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

TABLE OF CONTENTS

Suborder Nematocera, continued 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-16
  - 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-21
  - *Simulium* 11-13b-23
  - *Prosimulium* 11-13b-25
  - *Cnephia*/*Metacnephia* 11-13b-26
  - *Stegopterna* 11-13b-27
- Thaumaleidae – Trickle Midges 11-13b-27
- Psychodidae – Moth Flies and Sand Flies 11-13b-27

Summary 11-13b-29
Acknowledgments 11-13b-30
Literature Cited 11-13b-30

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^2 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).

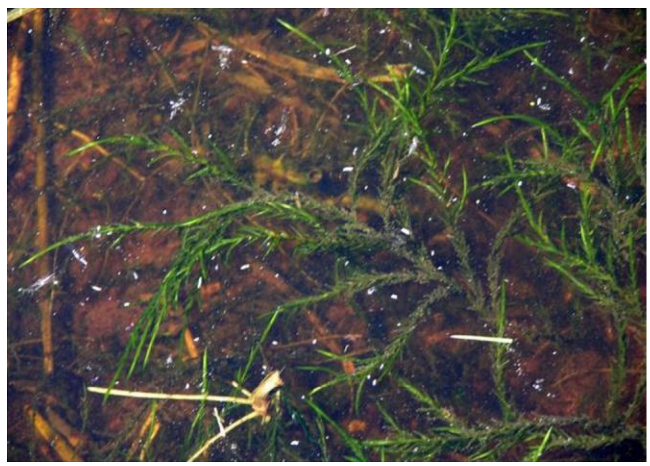

Figure 4. ***Fontinalis dalecarlica***, moss that is home to large numbers of **Chironomidae**. Photo by J. C. Schou, with permission.

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.

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.

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 (3months 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.

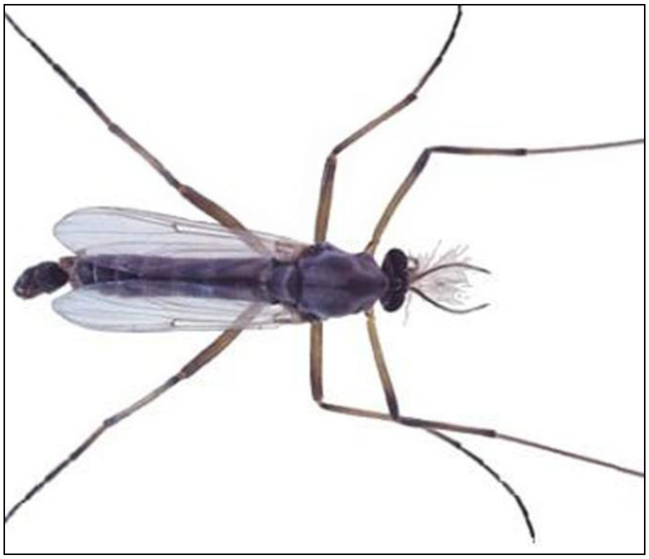

Figure 13. ***Chironomus tepperi*** adult male, an earlier emerger than ***Procladius paludicola***, thus separating their niches. Photo through Creative Commons.

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 18. ***Micropsectra*** larva, member of a genus with moss-dwelling species. Photo by NTNU University Museum, Department of Natural History, through Creative Commons.

Figure 16. ***Orthocladius*** *rubicundus*, a genus with larvae among bryophytes in cold water. Photo by J. K. Lindsey, with permission.

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 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 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. adaucta*** are cold-water species that are c**renobionts** (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

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.

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^{-1}.

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.

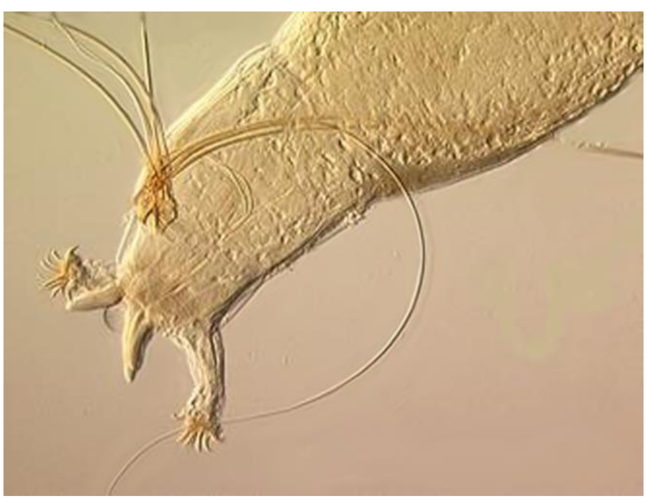

Figure 26. ***Krenosmittia*** larva posterior, an inhabitant of moss-filled seeps in Europe. Photo by Peter Cranston, with permission.

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. ***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, 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. ***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.

Taxon	Habitat	References
***Ablabesmyia costalis**	River Liffey, Ireland European alpine	Humphries & Frost 1937; Frost 1942; Thienemann 1936
Ablabesmyia mallochi	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
***Ablabesmyia minima**	European alpine streams; River Liffey, Ireland	Thienemann 1936; Humphries & Frost 1937; Frost 1942
Ablabesmyia nigropunctata	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Ablabesmyia sexannulata	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Belgica antarctica	Antarctic streams in moss beds	Rico & Quesada 2013
***Brillia alulata**	European alpine springs	Thienemann 1936
Brillia modesta	European alpine	Thienemann 1936
Camptocladius sp.	River Liffey, Ireland	Frost 1942
Cardiocladius albiplumus	fast water	Oliver & Bode 1985
Chaetocladius perennis	pupae in European alpine	Thienemann 1936
***Chironomus genuines**	River Liffey, Ireland	Frost 1942

