# CHAPTER 11-4
# AQUATIC INSECTS: HEMIMETABOLA – COLLEMBOLA AND EPHEMEROPTERA

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# CHAPTER 11-4 AQUATIC INSECTS: HEMIMETABOLA – COLLEMBOLA AND EPHEMEROPTERA

Figure 1. ***Serratella ignita***, a common moss dweller. Photo by J. C. Schou, with permission.

## COLLEMBOLA – Springtails

This group was traditionally considered to be one of the insect orders, but more recently they have been classified in the class **Entognatha**. **Collembola** are quite small and lack wings. They have three pairs of legs, like insects, but have only six abdominal segments (Thorp & Covich 1991). The young (**nymphs**) resemble the adults, changing to adults by breaking their outer covering (**exoskeleton**) and discarding it, then expanding while the new exoskeleton is still soft.. They are unique in having a **furcula** (Figure 3-Figure 5) that forms the spring and a **collophore** (cylindrical ventral tube; Figure 3, Figure 6). When at rest, the furcula bends forward under the abdomen and is held in place by the **tenaculum (**Figure 3), a midventral structure that clasps the furcula. The springtail accomplishes rapid distance movement by releasing the furcula, which springs backward, propelling the springtail forward several centimeters. This can be used even on the water surface. Some can be seen bouncing around on the snow in winter.

Figure 2. ***Podura aquatica*** moulting; note split in outer skeleton. Photo by Jan van Duinen, with permission.

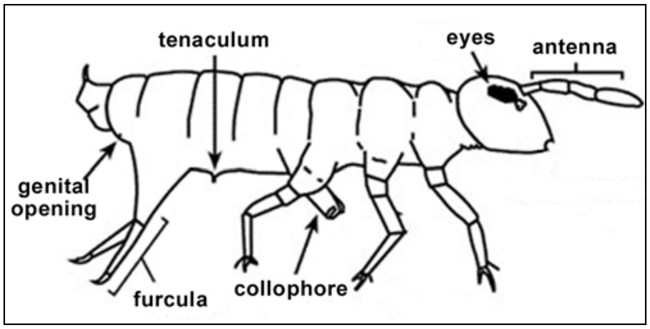


Figure 3. **Collembola** external anatomy. Modified from Cooperative Extension illustration, University of Missouri.

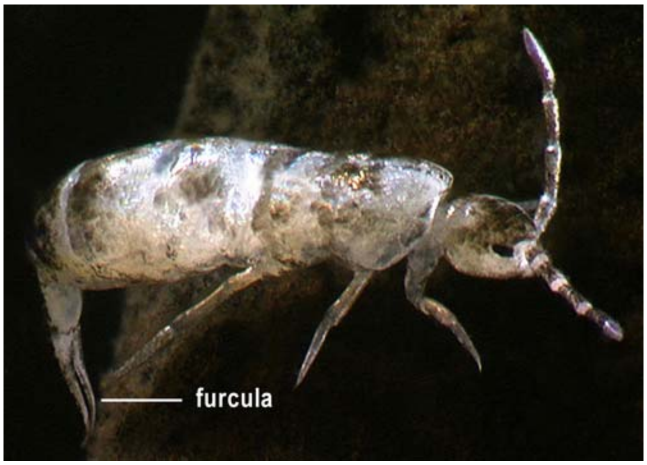


Figure 4. ***Arthropleona oruarangi*** showing furcula. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 5. ***Dicyrtomina ornata*** ventral side showing **furcula**. Photo by Jan van Duinen, with permission.

**Collembola** can be sexual or parthenogenetic. Sexual males deposit **spermatophores** in clusters or individually. Females stimulate this deposition by producing pheromones (Waldorf 1974). But among many of the soil **Collembola**, presumably including bryophyte dwellers, females lay eggs (Figure 7-Figure 8) that have not been fertilized, *i.e.*, are produed **parthenogenetically**. Since few reproductive studies exist, I cannot generalize of aquatic bryophyte dwellers. What makes this reproduction so interesting is the role of symbiotic bacteria in the genus ***Wolbachia*** (Werren *et al*. 1995). These bacteria live in and reproduce in the female reproductive organs and eggs of the springtail. It is these bacteria that control the parthenogenesis in the colonized species. That is, they feminize the springtails.

Figure 6. ***Isotoma*** (springtail) showing **collophore** (**arrow**). Photo by U. Burkhardt, through Creative Commons.

Figure 7. **Collembola** eggs. Photo by Jan van Duinen, with permission.

Figure 8. ***Sminthurides*** eggs in duckweed. Photo by Jan van Duinen, with permission.

The **Collembola** are predominately moist terrestrial organisms, but some can hop on the water surface (Figure 9) or live among wet mosses. Waltz and McCafferty (1979) considered only 10 species as semiaquatic and five as **riparian** (relating to bank of river or other moving water). The waxy cuticle (Chang 1966), coupled with small size, permits them to float on water. The **collophore** (ventral tube) serves a double function: absorption of water and respiration.

The **Collembola** seem to be particularly responsive to drawdown and drainage (Silvan *et al.* 2000). On older drained sites their numbers were up to 100 times as high compared to pre-drawdown. Other invertebrates were typically about ten times as high. The **Collembola** occurred mostly in the top 4 cm of the drained land.

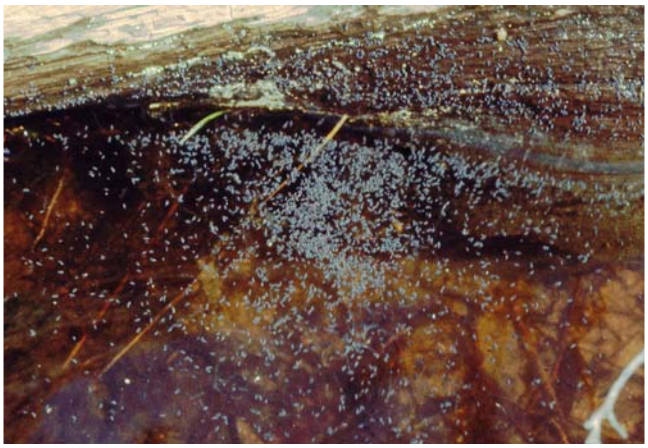

Figure 9. **Collembola** (springtails) on water where they can jump about on the surface tension. Photo by Janice Glime.

In my search for information on the bryophyte-dwelling springtails, I was surprised to find so little that related to aquatic habitats. In my own studies in the Appalachian Mountain, USA, streams, I found representatives of eight families, albeit not frequently. The species in these collections were ***Odontella lamellifera*** (Figure 10) (**Brachystomellidae**), ***Entomobrya griseoolivata*** (Figure 11) and ***Orchesella quinquefasciata*** (Figure 12) (**Entomobryidae**), ***Hypogastrura armatus*** (see Figure 13), and ***Schotella glasgowi*** (**Hypogastruridae**), ***Hydroisotoma schaefferi*** (Figure 14)**,** ***Isotoma violacea***, ***Isotoma viridis*** (Figure 15), and ***Isotomurus palustris*** (Figure 16) (**Isotomidae**), ***Pseudachorutes lunatus*** (**Neanuridae**; see Figure 17), ***Onychiurus subtenius*** (**Onychiuridae**), ***Sminthurides aquaticus*** (Figure 18) (**Sminthuridae**), and ***Tomocerus flavescens*** (Figure 19) (**Tomoceridae**). Of these taxa, only ***Isotomurus palustris*** was present in more than two collections. Nevertheless, I recorded ***Orchesella quinquefasciata*** in North America for the first time (Toliver Run, Garrett County, MD) (Richard Snider, pers. comm.). The ***Hydroisotoma schaefferi*** was an atypical blind form from Little Bennett Creek,. Montgomery Co., MD. Snider also found this species (not blind) in ponds surrounded with mosses in Michigan, USA (Snider 1967). It is likely that some of these springtails were living at the surface of emergent mosses. But the tiny size of these insects suggests they may have been missed in collections using insect nets. Others may have "sprung" away from surface locations as the collector approached.

