamesa prolongata pupae in European alpine Thienemann 1936
Diamesa steinboeki European alpine Thienemann 1936
Diamesa tonsa pupae among mosses in European alpine Thienemann 1936
Diplocladius cultriger *Drepanocladus revolvens*, Alberta, Canada Humphries & Frost 1937; Frost 1942
Endochironomus sp. European alpine streams Thienemann 1936
Eukiefferiella alpestris River Liffey, Ireland Thienemann 1936
Eukiefferiella brevicalcar River Liffey, Ireland Thienemann 1936
Eukiefferiella caerulea European alpine streams Thienemann 1936
*Eukiefferiella caerulea* larvae among Fontinalis; pupae among mosses River Liffey, Ireland Thienemann 1936
Eukiefferiella lobifera European alpine streams Thienemann 1936
Eukiefferiella minor European alpine streams Thienemann 1936
Eukiefferiella subalpina European alpine streams Thienemann 1936
*Eutanytarsus inmermepes* *Drepanocladus revolvens*, Alberta, Canada Humphries & Frost 1937; Frost 1942
Heterotrissocladius sp. River Liffey, Ireland Humphries & Frost 1937; Frost 1942
Heterotrissocladius changi Drepanocladus revolvens
Krenosmittia Drepanocladus revolvens
*Labrudinia pilosella* Drepanocladus revolvens
Limnophyes borealis Drepanocladus revolvens
Limnophyes globifer Drepanocladus revolvens
Limnophyes prolongatus Drepanocladus revolvens
Macropelopia sp. River Liffey, Ireland River Liffey, Ireland
Macropelopia advena River Liffey, Ireland
Macropelopia notata River Liffey, Ireland
Metriocnemus in high mosses of high mountain brooks of Europe Thienemann 1936
Metriocnemus cuneatus Colorado Rocky Mountain, USA, streams Elgmark & Sæther 1970
Metriocnemus fascipes Thienemann 1936
Metriocnemus hygropericus Thienemann 1936
Microspectra sp. European alpine streams Thienemann 1936
Microtendipes sp. River Liffey, Ireland Thienemann 1936
Microtendipes pedellus Europe European alpine streams Harper & Cloutier 1979
Nanocladius sp. River Liffey, Ireland
Nanocladius bicolor River Liffey, Ireland
Neostemplina thienemanni *Drepanocladus revolvens*, Alberta, Canada Boerger et al. 1982
Orthocladius luteus European alpine streams Thienemann 1936
Orthocladius obidens River Liffey, Ireland River Liffey, Ireland
Orthocladius rivicola European alpine streams Thienemann 1936
Orthocladius sasicola River Liffey, Ireland
Orthocladius thienemanni River Liffey, Ireland
Paraherochilus minutissimus European alpine streams Thienemann 1936
Paracricotopus sp. River Liffey, Ireland
Paracricotopus biformis larvae & pupae in alpine streams & waterfalls Welch 1976
Parachironomus sp. Holarctic mountain brooks Thienemann 1936
Parakiefferiella sp. *Drepanocladus revolvens*, Alberta, Canada; Boerger et al. 1982
Paramerina fragilis River Liffey, Ireland Humphries & Frost 1937; Frost 1942
Partanaytarsus sp. River Liffey, Ireland Humphries & Frost 1937; Frost 1942
Parochlus steinboeki River Liffey, Ireland
Polyplectilum scandaleum River Liffey, Ireland
Pectrocladius dilatatus River Liffey, Ireland
Pectrocladius psilopterus River Liffey, Ireland

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Notes</th>
</tr>
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<tbody>
<tr>
<td><em>Psectrocladius simulans</em></td>
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<td>European alpine waterfalls</td>
<td>Thienemann 1936</td>
</tr>
<tr>
<td><em>Tvetenia calvescens</em></td>
<td>semiterrestrial mosses in springs, Europe</td>
<td>Stur et al. 2005; Thienemann 1936; Humphries &amp; Frost 1937; Frost 1942</td>
</tr>
<tr>
<td><em>Tvetenia discoloripes</em></td>
<td>European streams; River Liffey, Ireland</td>
<td>Thienemann 1936, 1954; Humphries &amp; Frost 1937; Frost 1942</td>
</tr>
<tr>
<td><em>Xenochironomus xenolabis</em></td>
<td>Quebec highland stream</td>
<td>Elgmork &amp; Sæther 1970; Humphries &amp; Frost 1937; Frost 1942</td>
</tr>
</tbody>
</table>

Figure 33. *Ablabesmyia* larva, a common genus among bryophytes in Europe. Photo by Walter Pfiegl.</p>

Figure 34. *Ablabesmyia* egg sack, a common genus among bryophytes in Europe. Photo by Walter Pfiegl.
Figure 35. *Brillia bifida* adult, member of a genus that inhabits aquatic mosses in Europe. Photo by James K. Lindsey.

Figure 36. *Chaetocladius perennis* adult, a species whose larvae are known from bryophytes. Photo by James K. Lindsey.

Figure 37. *Corynoneura taranaki* larva, member of a genus with bryophyte dwellers. Photo by Stephen Moore, Landcare Research, NZ.