Cladotanytarsus	River Liffey, Ireland	Frost 1942
Conchapelopia flavifrons	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Conchapelopia puncticollis	European alpine	Thienemann 1936
Corynoneura sp.	River Liffey, Ireland larvae & pupae in European alpine	Humphries & Frost 1937; Frost 1942; Thienemann 1936
Corynoneura lobata	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Cricotopus sp.	***Drepanocladus revolvens***, Alberta, Canada; ***Fontinalis*** & ***Hygrohypnum*** in Russian lake outlets	Boerger *et al*. 1982 Vuori *et al*. 1999
Cricotopus bicinctus	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Cricotopus miricornis	European alpine	Thienemann 1936
Cricotopus prolongatus	European alpine	Thienemann 1936
Cricotopus trifasciatus	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Cryptochironomus sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Culicoides rivicola	European alpine	Thienemann 1936
Culicoides neglectus (*nom dub*)	European alpine	Thienemann 1936
Diamesa sp.	River Liffey, Ireland	Humphries & Frost 1937
Diamesa fissipes gr.	European alpine	Thienemann 1936
Diamesa prolongata	pupae in European alpine	Thienemann 1936
Diamesa steinboecki	European alpine	Thienemann 1936
Diamesa tonsa	pupae among mosses in European alpine	Thienemann 1936
Diplocladius cultriger	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Endochironomus sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
****Eukiefferiella alpestris***	European alpine streams	Thienemann 1936
Eukiefferiella brevicalcar	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Eukiefferiella caerulescens	larvae among ***Fontinalis***; pupae among mosses	Thienemann 1936
Eukiefferiella endobryonia	larvae & pupae in tubes made of ***Fontinalis*** spp.	Imada 2020
****Eukiefferiella longicalcar*** (nomen dubium)	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Eukiefferiella lobifera	European alpine	Thienemann 1936
Eukiefferiella minor	European alpine streams	Thienemann 1936
Eukiefferiella subalpina	European alpine streams	Thienemann 1936
****Eutanytarsus inmermepes***	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Heterotrissocladius sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Heterotrissocladius changi	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Krenosmittia	European springs & seeps	Ferrington 1984
****Labrudinia pilosella***	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Limnophyes borealis	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Limnophyes globifer	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Limnophyes prolongatus	European alpine	Thienemann 1936
Macropelopia sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Macropelopia adaucta	mosses in coldwater springs	Fittkau 1962; Lindegaard *et al*. 1975
Macropelopia notata	mosses in coldwater springs	Fittkau 1962; Lindegaard *et al*. 1975
Metriocnemus	in high mosses of high mountain brooks of Europe Colorado Rocky Mountain, USA, streams	Thienemann 1954 Elgmork & Sæther 1970
****Metriocnemus cuneatus***	European alpine springs	Thienemann 1936
Metriocnemus fuscipes	European alpine springs	Thienemann 1936
Metriocnemus hygropetricus	European alpine	Thienemann 1936
Micropsectra sp.	European alpine streams	Thienemann 1936
Microtendipes sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Microtendipes pedellus	emergences in mossy areas, Quebec, Canada	Harper & Cloutier 1979
Nanocladius sp.	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Nanocladius bicolor	high mountain streams in Europe	Thienemann 1954; Freeman 1956
Neostempellina thienemanni	exclusively alkaline springs & streams	Reiss 1984
Orthocladius luteus	European alpine streams	Thienemann 1936
Orthocladius oblidens	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Orthocladius rivicola	European alpine streams	Thienemann 1936
Orthocladius rivulorum	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Orthocladius saxicola	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Orthocladius thienemanni	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Paraboreochlus minutissimus	European alpine springs	Thienemann 1936
Paracladius quadrinodosus	moss & rock zones	Welch 1976
Paracricotopus sp.	larvae & pupae in alpine streams & waterfalls	Thienemann 1936
Parakiefferiella sp.	Holarctic mountain brooks ***Drepanocladus revolvens***, Alberta, Canada;	Thienemann 1944; Oliver 1963; Elgmork & Sæther 1970; Boerger *et al*. 1982
Parakiefferiella bathophila	River Liffey, Ireland	Frost 1942
Paramerina fragilis	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Paraphaenocladius	bog mosses, mountain streams, cold springs	Elgmork & Sæther 1970
Parapsectrocladius	mountain streams, Argentina	Epele *et al*. 2012
Paratanytarsus sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Parochlus steinenii	mosses on Antarctic lake bottoms	Rico & Quesada 2013

Polypedilum	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Polypedilum scalaenum	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Psectrocladius dilatatus	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Psectrocladius psilopterus	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Psectrocladius simulans	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Pseudodiamesa arctica	moss & rock zones	Welch 1976
Pseudodiamesa branickii	mid-mtn creeks,Colorado Rocky Mountain, USA	Elgmork & Sæther 1970
Pseudodiamesa nivosa?	European alpine	Thienemann 1936
Pseudokiefferiella parva	Colorado Rocky Mountain, USA, creeks and springs	Elgmork & Sæther 1970
Rheocricotopus effusus	pupae in alpine areas larvae in streams in high mountain areas	Thienemann 1936; Elgmork & Sæther 1970
Rheocricotopus fuscipes	River Liffey, Ireland European alpine	Humphries & Frost 1937; Frost 1942 Thienemann 1936
Rheotanytarsus sp.	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Rheotanytarsus distinctissimus	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Stempellina bausei	European alpine streams	Thienemann 1936
****Syndiamesa macronyx***	European alpine	Thienemann 1936
Synorthocladius semivirens	European alpine	Thienemann 1936
****Synorthocladius tipulatus***	River Liffey, Ireland, European alpine springs	Thienemann 1936; Humphries & Frost 1937; Frost 1942
Tanytarsus curticornis	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Tanytarsus dispar	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Tanytarsus gregarius	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Thienemannia gracilis	mountain streams in Europe & Iceland streams, Colorado Rocky Mountain, USA	Thienemann 1936,1954; Brundin 1956a, b; Elgmork & Sæther 1970
Thienemanniella fusca	European alpine	Thienemann 1936
Thienemannimyia	Russian streams	Vuori *et al.* 1999
****Trichocladius*** sp. (invalid genus)	River Liffey, Ireland	Humphries & Frost 1937; Frost 1942
Trissopelopia longimana	European alpine streams	Thienemann 1936
Trissopelopia ogemawi	***Drepanocladus revolvens***, Alberta, Canada	Boerger *et al*. 1982
Tvetenia bavarica	European alpine waterfalls	Thienemann 1936
Tvetenia calvescens	semiterrestrial mosses in springs, Europe European alpine streams; River Liffey, Ireland	Stur *et al*. 2005; Thienemann 1936; Humphries & Frost 1937; Frost 1942
Tvetenia discoloripes	European streams Colorado Rocky Mountain, USA, streams River Liffey, Ireland	Thienemann 1936, 1954 Elgmork & Sæther 1970 Humphries & Frost 1937; Frost 1942
Xenochironomus xenolabis	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.