Figure 10. ***Odontella*** cf. ***incerta***; ***O. lamellifera*** is a springtail that occasionally occurs among stream bryophytes in the Appalachian Mountains, USA. Photo by Andy Murray, through Creative Commons.

Figure 11. ***Entomobrya griseoolivata***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Domingo Zungri, through Creative Commons.

Figure 12. ***Orchesella quinquefasciata***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Malcolm Storey, through DiscoverLife Creative Commons.

Figure 13. ***Hypogastrura nivicola***; ***H. armatus*** is a springtail that sometimes occurs among Appalachian Mountain stream bryophytes in eastern USA. Photo by Scott Justis, with permission.

Figure 14. ***Hydroisotoma schaefferi***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Tom Murray, through Creative Commons.

Figure 15. ***Isotoma viridis***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Kyron Basu, through Creative Commons.

Figure 16. ***Isotomurus palustris***, an aquatic springtail that keeps its offspring together for two days after birth. Photo by Scott Justis, with permission.

Figure 17. ***Pseudachorutes*** sp.; ***Pseudachorutes lunatus*** lives among mosses in mountain streams. Photo by Jan van Duinen, with permission.

Figure 18. ***Sminthurides aquaticus***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Andy Murray, through Creative Commons.

Figure 19. ***Tomocerus flavescens***, a springtail that sometimes occurs among Appalachian Mountain stream bryophytes. Photo by Royce Bitzer, through Creative Commons.

## Isotomidae

The family **Isotomidae** was most frequently (almost exclusively among springtails) represented in the publications I found regarding bryophyte fauna. Among these, ***Isotomurus palustris*** (Figure 16) is most typically considered to be aquatic, although a few other species, including ***Sminthurus aquaticus*** (Figure 18), have names that suggest they are aquatic.

***Isotomurus palustris*** (Figure 16) is able to float on the water because of their non-wetting waxy epicuticle composed of a lipid monolayer that is extremely impermeable to water (Beament 1960). But Noble-Nesbitt (1963) provided evidence that the presence of wax gives it **hydrofuge** (shedding water) properties. A cementing substance contributes to this hydrofuge ability. The cuticle, combined with surface hairs, provides this springtail with a protective air layer that both makes these springtails **unwettable** (repelling water) and makes them float. Springtails also are very sensitive to desiccation, so the protection by the cuticle is important.

The **collophore** is **wettable** (doesn't repel water) and doubles as both a respiratory and water-taking organ (Noble-Nesbitt 1963). The air layer on the surface also behaves as a **plastron** (breast plate breathing apparatus). These springtails also take water by mouth and this may additionally supply dissolved oxygen. I wonder if they ever get hiccups! This tubule, combined with their small size, would permit them to drink water from the leaves of emergent mosses.

But it appears that the cuticle may also play an important role in their locomotion on the water surface (Noble-Nesbitt 1963). In the water, the furcula is used as a spring, much as it is on land. On the water surface the insect actually walks, using only its limbs.

***Isotomurus palustris*** (Figure 16) is **viviparous**, producing one egg at a time (Chang 1966). These eggs are carried internally and hatched inside the female with the nymph emerging from the genital pore. The female arches its body to permit the emerging nymph to reach the water surface. In observations on newborns of ***Isotomurus palustris*** (Figure 16) and *Folsomia fimetaria* (Figure 20), Chang found that the newborns stayed close to the mothers for the first two days. The young are able to float, walking on the surface tension with their **non-wetting** (repelling water) claws, but if they are forced to submerge they will sink. The cuticle does not develop until they spend time above water.

Figure 20. *Folsomia fimetaria*, a springtail whose newborns stay close to the mother for two days. Photo by Andy Murray, through Creative Commons.

Antennae are important in assessing the environment in both ***Isotomurus palustris*** (Figure 16) and *Folsomia fimetaria* (Figure 20). They are the sensory organ, often in consort with the post-antennal organ, that recognizes light intensity, wind direction, and heat. When one or the other of these organs is removed or cauterized, the springtails move about aimlessly or not at all, whereas those with both organs intact wiggle their antennae and exhibit a directional movement in response to the stimulus.

Some **Collembola** like it cold – ***Anurida frigida*** (**Neanuridae**) occurs under mosses on stones and on stones by melt-water brooks in the high alpine of Swedish Lapland (Fjellberg 1973). The greatest numbers of these were located under mosses that were wet by ice-cold meltwater. In the Nordic countries, ***Agrenia riparia*** prefers wet mosses, especially on lowland stream banks (Fjellberg 2007b)

## Bog Springtails

These tiny creatures seem often to be overlooked, but a treatment of **Collembola** in Michigan, USA, indicates that many species can occur in bogs (Snider 1967):

***Hypogastrura nivicola*** (**Onychiuridae**; Figure 21)
***Isotoma viridis*** (**Isotomidae**; Figure 15)
***Lepidocyrtus cyaneus*** (**Entomobryidae**; Figure 32)
***Lepidocyrtus lignorum*** (**Entomobryidae**; Figure 22)
***Lepidocyrtus unifasciatus*** (**Entomobryidae**)
***Lepidocyrtus violaceus*** (**Entomobryidae**; Figure 23) – in ***Sphagnum***
***Neelus minutus*** (Neelidae; see Figure 24)
***Orchesella ainsliei*** (**Entomobryidae**)
***Orchesella albosa*** (**Entomobryidae**)
***Pseudobourletiella spinata*** (**Sminthuridae**; Figure 25)
***Sminthurides aquaticus*** (**Sminthuridae**; Figure 18) – in ***Sphagnum***
***Sminthurides lepus*** (**Sminthuridae**)
***Sminthurides malmgreni*** (**Sminthuridae**; Figure 26) – semi-aquatic habitats
***Sminthurides occultus*** (**Sminthuridae**)
***Sminthurides penicillifer*** (**Sminthuridae**; Figure 27)
***Sminthurinus aureus*** (**Sminthuridae**; Figure 28)
***Sminthurinus bimaculatus*** (**Sminthuridae**; Figure 29)
***Tomocerus flavescens*** (**Tomoceridae**; Figure 19) – in ***Sphagnum***

Figure 21. ***Hypogastrura nivicola*** on snow. Photo by Charley Eiseman, through Creative Commons.

Figure 22. ***Lepidocyrtus lignorum***, a bog inhabitant. Photo by Jan van Duinen, with permission.

Figure 23. ***Lepidocyrtus violaceus***, a bog ***Sphagnum*** dweller. Photo by Jan van Duinen, with permission.

Figure 24. ***Neelus murinus*** carrying eggs; ***Neelus minutus*** is a bog dweller. Photo by Frans Janssens, with permission.

Figure 25. ***Pseudobourletiella spinata***, a bog inhabitant. Photo by Tom Murray, through Creative Commons.

Figure 26. ***Sminthurides malmgreni***, a bog inhabitant. Photo by Andy Murray, through Creative Commons.

Figure 27. ***Sminthurides*** nr. ***penicillifer*** female, a bog inhabitant. Photo by Andy Murray, through Creative Commons.