Figure 38. *Cricotopus lebetis* larva, member of a genus known from the mosses *Fontinalis* and *Hygrohypnum* in Russia. Photo by Jerry F. Butler.

Figure 39. *Cryptochironomus obreptans* female adult, member of a genus with larvae that can inhabit stream mosses. Photo by James K. Lindsey.
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. *Diplocadius cultriger*, a species whose larvae sometimes live among mosses. Photo by Tom Murray.

Figure 42. *Endochironomus* larva, a genus whose larvae sometimes live among mosses. Photo by J. C. Schou.

Figure 43. *Endochironomus* male adult, genus with larvae sometimes live among bryophytes. Photo by Don Loarie through Creative Commons.

Figure 44. *Eukiefferiella* (arrow) on *Nesameletus ebopohauapapa*. Several species of *Eukiefferiella* live among stream bryophytes. Photo by Stephen Moore, Landcare Research, NZ.
Figure 45. *Limnophyes habilis* adult, member of a genus with several species that live among bryophytes. Photo by James K. Lindsey.

Figure 46. *Macropelopia nebulosa* pupa, member of a genus with larvae of some species occurring among aquatic mosses. Photo by J. C. Schou.

Figure 47. *Macropelopia nebulosa* adult, member of a genus that sometimes lives among mosses as larvae. Photo by James K. Lindsey.

Figure 48. *Metriocnemus fusipes* male adult, a species whose larvae can occur among stream bryophytes. Photo by James K. Lindsey.

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.

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 51. *Paratanytarsus tenuis* male adult, member of a genus whose larvae inhabit stream bryophytes. Photo by James K. Lindsey.

Figure 52. *Polypedilum* larva in plant litter. *Polypedilum scalaenum* occurs among *Drepanoecladus revolvens*. Photo by Stephen Moore, Landcare Research NZ.

Figure 53. *Psectrocladius sordidellus* emerging female adult, member of a genus that sometimes occurs among stream bryophytes. Photo by James K. Lindsey.

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.

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. *Hydrohypnum ochraceum*, home of Chironomidae. Photo by Michael Lüth.

In their study of an Arctic stream (Alaska, USA), Lee and Hershey (2000) found that Chironomidae increased in density when the mosses (*Hydrohypnum*, 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 µm. 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 57. *Thienemanniymia* larva posterior, a moss dweller. Photo by Pete Cranston.

Figure 58. *Fissidens rigidulus*, a moss that houses abundant Chironomidae midstream in New Zealand. Photo by Bill & Nancy Malcolm.

Figure 59. *Fontinalis antipyretica*, a moss where Chironomidae are dominant in the Czech Republic. Photo by Michael Lüth.

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.](image)

![Figure 62. Sphagnum capillifolium, member of a genus that is eaten by Psectrocladius psilopterus in bogs. Photo by Blanka Shaw.](image)

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.](image)

![Figure 64. Tvetenia discoloripes larva, a bryophyte inhabitant. Photo by Walter Pfliegler.](image)

![Figure 65. Tvetenia discoloripes larva, a bryophyte inhabitant. Photo by Walter Pfliegler.](image)
Bryophytes are not typical habitats for the mosquitoes. Nevertheless, Elgmork and Sæther (1970) found that *Aedes excrucians* (Figure 68; a woodland mosquito that bites humans) occurred in bog pools and occasionally among *Sphagnum* mosses (Figure 69).

**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).

**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.

**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 70). 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 71) larvae (Anderson & Dicke 1960).
Chapter 11-13b: Aquatic Insects: Holometabola – Diptera, Suborder Nematocera

Figure 70. Simuliidae larvae on rock, showing how dense they can be. Photo by Janice Glime.

Figure 71. Simulium vittatum tribulatum complex larva, an abundant species on some bryophytes. Photo by D. S. Chandler <www.discoverlife.org>.

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 72), S. vittatum (Figure 71), 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 73). 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 72. Simulium venustum verecundum complex, blackflies that overwinter as eggs. Photo by David S. Chandler.

Figure 73. Ectemnia invenusta larva, a blackfly that uses dead mosses to form its pupal stalk. Photo by Tom Murray.

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 (CaCO₃) 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) (Niesiolowski 1980). Niesiolowski 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 74) and *Cocconeis* spp. (Figure 75). The latter is a common diatom adhering to moss leaves (pers. obs.).

**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 cm². 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 76) 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 77). In acid waters of the same river she found *S. venustum* (Figure 72) and *S. latipes* (Figure 78) 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 74.** *Rhoicosphenia abbreviata*, member of a genus that is food for moss-dwelling blackflies. Photo by Pauli Snoeijs through Creative Commons <www.nordicmicroalgae.org>.