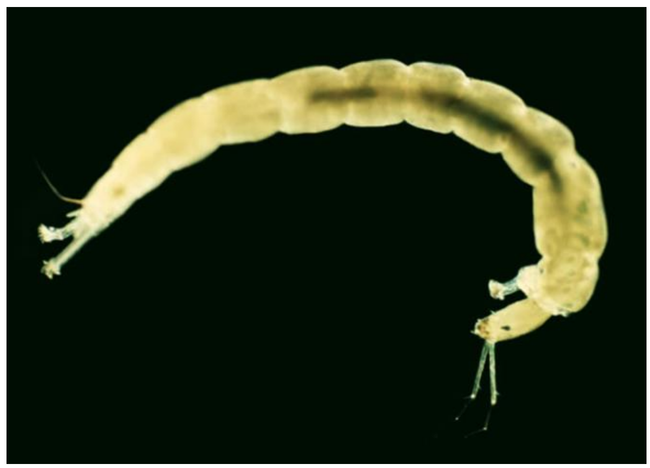

Figure 37. ***Corynoneura taranaki*** larva, member of a genus with bryophyte dwellers. Photo by Stephen Moore, Landcare Research, NZ, with permission.

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 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 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, 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 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.

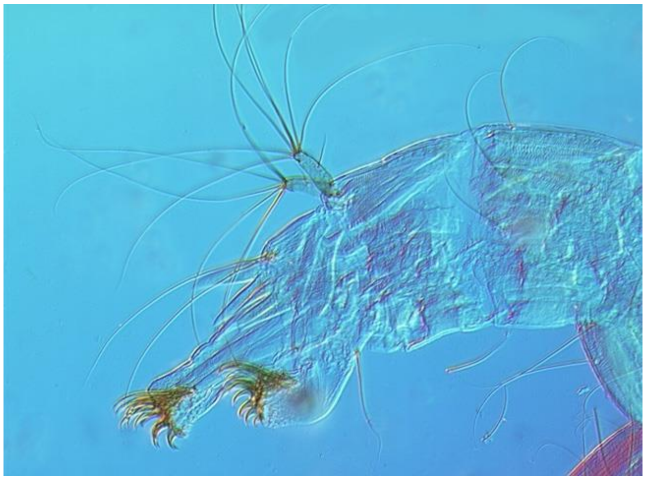

Figure 57. ***Thienemannimyia*** larva posterior, a moss dweller. Photo by Pete Cranston, with permission.

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 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 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.

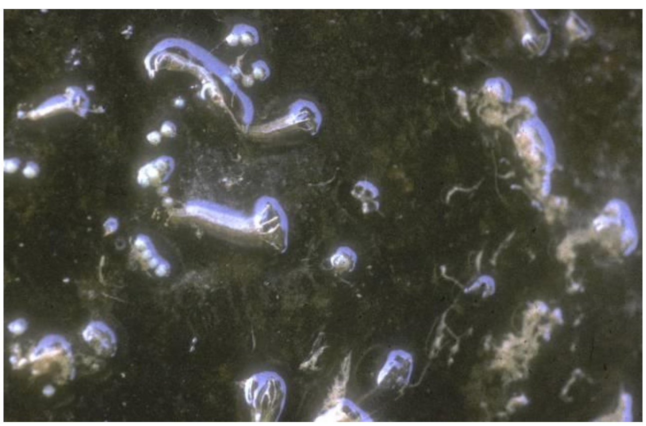

Figure 60. These tubes of **Chironomidae** are often present among mosses. The larvae live near the bottom of the moss clump and trap detritus in the net or use the moss as a trap, using the detrital matter for food. Photo by Janice Glime.

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.

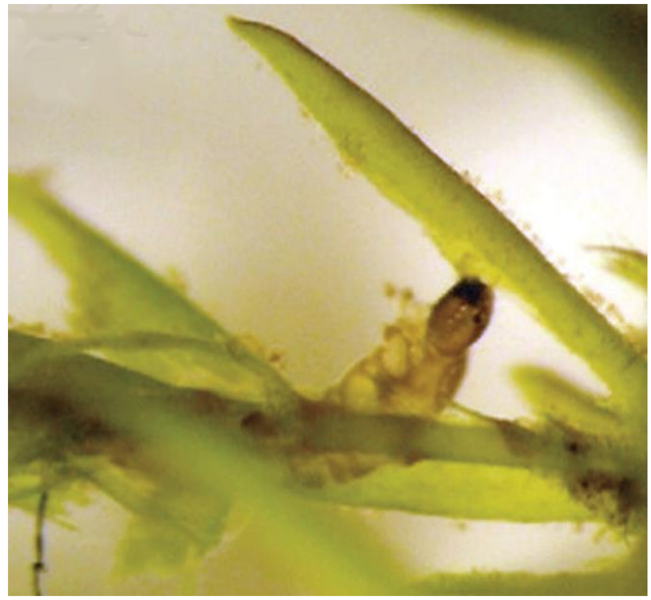

Figure 71. ***Eukiefferiella endobryonia*** fourth-instar larva feeding on leaf margin of ***Fontinalis dalecarlica***. Photo by Yume Imada, with permission.