Figure 28. ***Sminthurinus aureus***, a bog dweller. Photo by Andy Murray, through Creative Commons.

Figure 29. ***Sminthurinus bimaculatus***, a bog dweller. Photo by Andy Murray, through Creative Commons.

In his treatment of the **Collembola** of Fennoscandia and Denmark, Fjellberg (2007a) included ***Maristoma canaliculata*** as a species usually found in ***Sphagnum*** and ***Maristoma tenuicornis*** in ***Sphagnum*** bogs. The treatment for Nordic Collembola (Fjellberg 2007b) includes ***Marisotoma canaliculata*** in ***Sphagnum*** ponds; ***Marisotoma tenuicornis*** in boreal ***Sphagnum*** bogs; ***Desoria olivacea*** (**Isotomidae**; Figure 30) common in acidic forest bogs; ***Desoria blufusata*** (Figure 31) in bogs and wet meadows; ***Lepidocyrtus cyaneus*** (**Entomobryidae**; Figure 32) common in humid habitats including ***Sphagnum***/*Salix* bogs; ***Sminthurides schoetti*** common in bogs and damp meadows; ***Sminthurides pseudassimilis*** in boreal ***Sphagnum*** bogs and smaller lakes, boreal; ***Sminthurides parvulus*** uncommon in bogs, wet meadows, and shores of lakes; ***Neelides minutus*** uncommon in bogs; ***Arrhopalites cochlearifer*** and ***Arrhopalites principalis*** (common) in bogs; ***Isotomurus unifasciatus*** (Figure 33) in forest bogs; ***Isotomurus balteatus*** in boreal bogs and wetlands; ***Dicyrtomina minuta*** and ***Dicyrtoma fusca*** (Figure 34) common in bogs; ***Heterosminthurus insignis*** in wet meadows and bogs.

Figure 30. ***Desoria olivacea***, a species of acidic forest bogs. Photo by Jan van Duinen, with permission.

Figure 31. ***Desoria blufusata***, a common species in bogs and wet meadows. Photo by Arne Fjellberg, through Creative Commons.

Figure 32. ***Lepidocyrtus cyaneus***, a species of ***Sphagnum*** bogs. Photo by Steve Hopkin, with permission.

Figure 33. ***Isotomurus unifaciatus***, a species of boreal bogs and wetlands. Photo by Jan van Duinen, with permission.

Figure 34. ***Dicyrtoma fusca***, a species common in bogs. Photo by Jan van Duinen, with permission.

Greenslade *et al*. (2006) suggests that ***Mesaphorura macrochaeta*** may have been introduced to the Southern Hemisphere by human importations of soil and moss peat.

## HEMIMETABOLA

The **hemimetabolous** insects are those with **incomplete metamorphosis**. Instead of a larva, they have a **nymph** or **naiad** stage that resembles the adult except for having reduced wings or only wing pads. They lack a pupa stage and pass directly from the nymph or naiad stage to the adult stage. Most of the aquatic Hemimetabola have a stage with gills and wing pads and are distinguished as **naiads**.

## EPHEMEROPTERA – Mayflies

As in most of the names of insect orders, *optera* refers to wings. In the **Ephemeroptera**, *ephemera* refers to short-lived. Hence, these are insects that are short-lived in the winged, or adult, stage.

The immature mayflies, known as **naiads**, are all aquatic (Thorp & Covich 1991). They can be distinguished by their three (two in some) long caudal filaments that are also present in the adults. They are most similar to the stoneflies (**Plecoptera –** see subchapter on Plecoptera in this chapter), but differ in having abdominal gills (lacking in middle abdominal segments of stoneflies) and typically three tails (caudal filaments), which always number two in stoneflies. Most of the naiads are herbivores and some eat bryophytes.

The mayfly naiads are largely night-active and appear most often in the night-time drift (Elliott 1967). Adult mayflies emerge from the naiad first as a **sub-imago** (also known as a **dun**; Figure 35-Figure 40), a stage that often becomes a nuisance to motorists (Figure 36) in the area because of the large numbers that meet their demise (Figure 37) on the windshields. To complete emergence they must climb so they can pump fluids into their new wings (Figure 41). The adult does not eat – in fact lacking mouthparts – and typically lives for only a few days.

Figure 35. ***Baetis*** male subimago emerging to adult. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

Figure 36. Adult mayflies on emergence day. Photo by Jeff Reutter, through Ohio Sea Grant public domain.

In my own studies in the Appalachian Mountain streams, USA (Glime 1968, 1994), the **Ephemerellidae** was by far the most abundant of the mayflies. Frost (1942) reported the importance of the mayflies ***Ephemerella*** (*s.l.*) (Figure 45) and ***Baetis*** (**Baetidae**; Figure 35-Figure 40) among aquatic mosses, where they feed mostly on algae, but occasionally on bryophytes (Hynes 1961; Chapman & Demory 1963). Frost (1942) found about 530 mayfly nymphs per 200 g of mosses in Ireland. In a cool mountain stream of central Japan, Tada and Satake (1994) found that ***Baetis thermicus*** (Figure 38) and ***Ephemerella*** (*s.l.*) sp.

were more abundant among the moss ***Platyhypnidium riparioides*** (Figure 39) than in bare rock areas.

Figure 37. Mayflies that met their end on a travelling car during an emergence in August in Michigan, USA. Photo by Eileen Dumire, with permission.

Figure 38. ***Baetis thermicus*** naiad, a common moss dweller of the moss ***Platyhypnidium riparioides*** in Japan. Photo from Shiiba Research Forest. Permission requested.

Figure 39. ***Platyhypnidium riparioides*** partially submersed at the edge of a waterfall. Photo by Michael Lüth, with permission.

Figure 40. ***Baetis*** sub-imago showing huge eyes. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

Figure 41. Emerging **Ephemeroptera**. Mayflies live their immature lives as naiads in the water of streams and lakes. When they emerge as adults, they must climb, like these naiads, so they can pump up their wings once they have exited the naiad exuvia. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

With such a dwarfed lifespan, finding a mate quickly is paramount. This is accomplished by flying in giant swarms, facilitated by coordinated emergence time. At this time, they are a nuisance for motorists and a feast for birds (Figure 42). Those females that survive deposit their eggs, often among mosses.

Figure 42. Hermit thrush (*Catharus guttatus*) with mayfly subimago in its beak, enjoying the brief period of emergence. Photo by Bob Armstrong, with permission.

Increased biomass of bryophytes may increase some insects while having no effect on others. Lee and Hershey (2000) found that a dense growth of the moss ***Hygrohypnum*** (Figure 43-Figure 44) following stream fertilization in Alaska increased the density of the mayfly ***Ephemerella aurivillii*** (Figure 45) but not ***Baetis*** (Figure 46). In the fertilized zone, these mayflies both grew larger, a fact Lee and Hershey attributed to the greater growths of epiphytic diatoms. Furthermore, although the density of ***Ephemerella*** increased with increased moss density, the highest drift ratios were in the unfertilized zone with lower moss density. In enclosure experiments, they found that bare rock, mosses, and artificial mosses had no effect on any taxa except ***Ephemerella***. They considered that the ***Ephemerella*** benefitted from the increased complexity of the moss habitat.

Figure 43. ***Hygrohypnum ochraceum***, home for a variety of stream insects. Photo by Michael Lüth, with permission.

Figure 44. Close view of ***Hygrohypnum ochraceum***, home for a variety of insects. Photo by Michael Lüth, with permission.