**Figure 75.** *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/> (Mikroscopie).

**Figure 76.** *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 through Discover Life.

**Figure 77.** *Simulium ornatum / intermedium / trifasciatum* adult, a blackfly complex whose larvae are common on bryophytes. Photo by Malcolm Storey through Discover Life.
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 81), *S. venustum*–*S. verecundum* complex (Figure 72), and *S. vittatum* (Figure 71). The most widespread of these is *S. tuberosum*, appearing among all the common bryophytes: *Fontinalis dalecarlica* (Figure 4), *Hygroamblystegium fluviale* (Figure 5) – *Platyhypnidium riparioides* (Figure 6), and *Scapania undulata* (Figure 7).

The *Simuliidae* require a relatively rapid flow rate. For *Simulium ornatum* (Figure 77) 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 82) (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 72), *S. verecundum* (Figure 72), *S. vittatum* (Figure 71), *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 71). 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 83–Figure 84)] crawled out of the water onto various substrata to dry their wings before their first flight.
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.

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**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 Rajcianka in Slavakia.

*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 87) 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 88), an inhabitant of slower streams, that builds a somewhat weaker cocoon. Of these three, *P. fontanum* makes the weakest cocoon.

![Figure 87. *Prosimulium fuscum*, a species that lives on bryophytes in very fast water. Photo by Donald S. Chandler.](image)

![Figure 88. *Prosimulium mixtum* larva lives on bryophytes in slower streams than those of *Prosimulium fuscum*. Photo by Donald S. Chandler.](image)

The genus *Prosimulium* was common among bryophytes in Appalachian Mountain, USA, streams (Glime 1968). The most common was *Prosimulium hirtipes* (Figure 89-Figure 90, 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 88), and *P. rhizophorum*.

![Figure 89. *Prosimulium hirtipes* among leafy liverworts. Photos by Janice Glime.](image)

![Figure 90. *Prosimulium hirtipes* is a common blackfly on stream mosses. Photos by Janice Glime.](image)

*Prosimulium hirtipes* (Figure 89-Figure 90) 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 89-Figure 90) 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 89-Figure 90), *P. tomosvaryi*, and *P. subrufipes* use moist terrestrial mosses, mostly *Brachythecium rivulare* (Figure 91), 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 x 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 91. *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 92) among mosses in my Appalachian stream study, but they were not as abundant as *Prosimulium* (Figure 87-Figure 90) or *Simulium* (Figure 76-Figure 85) (Glime 1968). Other aquatic bryophyte habitat studies I have found do not mention them.

![Cnephia adult; larvae of *C. mutata* occasionally occur among mosses in mid-Appalachian, USA, streams. Photo by Sam Houston.](image)

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 93) 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\(^{-1}\). 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).

![Rhyacophila nubila larva, a predator that cohabits with the blackfly *Metacnephia pallipes* on mosses. Photo by Niels Sloth.](image)

**Stegopterna**

Pupae of the *Stegopterna mutata* complex (Figure 94-Figure 95) 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.

![Stegopterna, a genus that often moves to mosses to pupate. Photo courtesy of the State Hygienic Laboratory, University of Iowa.](image)
Chapter 11-13b: Aquatic Insects: Holometabola – Diptera, Suborder Nematocera

Figure 95. Stegopterna mutata-diplomutata complex, with larvae that move to mosses to emerge from streams in Pennsylvania, USA. Photo by Donald S. Chandler.

In Slovakia, in the River Rajcianka, Krno (1990) found the genus Odagmia, 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 96) as occurring along streams, particularly those bordered by mosses. In the Appalachian Mountains, USA, I occasionally found larvae of this genus (Figure 97) 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 96. Thaumalea adult, an occupant along streams bordered by mosses. Photo by Kirk C. Tonkel through Creative Commons.

Figure 97. Thaumalea larva, an occasional bryophyte dweller. Photo by Ton van Haaren.

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 98) 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 98. Leptodictyum riparium, a stream and lake moss that is home for such nuisance Diptera as Psychodidae and Chironomidae. Photo by Michael Lüth.

Thorup (1963) found Pericoma blandula (Figure 99), 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 99. Pericoma blandula adult female; larvae live among mosses. Photo by Walter Pfiegl.
**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, swamplike meadows, bottomlands of brooks, and reservoirs. In the streams of the Appalachian Mountains, USA, its larvae are fairly frequent among *Hygroamblystegium fluviale* (Figure 5) and *Platypnidium 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 100) 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 101) on a dripping rock cliff among mosses where diatoms were abundant. Egglishaw (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.

Larvae of the moth fly *Sycorax silacea* (see Figure 102) 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 100.** *Pericoma* larva, a frequent bryophyte dweller. Photo from <www.dfg.ca.gov.png>.

**Figure 101.** *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.

**Figure 102.** *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 crispi* 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 103) 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, swamplike meadows, and forest pools.

**Figure 103.** *Ulomyia fuliginosa* adult, a species whose larvae live among mosses in running water. Photo by James K. Lindsey.
Berdeniella (Figure 104) 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 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 104. Berdeniella sp., as genus whose larvae live among alpine stream bryophytes, showing the posterior of the larva. Photo by Urma S. Kruus.

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 families of much less importance include the Culicidae (quiet water), Thaumaleidae (beside waterfalls), and Psychodidae (quiet or slow-moving water).

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Literature Cited


Reg. 3(1): 1-16.