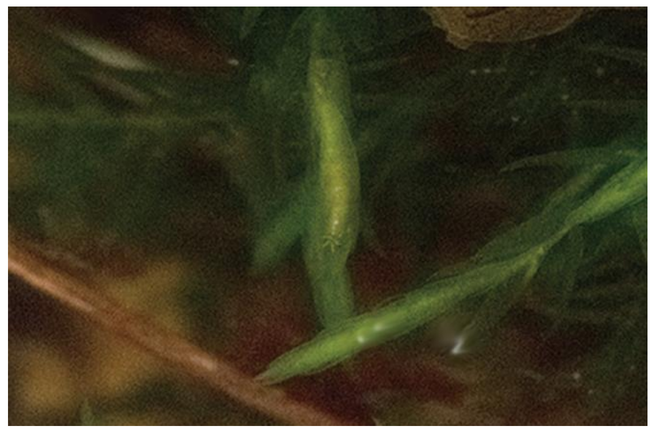

Figure 72. ***Eukiefferiella endobryonia*** early fourth instar larva with undulating body in tube. Photo by Yume Amada, with permission.

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.

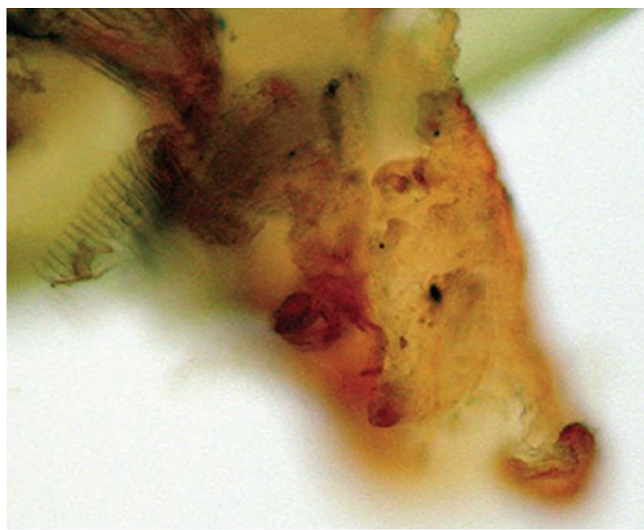

Figure 77. ***Eukiefferiella endobryonia*** amorphous, jelly-like silk mass spotted with detritus and diatoms, ripped off inner wall of end of pupal case. Photo by Yume Imada, with permission

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).

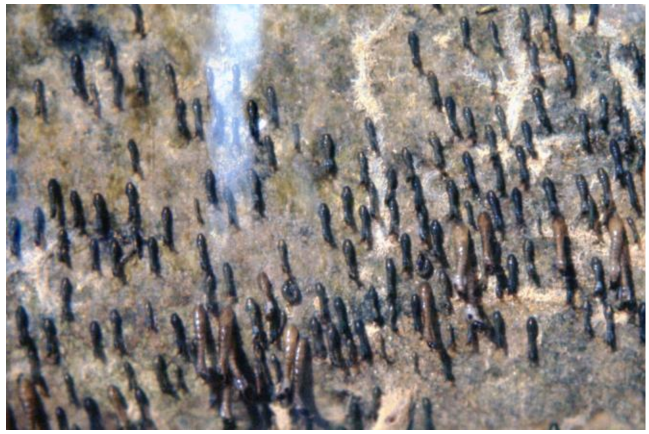

Figure 80. **Simuliidae** larvae on rock, showing how dense they can be. Photo by Janice Glime.

Figure 81. ***Simulium vittatum tribulatum*** complex larva, an abundant species on some bryophytes. Photo by D. S. Chandler <www.discoverlife.org>, 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 ($CaCO_3$) 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.).

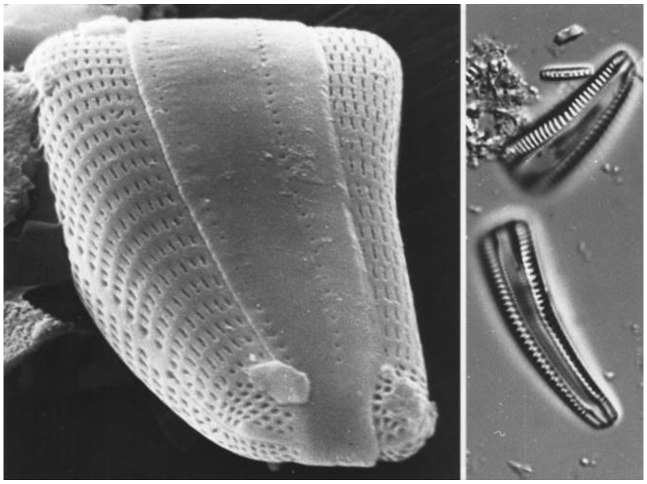

Figure 84. ***Rhoicosphenia abbreviata***, member of a genus that is food for moss-dwelling blackflies. Photo by Pauli Snoeijs, through Creative Commons <www.nordicmicroalgae.org>.

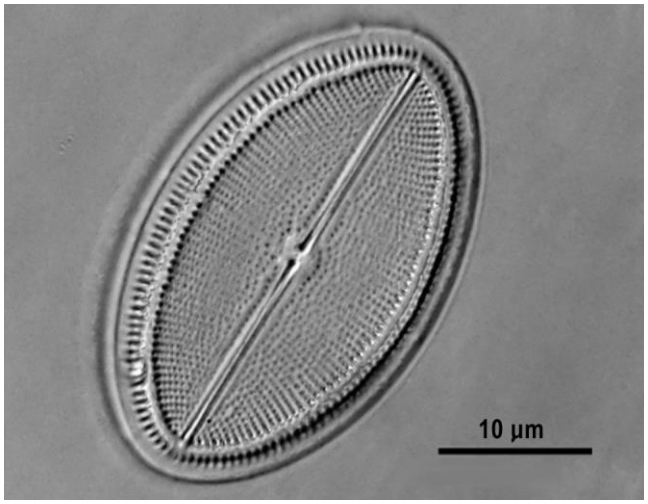

Figure 85. ***Cocconeis placentula***, a diatom that embeds itself in the surface of bryophyte leaves and also serves as food for blackflies in streams. Photo by Ralf Wagner at <http://www.dr-ralf-wagner.de/> (Mikroscopie).

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^2. 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 **Ephydridae** 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.