Figure 45. ***Ephemerella aurivillii*** naiad, a mayfly that increased with increased coverage of ***Hygrohypnum*** in Alaska. Photo by Tom Murray, through Creative Commons.

Figure 46. ***Baetis*** naiad, a bryophyte inhabitant in many streams. Photo by Bob Henricks, with permission.

Jones (1950) did extensive gut analysis of insects from the River Rheidol. Among the **Ephemeroptera**, none of the five species examined had fragments of the common moss ***Fontinalis antipyretica*** (Figure 47) in the gut. Detritus was the most common food. Gilpin and Brusven (1970) found six mayfly species with ***Fontinalis*** sp. in their guts, but these all amounted to less than 1% of the gut contents.

Figure 47. ***Fontinalis antipyretica***, a moss found in the guts of some mayflies in the River Rheidol. Photo by Kristian Peters, with permission.

It is surprising to find such flattened, rock-adapted genera as ***Heptagenia*** (Figure 48) among mosses, but Muttkowski and Smith (1929) did find it several times among mosses in trout streams of Yellowstone National Park, USA.

Figure 48. ***Heptagenia dalecarlica*** naiad, a flattened species adapted for smooth rocks, but that occasionally visits mosses. Photo by Urmas Kruus, with permission.

## Suborder Furcatergalia

### Leptophlebiidae – Prong-gilled Mayflies

This is a family that lives in freshwater streams and lakes where the naiads eat detritus and algae (Leptophlebiidae 2013). Their length is up to 20 mm; they are **nocturnal** (active at night) and are poor swimmers, generally clinging to rocks. Only a few seem to live among bryophytes.

***Paraleptophlebia*** (Figure 49) was a minor component of the bryophyte communities in my own Appalachian, USA, stream studies (Glime 1968). Maurer & Brusven (1983) found ***Paraleptophlebia heteronea*** (Figure 49) frequently in the clumps of ***Fontinalis neomexicana*** (Figure 79) in an Idaho stream. In their study of four Appalachian streams, Woodall and Wallace (1972) found this genus where there was moderate or slow current among decaying leaves, bark, and wood. Its food is predominately detritus (Chapman & Demory 1963).

Figure 49. ***Paraleptophlebia*** sp. naiad, a frequent dweller among ***Fontinalis neomexicana***. Photo by Jason Neuswanger, with permission.

Macan (1957) found ***Leptophlebia*** (Figure 50) among mosses in Ford Wood Beck, UK. Berner (1959) described this genus as one that would live in submerged mossy banks and other quiet areas. The genus is negatively **phototactic** (movement of organism toward or away from source of light), explaining their presence in the secluded shade of streambank mosses. When it is time for the naiads to emerge into adults, they become positively phototactic and crawl upward onto sticks, logs, or other protruding structure, probably including emergent bryophytes.

Vuori *et al.* (1999) considered ***Leptophlebia marginata*** (Figure 50) to be among the dominant moss dwellers in the Tolvajärvi region of the Russian Karelia. Bengtsson (1981) found that ***L. marginata*** demonstrated a steady growth rate throughout winter, permitting it to thrive in such northern regions.

Figure 50. ***Leptophlebia marginata*** naiad on waterweed. Photo by Niels Sloth, with permission.

One advantage enjoyed by some members of this family is tolerance of somewhat low *p*H. Mayflies in general are indicators of fresh, unpolluted water. They do not generally tolerate extremes, low *p*H included (Raddum & Fjellheim 1988; Raddum *et al.* 1988; Braukmann 1992; Lingdell & Engblom 1995). Thus the streams that drain ***Sphagnum*** fens and bogs (Figure 51) are generally **depauperate** (lacking in numbers or kinds of species) of mayflies. However, this habitat is suitable for a few, including ***Leptophlebia vespertina*** (Figure 52) (Bauernfeind & Moog 2000). This intolerance of low *p*H may explain its relative rarity among bryophytes in the mid-Appalachian Mountain streams (Glime 1968).

Figure 51. ***Sphagnum affine***, member of a genus that contributes $H^+$ ions, lowering the *p*H of bogs and their outflow waters. Photo by Michael Lüth, with permission.

Figure 52. ***Leptophlebia vespertina*** adult, a species whose naiads can inhabit the acid outflows of acid bog lakes. Photo by Niels Sloth, with permission.

In New Zealand ***Austroclima sepia*** (see Figure 53) frequently lives among mosses in small waterfalls (Winterbourn & Gregson 1981). Similarly, Towns (1987) reported this species along with ***A. jollyae*** and ***Mauiulus luma*** (Figure 54) as 72%, 13%, and 9%, respectively, of the fauna from mosses in rapid flow (where only 4 insect species lived!) on the Great Barrier Island, New Zealand.

Figure 53. ***Austroclima*** naiad, a genus with moss dwellers in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 54. ***Mauiulus luma*** naiad, a mayfly that lives among mosses in small waterfalls in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.

In his study of the River Rajcianka, Krno (1990) found a genus I have not encountered elsewhere – ***Habroleptoides***. ***Habroleptoides modesta*** (Figure 55) is a bryophyte dweller in the river, but like many of the mayfly genera, it is unable to live among the wet mosses above the water level.

Figure 55. ***Habroleptoides modesta*** naiad, a mayfly that sometimes lives among bryophytes in rivers. Photo by Alfeo Busilacchio, with permission.

## Caenidae - Small Squaregill Mayflies

The **Caenidae** are small sprawlers in quiet and sometimes stagnant water as well as streams (Caenidae 2014). They are adapted to the relatively low oxygen of silt.

***Caenis*** (Figure 56) seems to prefer loose mosses (Percival & Whitehead 1929). Frost (1942) found that it was most likely to occur among mosses that had accumulated considerable silt. In the River Rajcianka in Slovakia, ***Caenis beskidensis*** (Figure 56) lives among submerged bryophytes but is not found, like some mayflies, among the wet emergent bryophytes (Krno 1990). In the Appalachian Mountain, USA, streams naiads of ***Caenis*** were among the lesser of the moss inhabitants, appearing mostly among ***Fontinalis dalecarlica*** (Figure 69).

Figure 56. ***Caenis lactea*** naiad, a mayfly that prefers loose mosses. Photo by Niels Sloth, with permission.

## Neoephemeridae

The rare genus ***Neoephemera*** (Figure 57) sometimes lives deep within submerged moss mats in rapid water in eastern North America (Berner 1959), including

***Neoephemera compressa*** (Figure 57) among mosses on submersed parts of trees (Berner 1956). The naiad moves slowly, but when it bends its 3 tails over its abdomen, then suddenly lashes them back, this action propels it forward (see Figure 60).

Figure 57. ***Neoephemera compressa***, an inhabitant of mosses on submersed parts of trees. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

In Australia, ***Neoephemera*** (Figure 57) naiads live in protected parts of streams with slow to moderate flow where they hide among debris, plant roots, and mosses (Edmunds *et al*. 1976). These naiads are difficult to dislodge from the mosses, partly because they grip the mosses. The membranous respiratory gills are fragile and they need the protection that is provided by the fused, sclerotized **opercula** (gill covers) (Notestine 1994). This genus relies heavily on these gills for respiration.

## Ephemerellidae – Spiny Crawlers

This family occurs throughout North America as well as the United Kingdom (Ephemerellidae 2014). These collector-gatherers occur where there is moving water, including lake shores subject to wave action, but seem to require reduced flow. They are able to live in fast water by accepting the protection of bryophytes.

When these mayfly naiads are threatened by a predator, they raise their three tails like a scorpion, arching them up and over their backs, making them appear larger (Ephemerellidae 2014). They will then project the tails forward to poke the enemy. Spines on the back of the abdomen (Figure 58) may contribute to their protection. One suggestion is that the spines help the mayflies hold their positions when attacked from behind by a predator.

This family takes advantage of the protection of the bryophyte habitat while modulating the oxygen and keeping its tuft of gills clean with its gill covers. When oxygen concentrations become too low, the **Ephemerellidae** move the gill covers (Figure 58) up and down to keep fresh water circulating across the gills (Figure 59) (Ephemerellidae 2014). Their bodies are somewhat flattened dorsiventrally and are adapted to crawling among the chambers of their mossy habitat. When they are in open water and need to move quickly, mayflies in this family flip their tails upward over their backs and down to act like a paddle (Figure 60), thrusting them forward.

Figure 58. ***Ephemerella subvaria*** naiad gill covers, closed over gills. Photo by Tom Murray, through Creative Commons.

Figure 59. ***Drunella*** sp. naiad with gill covers up to expose the tufts of gills. Photo by Bob Henricks, with permission.

Figure 60. ***Ephemerella subvaria*** naiad in a swimming position with its tails flipped upward. Photo by Bob Henricks, with permission.

Berner (1959) described some members of this family as living on the tops of rocks, deep within the moss. Arnold and Macan (1969) found that **Ephemerellidae** (Figure 58-Figure 64) were common among mosses in a

Shropshire Hill stream in the UK. In a study of the McKenzie River, Oregon, USA, Hawkins (1984) reported that 5 species [***Serratella teresa***, ***C. hystrix*** (Figure 61), ***Caudatella cascadia*** (now a synonym of ***C. hystrix***), ***C. edmundsi*** (Figure 62), and ***Drunella spinifera*** (Figure 63)] out of 12 **Ephemerellidae** species were common among mosses, including ***Fontinalis*** sp. (Figure 79) and others. Gilpin and Brusven (1970) likewise found ***C. edmundsi*** among clumps of ***Fontinalis***. Hawkins (1984) found those restricted to mosses were usually at upstream locations where the mosses were abundant. However, two moss dwellers [***Caudatella edmundsi*** (100% moss usage - found only on ***Fontinalis***), ***Drunella spinifera*** (54%)] were most abundant downstream, living among mats of the moss ***Fontinalis*** sp. For other species with more than 5% use of bryophyte habitats he found ***Serratella teresa*** (85%), ***Caudatella cascadia*** (46%), and ***Caudatella hystrix*** (22%).

Brittain and Saltveit (1989) found that river impoundments had "profound" effects on the **Ephemerellidae** (Figure 58-Figure 64) living there. Changes in temperature, discharge, flow patterns, food availability, and predator density all contribute to changes in living conditions for the mayflies. Increased growth of mosses and additional available substrata for periphyton below the dams often favor some of the **Ephemerellidae** while reducing suitable habitat for **Heptageniidae** (Figure 48). The mayflies living under these changeable regimes often have flexible life cycles or shorter periods of rapid growth with a long period of egg development that permit them to survive unsuitable periods.

Figure 61. ***Caudatella hystrix*** naiad, a common moss dweller in the McKenzie River, Oregon, USA. Photo by Bob Newell, with permission.

Figure 62. ***Caudatella edmundsi*** naiad, a common moss dweller. Photo by Bob Newell at <Troutnut.com>, with permission.

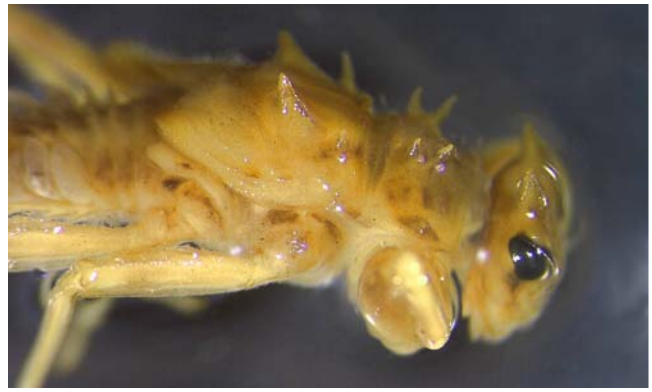

Figure 63. ***Drunella spinifera*** naiad. Photo by Bob Newell at <Troutnut.com>, with permission.

Percival and Whitehead (1929) considered mosses and algae to be the main food of the **Ephemerellidae** (Figure 58-Figure 64). Woodall and Wallace (1972) found ***Eurylophella funeralis*** (=***Ephemerella funeralis***, Figure 64) to be the most abundant ***Ephemerella*** species among mosses in the southern Appalachian Mountains, USA, and I found a similar relationship for ***E. funeralis*** and ***E. temporalis*** in the middle Appalachian Mountain streams (Glime 1968). The members of ***Ephemerella*** tended to avoid the heavily shaded hardwood stream where mosses and algae were scarce.

Figure 64. ***Eurylophella funeralis***, a common mayfly among mosses in the southern Appalachian Mountain, USA, streams. Photo by Donald S. Chandler, with permission.

Brittain and Saltveit (1989) found that growth of mosses and associated periphyton below dams favored presence of **Ephemerellidae** (Figure 58-Figure 64). They reasoned that flexible life cycles permitted them to survive adverse conditions, including rapid nymphal growth and long period of egg development. Eggs typically form a ball (Figure 65).

Percival and Whitehead (1929) found ***Eurylophella funeralis*** (=***Ephemerella funeralis***) (Figure 64) to be the most abundant species of the ***Ephemerella*** genus group in their study of UK streams. The main foods of ***Ephemerella*** species are algae and mosses (Percival & Whitehead 1929; Jones 1949, 1950; Gerson 1969). This is convenient because this genus is common among mosses, but it also occurs on the pebbles on the bottom. Jones (1949, 1950) found that ***Ephemerella*** *s.l.* fed primarily on ***Fontinalis*** (Figure 47) and the alga *Ulothrix* (Figure 66) in **calcareous** (having dissolved chalk or limestone) streams of South

Wales. Among 14 specimens examined on 14 July the moss was the primary food, but they concluded that ***Ephemerella*** feeds on *Ulothrix* when it is abundant but switches to ***Fontinalis antipyretica*** (Figure 47) when the *Ulothrix* becomes scarce.

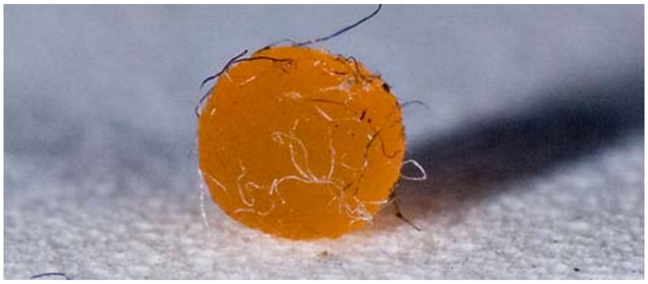

Figure 65. ***Ephemerella*** egg mass with debris stuck to it. Photo by Jason Neuswanger at <Troutnut.com>, with permission.