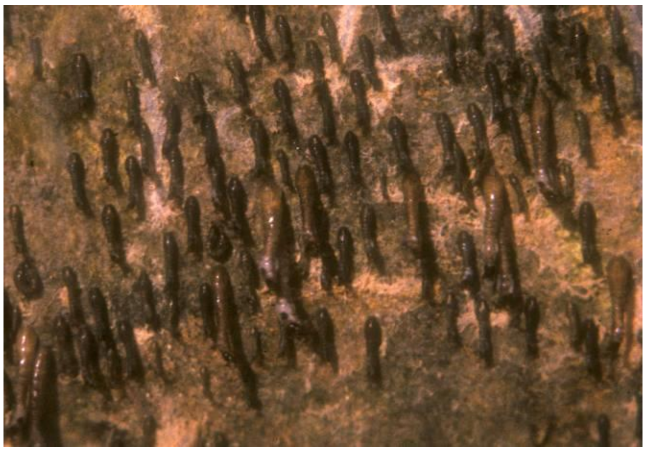

Figure 95. Blackfly (**Simuliidae**) larvae attach by tiny posterior hooks in fast current. Their heads with head fans point downstream and trap small particles of detritus, bacteria, algae, and even mosses for food. Photo by Janice Glime.

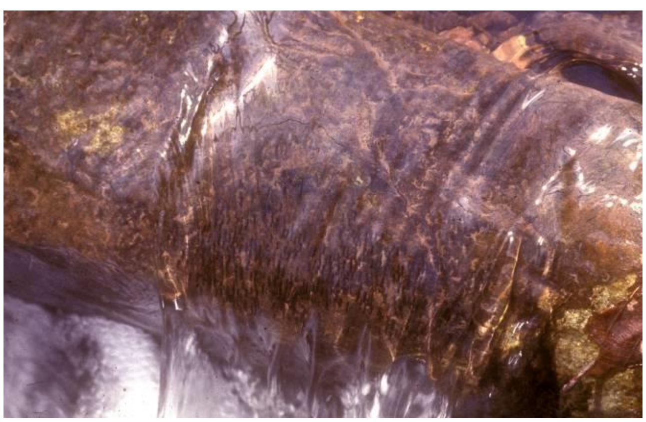

Figure 96. These blackfly larvae (**Simuliidae**) are just as common on these mosses as they often are on rocks in fast water. Larvae of the blackflies, **Simuliidae**, can use leaves of ***Fontinalis*** (Figure 59) in place of the usual net-like cocoon used to house the pupa. Photo by Janice Glime.

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 Rajcianka in Slavakia.

Prosimulium fontanum lives in forest and bog-fed streams (Davies & Syme 1958) where ***Sphagnum*** (Figure 62) influences the *p*H 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 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 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^{-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).

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 ***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 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. 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.

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 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 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 Urma 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).

Acknowledgments

Douglas M. Davies verified the Simuliidae and Julian P. Donahue verified some of the remaining Diptera from my mid-Appalachian Mountain study. Eileen Dumire helped me pull the numerous **Chironomidae** from the bryophytes. She proofread the chapter and offered suggestions to make it clearer.

Literature Cited

Adler, P. H. and Kim, K. C. 1986. The black flies of Pennsylvania (Simuliidae, Diptera). Bionics, Taxonomy, and Distribution. Bulletin 856 of The Pennsylvania State University, College of Agriculture, Agricultural Experiment Station, University Park, PA, 88 pp.

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

Anderson, A. M., Kranzfelder, P., Bouchard R. W. Jr., and Ferrington, L. C. Jr. 2013. Survivorship and longevity of *Diamesa mendotae* Muttkowski (Diptera: Chironomidae) under snow. J. Entomol. Acarol. Res. 45(1): e6.

Anderson, J. R. and Dicke, R. J. 1960. Ecology of the immature stages of some Wisconsin black flies (Simuliidae: Diptera). Ann. Entomol. Soc. Amer. 53: 386-404.

Armitage, P. D., Cranston, P., and Pinder, L. C. V. (eds.). 1995. The Chironomidae. The Ecology and Biology of Non-biting Midges. Chapman & Hall, London, 585 pp.

Arnold, F. and Macan, T. T. 1969. Studies on the fauna of a Shropshire Hill stream. Field Stud. 3: 159-184.

Baba, M. and Takaoka, H. 1989. Oviposition sites and the number of larval instars of two mountain blackfly species, *Simulium japonicum* and *S. rufibasis* (Diptera: Simuliidae). Jap. J. Sanit. Zool. 40(4): 307-313.

Baba, M. and Takaoka, H. 1991. Oviposition habits of a univoltine blackfly, *Prosimulium kiotoense*. Med. Vet. Entomol. 5: 351-357.

Bartlett, Troy. 2004a. Family Culicidae – Mosquitoes. BugGuide. Accessed 31 January 2015 at <http://bugguide.net/node/view/169>.

Bartlett, Troy. 2004b. Family Psychodidae – Moth Flies and Sand Flies. BugGuide. Accessed 31 January 2015 at <http://bugguide.net/node/view/3128>.

Becker, C. and Wagner, R. 2004. Chironomidae (Diptera) emergence from two adjacent stream reaches with contrasting bottom substrata of a brook in Hesse/Germany in 1983. Entomol. Gen. 27: 105-122.

Boerger, H., Clifford, H. F., and Davies, R. W. 1982. Density and microdistribution of chironomid larvae in an Alberta, Canada, brown-water stream. Can. J. Zool. 60: 913-920.

Brundin, L. 1956a. Zur Systematik der Orthocladiinae (Dipt. Chironomidae). Rept. Inst. Freshw. Res. Drottningh 37: 5-185.

Brundin, L. 1956b. Die bodenfaunistischen Seentypen und ihre Anwendbarkeit auf die Südhalbkugel. Zugleich ein Theorie der produktionbiologischen Bedeutung der glazialen Erosion. Rept. Inst. Freshw. Res. Drottningh 37: 186-235.

Brusven, M. A., Meehan, W. R., and Biggam, R. C. 1990. The role of aquatic moss on community composition and drift of fish-food organisms. Hydrobiologia 196: 39-50.

Butcher, R. W., Longwell, J., and Pentelow, F. T. K. 1937. Survey of the R. Tees. Part III. The non-tidal reaches. Chemical and Biological. Water Poll. Res. Tech. Pap. 6.