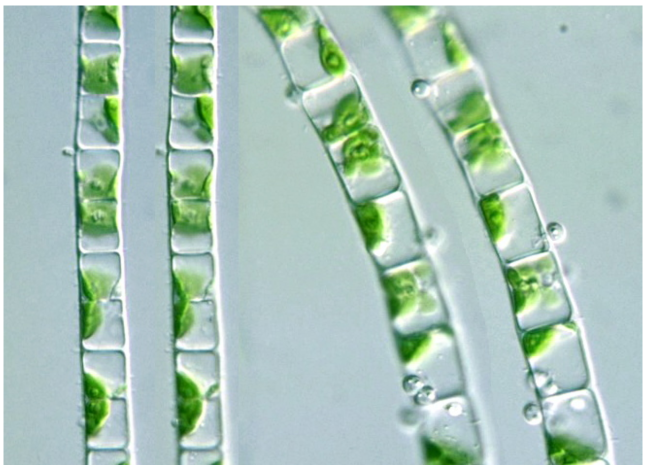

Figure 66. ***Ulothrix***, food for ***Eurylophella funeralis***. Photo by Yuuji Tsukii, with permission.

Reproduction in the mayflies involves swarming, a behavior that maximizes contact of males and females that typically live for only one day as adults. In ***Serratella ignita*** (Figure 67) this swarming occurs in the late afternoon and evening (Elliott & Humpesch 1980). The egg mass is a greenish ball. Once fertilized, eggs are laid in turbulent water, usually where there are mosses. The female flies upstream to deposit the eggs on the water surface. She then usually falls on the surface and is vulnerable to fish predation. The egg mass separates when it enters the water and each egg attaches to the substrate with its polar anchoring cap.

Figure 67. ***Serratella ignita*** naiad. Photo by J. C. Schou, through Creative Commons.

The family **Ephemerellidae** (Figure 58-Figure 64) seems to have bryological preferences, or preferences that match those of the bryophytes. They reach extremely high numbers among ***Hygroamblystegium fluviatile*** (Figure 68) in mid-Appalachian streams, but are nearly absent in ***Fontinalis dalecarlica*** (Figure 69) and ***Scapania undulata*** (Figure 70) in different streams (Glime 1968).

Figure 68. ***Hygroamblystegium fluviatile***, home to large numbers of **Ephemerellidae**. Photo by Michael Lüth, with permission.

Figure 69. ***Fontinalis dalecarlica***, a stream moss that houses some of the larger insects. Photo by Jan-Peter Frahm, with permission.

Figure 70. ***Scapania undulata***, a leafy liverwort that has few of the typical moss-dwelling **Ephemerellidae**. Hermann Schachner, through Creative Commons.

D. N. Bennett (pers. comm. 19 April 2011) described her field experience with an aquatic entomologist, Bob Henricks. Henricks was attempting to distinguish between mosses and grasses, so she began looking at the inhabitants of the mosses. When the moss-covered rocks were removed from the stream, the insects began moving about and became more noticeable. There were often 40-50 **Ephemerellidae** naiads on a single moss-covered rock – determined to be ***Hygroamblystegium***, probably ***H. tenax*** (Figure 71-Figure 72). The moss grew on and "under" the rock, and it was the submersed "under" portion that housed the many mayflies. She observed the naiads rolling up the algae from the moss leaf surface, starting at the leaf tip and moving to the stem.

Figure 71. ***Hygroamblystegium tenax*** in a dry stream bed. Photo by Janice Glime.

Figure 72. ***Hygroamblystegium tenax***, home to many kinds of stream insects, including **Ephemerellidae**. Photo by Jan-Peter Frahm, with permission.

## Seasons

Seasonal differences in the life cycle stages spent in the water are often the key to success for these species. Timing differences in emergence times and hatching times can separate realized niches in closely related species. In the **Ephemerellidae** (Figure 58-Figure 64), the life cycle is typically one year with one brood per year (**univoltine**). For example, ***Serratella ignita*** (Figure 1) has an annual cycle with the eggs spanning the winter in a dormant state, hatching in April and May in the River Endrick in Scotland (Maitland 1955). The naiads develop quickly, emerging in July and August, and adults typically lay eggs within 24 hours of emergence. These eggs are often laid among mosses in abundance (Percival & Whitehead 1928). The eggs are laid in evening light and are caught by ***Platyhypnidium riparioides*** (Figure 39) and ***Fontinalis*** species (Figure 47) where they adhere as a greenish gelatinous mass.

In a Shropshire Hill stream in the UK, Arnold and Macan (1969) found that the longest stage in ***Serratella ignita*** (Figure 1) was the egg, a stage that remained from late summer one year to late spring the next year, hence overwintering as an egg (Elliott 1967). Rosillon (1988) found that completion of naiad development on a diatom diet required about 950 **degree-days** above a temperature of 3.5°C (range 9.5-18°C). [Degree days for insect development can be calculated by adding the minimum and maximum temperature of the day and dividing by 2. The minimum required for development is subtracted from that number to determine how many degree-days have been added that day. (Townsend *et al*. 2010)]. Those reared on detritus rarely achieved adult stage. Rosillon suggested that poor food quality would reduce **fecundity** (reproductive rate) of females. Furthermore, it appears that under ideal conditions ***Serratella ignita*** could have a **bivoltine** (2 broods per year) life cycle.

Emergence patterns can be gleaned from the stages of the naiad development of mayflies in samples. Based on such sampling, Gurtz & Wallace (1984) estimated that in a stream in the southern Appalachian Mountains, USA, the moss inhabitants ***Ephemerella catawba*** (Figure 73) probably emerged from May to July, ***E. hispida*** from April to June, ***E. excrucians*** (Figure 81) in May and June, and ***Drunella tuberculata*** (Figure 74) from June to September. Both ***Ephemerella catawba*** and ***Ephemerella invaria*** occurred among mosses in the acidic mid Appalachian streams in my own studies (Glime 1968). ***Ephemerella invaria*** (Figure 75) increased in Big Hurricane Branch following a clearcut, but no specimens with fully developed wing pads were ever collected, suggesting that nymphs of this species might complete their development farther downstream in Shope Creek (Gurtz & Wallace 1984).

Figure 73. ***Ephemerella catawba***, a moss inhabitant as a naiad that emerges May to July in the southern Appalachian Mountains, USA. Photo by Biodiversity Institute of Ontario, through Creative Commons.

Figure 74. ***Drunella tuberculata***, a summer emerger. Photo by Bob Henricks, with permission.

Figure 75. ***Ephemerella invaria*** naiad. Photo by Bob Henricks, with permission.

***Ephemerella invaria*** (Figure 75) occurred both above and below a hydroelectric plant on the Sturgeon River in northern Michigan, USA, with similar abundance and growth (Mundahl & Kraft 1988). ***Ephemerella subvaria*** (Figure 76) naiads were 4x as abundant below the plant (136 $m^{-2}$ below vs. 33 $m^{-2}$ above), but grew more slowly there. Nevertheless, the growth rate increased with distance downstream from the power plant for nearly 10 km. Extensive beds of ***Fontinalis*** (pers. obs.) may have contributed to the improved growth rates, with the mosses serving as traps for **seston** (swimming or floating living organisms and non-living matter) being released from the reservoir. Both of these species occur among bryophytes in streams of the mid Appalachian Mountains, USA (Glime 1968).

Figure 76. ***Ephemerella subvaria*** naiad. Photo by Donald S. Chandler, through Creative Commons.