Butler, M. G. 1982. A 7-year life cycle for two *Chironomus* species in Arctic Alaskan tundra ponds (Diptera: Chironomidae). Can. J. Zool. 60: 58-70.

Carlson, G. 1967. Environmental factors influencing blackfly populations. Bull. World Health Org. 37: 139-150.

Carr, John. 2013. Family Thaumaleidae – Trickle Midges. BugGuide. Accessed 31 January 2015 at <http://bugguide.net/node/view/740925>.

Chantha, S.-C., Cloutier, L., and Cattaneo, A. 2000. Epiphytic algae and invertebrates on aquatic mosses in a Quebec stream. Arch. Hydrobiol. 147: 143-160.

Clifford, H. F. 2014. Aquatic Insects of Alberta. Accessed 16 August 2014 at <http://sunsite.ualberta.ca/Projects/Aquatic_Invertebrates/?Page=45>.

Čmrlec, K., Ivković, M., Šemnički, P., and Mihaljević, Z. 2013. Emergence phenology and microhabitat distribution of aquatic Diptera community at the outlets of barrage lakes: Effect of temperature, substrate and current velocity. Polish J. Ecol. 61: 135-144.

Cotinis. 2004. Family Chironomidae – Midges. BugGuide. Accessed 31 January 2015 at <http://bugguide.net/node/view/3163>.

Cowie, B. and Winterbourn, M. J. 1979. Biota of a subalpine springbrook in the Southern Alps. N. Z. J. Marine Freshwat. Res. 13: 295-301.

Crosskey, R. W. 1990. The Natural History of Black Flies. John Wiley and Sons. Chichester, ix + 771 pp.

Curran, C. H. 1927. Synopsis of Canadian Stratiomyidae (Diptera). Trans. Can. Royal Soc. Entomol. Sec. 5: 191-228.

Danks, H. V. and Oliver, D. R. 1972. Seasonal emergence of some high Arctic Chironomidae (Diptera). Can. Entomol. 104: 661-686.

Davies, D. M. 1949. The ecology and life history of blackflies (Simuliidae, Diptera) in Ontario with a description of a new species. Ph.D. Thesis. University of Toronto.

Davies, D. M. and Syme, P. D. 1958. Three new Ontario black flies of the genus *Prosimulium* (Diptera: Simuliidae). Part II. Ecological observations and experiments. Can. Entomol. 90: 744-759.

Davies, D. M., Peterson, B. V., and Wood, D. M. 1962. The black flies (Diptera: Simuliidae) of Ontario. Pt. 1. Adult identification and distribution with descriptions of six new species. Proc. Entomol. Soc. Ont. 92: 70-130.

Egglishaw, H. J. 1969. The distribution of benthic invertebrates on substrata in fast flowing streams. J. Anim. Ecol. 38: 19-33.

Elgmork, K. and Sæther, O. R. 1970. Distribution of invertebrates in a high mountain brook in the Colorado Rocky Mountains. Univ. Colorado Stud. Ser. Biol. 31: 1-55.

Epele, L. B., Miserendino, M. L., and Brand, C. 2012. Does nature and persistence of substrate at a mesohabitat scale matter for Chironomidae assemblages? A study of two perennial mountain streams in Patagonia, Argentina. J. Insect Sci. 12: 68-.

Ertlova, E. 1984. Charakteristik der Chironomiden-gemeinschaften des Flusses Bela. [Characteristics of Chironomid communities of the River Bela.]. Ertl M(ed) (limnology of the Bela River.)., Limnologie Des Flusses Bela.- Limnologia Rieky Bela. Pr. Lab. Ryb. Hydrobiol., Bratisl./works Lab. Fish. Res. Hydrobiol., Bratisl. 4: 213-230.

Ferrington, L. C. Jr. 1984. Evidence for the hyporheic zone as a microhabitat of *Krenosmittia* spp. larvae (Diptera: Chironomidae). J. Freshwat. Ecol. 2: 353-358.

Fittkau, E. J. 1962. Die Tanypodinae (Diptera: Chironomidae) (Die Tribus Anatopyggiini, Macropelopiini und Pentaneurini). Abhandlungen zur Larvalsystematik der Insekten 6: 1-453.

Fredeen, F. J. H. 1960. Bacteria as a source of food for black-fly larvae. Nature 4741: 963.

Fredeen, F. J. H. 1964. Bacteria as food for blackfly larvae (Diptera: Simuliidae) in laboratory cultures and in natural streams. Can. J. Zool. 42: 527-548.

Freeman, P. 1956. A study of the Chironomidae (Diptera) of Africa south of the Sahara. Part IV. Bull. Brit. Mus. Nat. Hist. Entomol. 4(7): 285-368.

Frost, W. E. 1942. River Liffey survey IV. The fauna of submerged "mosses" in an acid and an alkaline water. Proc. Roy. Irish Acad. Ser. B13: 293-369.

Gardenfors, U. 2001. Noi larve de Chironomide (Diptera) gasite in fauna Romaniei. [New Chironomidae (Diptera) larvae found in Romania's fauna.]. Classifying threatened species at national versus global levels. Hidrobiologia (Bucur.) 14: 225-243; Trends Ecol. Evol. 16(9): 511-516.

Gerson, U. 1969. Moss-arthropod associations. Bryologist 72: 495-500.

Gerson, U. 1982. Bryophytes and invertebrates. In: Smith, A. J. E. (ed.). Bryophyte Ecology. Chapman & Hall, New York, pp. 291-332.

Glime, J. M. 1968. Aquatic Insect Communities Among Appalachian Stream Bryophytes. Ph.D. Dissertation, Michigan State University, East Lansing, MI, 180 pp.

Glime, J. M. 1994. Bryophytes as homes for stream insects. Hikobia 11: 483-497.

Haefner, J. D. and Wallace, J. B. 1981. Shifts in aquatic insect populations in a first-order southern Appalachian stream following a decade of old field succession. Can. J. Fish. Aquat. Sci. 38: 353-359.

Harper, P. P. and Cloutier, L. 1979. Chironomini and Pseudochironomini of a Québec highland stream (Diptera: Chironomidae). Entomol. Scand. Suppl. 10: 81-94.

Harrod, J. J. 1965. Effect of current speed on the cephalic fans of the larvae of *Simulium ornatum* var. *nitidifrons* Edwards (Diptera: Simuliidae). Hydrobiologia 26: 8-12.

Humphries, C. F. and Frost, W. E. 1937. River Liffey Survey. The chironomid fauna of submerged mosses. Proc. Roy. Irish Acad. Ser. B 43: 161-181.

Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 57: 344-388.

Hynes, H. B. N. 1970. The ecology of stream insects. Ann. Rev. Entomol. 15: 25-42.

Imada, Y. 2020. A novel leaf-rolling chironomid, *Eukiefferiella endobryonia sp. nov*. (Diptera, Chironomidae, Orthocladiinae), highlights the diversity of underwater chironomid tube structures. ZooKeys 906: 73-111.

Irons, J. G. III, L. K. Miller, L. K., and Oswood, M. W. 1993. Ecological adaptations of aquatic macro-invertebrates to overwintering in interior Alaska (U.S.A.) subarctic streams. Can. J. Zool. 71: 98-108.

Jamnback, H. A. and Stone, A. 1955. The blackflies of New York state. Bull. N. Y. State Mus. 349: 144 pp.

Ježek, J., Lukáš, J., Kvifte, G. M., and Oboňa, J. 2012. New faunistic records of non-biting moth flies (Diptera: Psychodidae) from the Czech Republic and Slovakia. [Nové faunistické nálezy koutulí (Diptera: Psychodidae) z České republiky a Slovenska.]. Klapalekiana 48: 121-126.

Johannsen, O. A. 1969. Aquatic Diptera. Entomological Reprint Specialists, East Lansing, MI. 5 parts.

Jones, E. 1949. A further ecological study of calcareous streams in the Black Mountain district of South Wales. J. Anim. Ecol. 18: 142-159.

Jones, J. R. E. 1950. A further ecological study of the river Rheidol: The food of the common insects of the mainstream. J. Anim. Ecol.19: 159-174.

Jung, H. F. 1958. Psychodidae – Trichomyiinae. Fliegenpal. Reg. 3(1): 1-16.

Kalachova, G. S., Gladyshev, M. I., Sushchik, N. N., and Makhutova, O. N. 2011. Water moss as a food item of the zoobenthos in the Yenisei River. Central Eur. J. Biol. 6: 236-245.

Kelly, M G. and Huntley, B. 1987. *Amblystegium riparium* in brewery effluent channels. J. Bryol. 14: 792-793.

Kits, Joel. 2005. Family Simuliidae – Black Flies. BugGuide. Accessed 31 January 2015 at <http://bugguide.net/node/view/16613>.

Krno, I. 1990. Longitudinal changes in the structure of macrozoobenthos and its microdistribution in natural and moderately eutrophicated waters of the River Rajcianka (Strázovské vrchy). Acta Fac. Rer. Natur. Univ. Comen. Zool 33: 31-48.

Kurtak, D. 1974. Overwintering of *Simulium pictipes* Hagen (Diptera: Simuliidae) as eggs. J. Med. Entomol. 11: 383-384.

Lee, J. O. and Hershey, A. E. 2000. Effects of aquatic bryophytes and long-term fertilization on Arctic stream insects. J. N. Amer. Benthol. Soc. 19: 697-708.

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

Lindegaard, C., Thorup, J., and Bahn, M. 1975. The invertebrate fauna of the moss carpet in the Danish spring Ravnkilde and its seasonal, vertical and horizontal distribution. Arch. Hydrobiol. 75: 109-139.

Linhart, J., Fiurásková, M., and Vlcková, S. 2000. Meiofauna osídlující vodní mech Fontinalis antipyretica: Predbezné vysledky. [Meiofauna inhabiting an aquatic moss Fontinalis antipyretica: Preliminary results.] In: Rulík, M. (ed.). Sborník referátu z XII. Limnologické konference. Limnologie na prelomu tisíciletí, Kouty nad Desnou. Univerzita Palackého, Olomouc, pp. 190-193.

Linhart, J., Fiurásková, M., and Uvíra, V. 2002a. Moss- and mineral substrata-dwelling meiobenthos in two different low-order streams. Arch. Hydrobiol. 154: 543-560.

Linhart, J., Vlčková, Š., and Uvíra, V. 2002b. Moss-dwelling meiobenthos and flow velocity in low-order streams. Biologica 39: 111-122.

Lods-Crozet, B., Lencioni, V., Olafsson, J. S., Snook, D. L., Velle, G., Brittain, J. E., Castella, E., Rossaro, B. 2001. Chironomid (Diptera: Chironomidae) communities in six European glacier-fed streams. Freshwat. Biol. 46: 1791-1809.

Maurer, M. A. and Brusven, M. A. 1983. Insect abundance and colonization rate in *Fontinalis neo-mexicana* (Bryophyta) in an Idaho batholith stream, USA. Hydrobiologia 98: 9-15.

Meissner, K., Juntunen, A., Malmqvust, B., and Muotka, T. 2009. Predator-prey interactions in a variable environment: Responses of a caddis larva and its blackfly (*Cnephia pallipes*) prey to variations in stream flow. Ann. Zool. Fennici 46: 193-204.

Moore, M. V. and Lee, R. E. Jr. 1991. Surviving the big chill: Overwintering strategies of aquatic and terrestrial insects. Amer. Entomol. 37: 111-118.

Needham, J. G. and Christenson, R. O. 1927. Economic insects in some streams of northern Utah. Bull. Utah Agric. Exper. Stat., Logan, Utah 201: 36 pp.

Niesiołowski, S. 1980. Studies on the abundance, biomass and vertical distribution of larvae and pupae of black flies (Simuliidae, Diptera) on plants of the Grabia River, Poland. Hydrobiologia 75: 14-156.

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

Nolte, U. and Hoffmann, T. 1992. Life cycle of *Pseudodiamesa branickii* (Chironomidae) in a small upland stream. Netherlands J. Aquat. Ecol. 26: 309-314.