## Food

The **Ephemerellidae** (Figure 58-Figure 64) are the most commonly reported mayflies among the bryophyte consumers (Table 1). ***Caudatella hystrix*** (as ***C. cascadia***; Figure 61) varies its diet depending on the site (Coffman *et al*. 1971; Hawkins 1985). Detritus is important in its diet, but the proportion decreases when that of moss increases (Hawkins 1985). The naiads of ***Caudatella edmundsi*** (Figure 62, Figure 101) feed primarily on diatoms, but also include detritus and mosses in their diet. Hawkins found that as size increased in the **Ephemerellidae**, especially in ***Caudatella edmundsi*** and ***Ephemerella dorothea infrequens*** (Figure 80), the consumption of both animal matter and mosses increased. Hawkins found that eight species demonstrated a correlation between moss consumption and size. López-Rodríguez *et al.* (2008) likewise found that the proportion of mosses in the diet increases in **Ephemerellidae** as naiads age. Several researchers (Hynes 1941; Chapman & Demory 1963; Gaevskaya 1969) found that mosses are eaten by members of this family more often than other aquatic macrophytes (not including algae). But it is not clear if the moss is eaten for its own food value or for the attached periphyton. Percival and Whitehead (1929) found that two species in this family ingested large amounts of moss, suggesting that the moss itself was an important food source. Among the members of **Ephemerellidae** studied by Hawkins (1985), ***Caudatella edmundsi***, ***C. heterocaudata***, ***C. hystrix***, and ***Serratella teresa*** were moss shredders. Others living among the mosses and ingesting them were detritus shredders, including ***Attenella margarita*** (Figure 77), ***Ephemerella dorothea infrequens***, ***E. excrucians*** (Figure 81), ***E. velmae***, ***Serratella tibialis*** (Figure 84), and ***Timpanoga hecuba*** (Figure 78). ***Drunella pelosa*** is a diatom scraper, permitting it to eat the many diatoms adhering to the moss leaves.

Table 1. Correlations between size (mm) and percent composition of major food items in the gut. Values are correlation coefficients ($r$). * = $P<0.05$; ** = $P < 0.01$. Percentages arcsine-transformed prior to analysis. From Hawkins 1985.

| Species | n | diatoms | detritus | animal | moss | wood | fungus |
|---|---|---|---|---|---|---|---|
| *Caudatella cascadia* (=*C hystrix*) | 18 | 0.191 | 0.149 | – | -0.369 | 0.027 | -0.518* |
| *Caudatella hystrix* | 23 | -0.550** | 0.166 | 0.203 | 0.398 | -0.213 | -0.117 |
| *Caudatella edmundsi* | 17 | -0.115 | -0.609** | 0.313 | 0.573* | – | – |
| *Serratella teresa* | 21 | 0.660** | -0.550** | -0.183 | 0.001 | – | -0.412 |
| *Serratella tibialis* | 13 | -0.095 | -0.199 | 0.160 | 0.424 | – | – |
| *Ephemerella dorothea infrequens* | 60 | -0.129 | -0.177 | 0.109 | 0.295* | 0 | 0.080 |
| *Drunella spinifera* | 33 | 0.037 | 0.050 | -0.016 | -0.057 | -0.035 | -0.128 |
| *Drunella doddsi* | 36 | -0.067 | -0.324 | 0.211 | -0.255 | – | -0.165 |
| *Drunella coloradensis* | 65 | -0.313** | -0.138 | 0.433** | 0.144 | -0.168 | -0.142 |
| *Drunella pelosa* | 29 | -0.463* | 0.256 | 0.179 | 0.330 | – | – |
| *Drunella grandis* | 5 | -0.863 | -0.371 | 0.394 | 0.245 | – | 0.158 |
| All species | 359 | -0.115* | -0.099 | 0.257** | 0.008 | -0.034 | -0.067 |

Figure 77. ***Attenella margarita*** naiad, a moss shredder. Photo by Donald S. Chandler, with permission.

Figure 78. ***Timpanoga hecuba*** naiad, a detritus shredder. Photo by Bob Newell, with permission.

### *Ephemerella*

***Ephemerella*** and its segregates are usually the most common mayflies among mosses. Needham & Christenson (1927) reported ***Ephemerella*** s.l. from moss-covered boulders in streams of northern Utah, USA. In their study of colonization of ***Fontinalis neomexicana*** (Figure 79) in Idaho, USA, Maurer and Brusven (1983) found ***E. dorothea infrequens*** (Figure 80) to be common among these mosses. In the St. Maries River of Idaho, USA, Gilpin and Brusven (1970) occasionally found ***E. excrucians*** (Figure 81) and ***E. dorothea infrequens*** clinging to ***Fontinalis*** and other vegetation, but mostly they were on submerged logs and rocks. Nevertheless, mosses comprised 8% of the diet of this variety (Hawkins 1985).

Figure 79. ***Fontinalis neomexicana***, home to several species of ***Ephemerella*** naiads. Photo by Belinda Lo, through Creative Commons.

Figure 80. ***Ephemerella dorothea infrequens*** naiad. Photo by Bob Henricks, with permission.

Figure 81. ***Ephemerella excrucians***, a common inhabitant of ***Fontinalis neomexicana*** in streams of Idaho, USA. Photo by Jason Neuswanger, with permission.

In Straffan, UK, ***Ephemerella notata***, a species once considered close to ***Serratella ignita***, lived among mosses (Frost 1942; Kimmins & Frost 1943), including ***Fontinalis*** (Figure 47) (Kimmins & Frost 1943). Although ***Ephemerella*** sometimes eats a considerable diet of bryophytes, Jones (1950) did not find moss tissue in the guts of any of the five species of mayflies, including ***Ephemerella notata***, in the River Rheidol, UK.

Bob Henricks reported 40-50 spiny crawlers (***Ephemerella***) on a mossy rock in a stream. He noted that in this stream the mosses held tiny sand grains and minute rocks instead of fine silt. In the mountain streams the mosses held fine silt and organic matter with many fewer of these mayflies. They avoid the mosses that grow on the tops of rocks and that float on the surface where the moss reaches the air. Rather, they tend to be on the under-surface of the mosses that wrap around the rocks in the water (Figure 82).

Figure 82. ***Ephemerella*** on rock with mosses. The mayflies blend with the algal-detrital mat on the mosses. Photo by D. N. Bennett, with permission.

Bengtsson (1981) found that ***Ephemerella mucronata*** (Figure 83) demonstrated a steady growth rate throughout winter in Sweden. This species has an interesting niche in the River Rajcianka, Slovakia, where it occurs among the wet emergent bryophytes but not among the submerged ones (Krno 1990).

Figure 83. ***Ephemerella mucronata***, a mayfly that continues to grow throughout winter in Sweden. Photo by Biodiversity Institute of Ontario, through Creative Commons.

### *Serratella*

***Serratella tibialis*** (Figure 84) is a collector-gatherer, feeding on detritus (Aquatic Insects 2008). Both early instars and mature naiads are common among mosses, including ***Platyhypnidium riparioides*** (Figure 39) and ***Fontinalis antipyretica*** (Figure 47) (Langford & Bray 1969). ***Serratella teresa*** occurs on mosses and other vegetation in swiftly-flowing streams (Allen & Edmunds 1963). In the McKenzie River, Oregon, USA, Hawkins (1984) found that 85% of the individuals of this species sampled were in clumps of ***Fontinalis*** sp. (Figure 79). Furthermore, 17% of the food for ***S. teresa*** in Oregon was mosses (Hawkins 1985).

Figure 84. ***Serratella tibialis***, a naiad common among mosses in both its young and older stages. Photo by Bob Henricks, with permission.

In Straffan, UK, Frost (1942) found that ***Serratella ignita*** (Figure 67) lived among mosses. Percival and Whitehead (1929) found that mosses form the primary habitat for ***S. ignita***, and that the moss also is its dominant food, an observation consistent with that of López-Rodríguez *et al*. (2008). Langford and Bray (1969) found this species among ***Fontinalis antipyretica*** (Figure 47) and ***Platyhypnidium riparioides*** (Figure 39) as well as on bare sand and tracheophytes in Britain.