O'Kane, W. C. 1926. Black flies in New Hampshire. University of New Hampshire Technical Bulletin 32: 24 pp.

Oliver, D. R. 1963. Entomological studies in the lake Hazen area, Ellesmere Island, including lists of species of Arachnida, Collembola, and Insecta. Arctic 16: 175-180.

Oliver, D. R. and Bode, R. W. 1985. Description of the larva and pupa of *Cardiocladius albiplumus* Saether (Diptera: Chironomidae). Can. Entomol. 117: 803-809.

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

Pentelow, F. T. K. 1935. Notes on the distribution of the larvae and pupae of *Simulium* spp. on R. Tees and its tributaries. Parasitology 27(4).

Percival, E. and Whitehead, H. 1929. A quantitative study of the fauna of some types of stream-bed. J. Ecol. 17: 282-314.

Peterson, B. V. 1956. Observations on the biology of Utah black flies. (Diptera: Simuliidae). Can. Entomol. 88: 496-507.

Puri, I. M. 1925. On the life-history and structure of the early stages of Simuliidae (Diptera, Nematocera). Part 1. Parasitology 25: 295-369.

Reisen, W. K. and Prins, R. 1972. Some ecological relationships of the invertebrate drift in Praters Creek, Pickens County, South Carolina. Ecology 53: 876-884.

Reiss, F. 1984. *Neostempellina thienemanni* n. gen., n. sp., eine europäische Chironomide mit gehäusetragenden Larven (Diptera, Insecta). Spixiana 7: 203-210.

Rico, E. and Quesada, A. 2013. Distribution and ecology of chironomids (Diptera, Chironomidae) on Byers Peninsula, Maritime Antarctica. Antarct. Sci. 25: 288-291.

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

Rosa, B. F. J. V., Silva, M. V. D. da, Oliveira, V. C. D., Martins, R. T., and Alves, R. D. G. 2011. Macroinvertebrates associated with Bryophyta in a first-order Atlantic Forest stream. Zoologia (Curitiba) 28: 351-356.

Rosa, B. F. J. V., Dias-Silva, M. V. da, and Alves, R. G. 2013. Composition and structure of the Chironomidae (Insecta: Diptera) community associated with bryophytes in a first-order stream in the Atlantic Forest, Brazil. Neotrop. Entomol. 42: 15-21.

Rubtsov, I. A. 1962. Kratkii opredelitel krovososushchikh moshek fauny SSSR. [Short keys to the bloodsucking Simuliidae of the USSR.]. Acad. Sci. USSR. pp. 1-228.

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

Schroeder, P. 1988. Gut-passage, particle selection and ingestion of filter-feeding blackfly (Dipt., Simuliidae) larvae inhabiting a waterfall in Tahiti (French Polynesia). Aquat. Ins. 10: 1-16.

Smirnov, N. N. 1961. Food cycles in sphagnous bogs. Hydrobiologia 17: 175-182.

Stern, M. S. and Stern, D. H. 1969. A limnological study of a Tennessee cold springbrook. Amer. Midl. Nat 82: 62-82.

Stevens, M. M. 1994. Emergence phenology of *Chironomus tepperi* Skuse and *Procladius paludicola* Skuse (Diptera: Chironomidae) during rice crop establishment in southern New South Wales. Anim. Produc. Sci. 34: 1051-1056.

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

Suren, A. M. 1988. Ecological role of bryophytes in high alpine streams of New Zealand. Internat. Ver. Theor. Angew. Limnol. 23: 1412-1416.

Suren, A. 1993. Bryophytes and associated invertebrates in first-order alpine streams of Arthur's Pass, New Zealand. N. Z. J. Marine Freshwat. Res. 27: 479-494.

Tarshis, I. B. and Neil, W. 1970. Mass movement of black fly larvae on silken threads (Diptera: Simuliidae). Ann. Entomol. Soc. Amer. 63: 607-610.

Thienemann, A. 1936. Alpine chironomiden. (Ergebnisse von Untersuchungen in der Gegend von Garmisch-Partenkirchen, Oberbayern.). Arch. Hydrobiol. 30: 167-262.

Thienemann, A. 1944. Bestimmungstabellen für die bis jetzt bekannten Larven und Puppen der Orthocladiinen. Arch. Hydrobiol. Suppl. 39: 551-664.

Thienemann, A. 1954. *Chironomus*. Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. Binnengewässer 20: 1-834.

Thorup, J. 1963. Growth and life-cycle of invertebrates from Danish springs. Hydrobiologia 22: 55-84.

Tilbrook, P. J. 1967. The terrestrial invertebrate fauna of the maritime Antarctic. Philosoph. Trans. Royal Soc. London Ser. B Biol Sci. 252: 261-278.

Troiano, G. 1981. Studies of karyotype and male meiosis in three species of subfamily Psychodinae (Diptera: Psychodidae). Caryologia 3: 197-206.

Usinger, R. L. 1974. Aquatic Insects of California. University of California Press, Berkeley.

Vaillant, F. 1959. The larvae of three Nearctic Diptera of the family Psychodidae. N. Y. Entomol. 67: 39-47 + 7 plates.

Vuori, K. M., Luotonen, H., and Liljaniemi, P. 1999. Benthic macroinvertebrates and aquatic mosses in pristine streams of the Tolvajärvi region, Russian Karelia. Boreal Environ. Res. 4: 187-200.

Wagner, R., Marxsen, J., Zwick, P., and Cox, E. J. (eds.). 2011. Central European Stream Ecosystems: The Long Term Study of the Breitenbach. John Wiley & Sons, New York.

Welch, H. E. 1976. Ecology of Chironomidae (Diptera) in a polar lake. J. Fish. Bd. Can. 33: 227-247.

Withers, P. 2005. New records of Psychodidae (Diptera) for Switzerland. Rev. Suisse Zool. 112: 183-188.

Wolfe, L. S. and Peterson, D. G. 1959. Black flies (Diptera: Simuliidae) of the forests of Quebec. Can. J. Zool. 37: 137-159.

Wotton, R. S. 1982. Different life history strategies in lake-outlet blackflies. Hydrobiologia 96: 243-251.