Macan (1957) found that among the streams he studied in Ford Wood Beck, UK, the abundance of ***Serratella ignita*** (Figure 1, Figure 67) increased as the flow became more sluggish and the vegetation became thicker. In all streams, this species was more common when either tracheophytes or mosses were present. In faster streams, this relationship with mosses might explain the presence of this species. Furthermore, this species is able to move about in the wet moss mats above the water level (Krno 1990). ***Serratella ignita*** is among the species that not only live among mosses, but it also eats them (Percival & Whitehead 1929).

***Serratella ignita*** (Figure 1, Figure 67) usually lays its eggs where moss is present in fast-flowing water (Elliott 1978). The development time for the eggs depends on the temperature, with hatching time decreasing with increasing water temperature in the range of 5.9-14.2°C. However, at higher temperatures the hatching time increases with temperature. Correlations of naiad numbers with moss coverage may be a correlation with temperature.

***Serratella ignita*** (Figure 67) prefers a flow of 10-30 cm $sec^{-1}$ (Macan 1962). Willoughby and Mappin (1988) were unable to find it in upland streams of the River Duddon where the *p*H was low (4.8-5.2), but it did occur in lowland streams with *p*H values of 6.6 and higher. But it appears that the *p*H was not the direct cause of its absence. In the lab, it was very tolerant of low *p*H and low ion content, and growth rates were equally good whether food supplied was that available in low *p*H streams (liverwort ***Nardia compressa*** (Figure 85) plus the filamentous alga ***Klebsormidium subtile*** (**Charophyta**; see Figure 86) or that available in high *p*H streams [moss ***Platyhypnidium riparioides*** (Figure 39) with the epiphytic diatom ***Cocconeis placentula*** (**Bacillariophyta**; Figure 87). Nevertheless the absence of ***K. subtile*** as a food at the higher *p*H seems to account for the absence of ***S. ignita*** there. Percival and Whitehead (1929) found mosses in the guts of ***Serratella ignita*** in Great Britain. But are the mosses really a preferred food? In preference experiments, Rosillon (1988) found that ***S. ignita*** preferred diatoms over detritus. In these experiments, the growth rate was significantly higher on the diatom diet than that on the detritus diet, no matter what the temperature. In fact, larvae reared on the detritus diet had slower development and usually failed to reach the adult stage. If diatoms are the preferred food, eating the moss may simply be the most efficient means of obtaining them.

Figure 85. ***Nardia compressa***, a leafy liverwort in low *p*H streams where ***Serratella ignita*** feeds. Photo by David T. Holyoak, with permission.

Figure 86. ***Klebsormidium flaccidum***, a congener of ***K. subtile*** that is an important food for ***Serratella ignita*** in the bryophyte habitat. Photo by Sarah Kiemle, with permission.

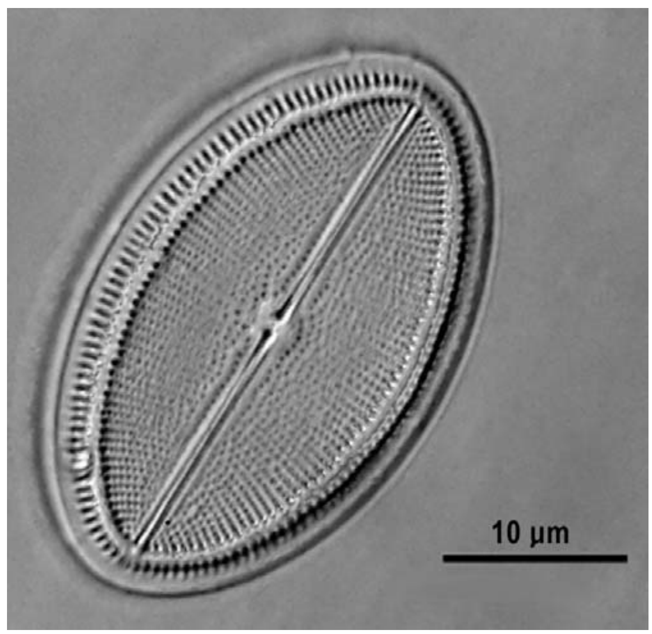


Figure 87. ***Cocconeis placentula***, a common epiphyte on aquatic bryophytes and important food for ***Serratella ignita***. Photo by Ralf Wagner, with permission.

Rosillon (1988) demonstrated that temperature was an important factor in determining mortality for ***Serratella ignita*** (Figure 67). Furthermore, as the temperature increased, mortality was higher on the detritus diet than on the diatom diet. The bryophytes are more likely to be abundant in the cooler habitats, often being overtaken by algal and microbial growth where it is warmer.

***Serratella serratoides*** (Figure 88) occurs primarily among ***Hygroamblystegium fluviatile*** (Figure 68) – ***Platyhypnidium riparioides*** (Figure 39) mats in Appalachian Mountain, USA, streams (Glime 1968). In the southeastern USA it burrows into the moss mats a few cm below the surface (Berner & Allen 1961).

Figure 88. ***Serratella serratoides*** naiad. Photo by Bob Henricks, with permission.

Even for this common moss-dwelling genus, other substrata are often acceptable as well. ***Serratella spinosa nevadensis*** (as *Ephemerella ikonomovi nevadensis*) only occurred in soft water in Spain, living at margins or midstream where roots, moss, algae, or other form of vegetation, along with detritus, was present (Alba-Tercedor 1990; López-Rodríguez *et al*. 2008). Unlike most of the **Ephemerellidae** that increase moss consumption with size, the naiads of ***S. spinosa nevadensis*** increase the percentage of detritus in the diet as they grow larger.

Some **Ephemerellidae** take advantage of ecosystem engineering by other insects. They are poor swimmers that need to cling to vegetation or other objects for support in the current (DEP 2014). ***Serratella setigera*** prefers slow flow (Nakano *et al*. 2005). In field experiments on artificial substrata, this species took advantage of the flow reduction in retreats of the net-spinning caddisfly ***Hydropsyche orientalis*** (Figure 89). In the experiments, those living on experimental plates with no caddisflies were mostly lost during high flow events, whereas none of the naiads in the caddisfly retreats were lost. It is likely that bryophytes provide similar retreats on rocks for some members of this genus. The researchers suggested that in the complex habitat created by mosses, the advantages provided by the ***Hydropsyche*** retreats would weaken. ***Hydropsyche orientalis*** occurs in moss mats of ***Platyhypnidium riparioides*** (Figure 39) in Japan (Takemon & Tanida 1992), but I could find no documentation that ***Serratella setigera*** likewise occurs there.

Figure 89. ***Hydropsyche orientalis*** larva, provider of retreats for ***Serratella setigera***. Photo by Takao Nozaki, with permission.

### *Teloganopsis*

***Teloganopsis*** (=*Serratella*) ***deficiens*** (Figure 90-Figure 91) is known from bryophytes in eastern North America (Allen & Edmunds 1963; Glime 1968). In the southeastern states it lives primarily among mosses and other plants in rocky, swift streams, but in Michigan it also occurs among detritus (Allen & Edmunds 1963). Among the mosses they are protected from the current and find a sufficient food supply.

Figure 90. ***Telogonopsis deficiens*** naiad, a ***Fontinalis*** inhabitant. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 91. ***Teloganopsis deficiens*** naiad, a ***Fontinalis*** inhabitant. Photo by Bob Henricks, with permission.

### *Cincticostella*

In Japan, the narrowly distributed ***Cincticostella nigra*** (Figure 92) occurs in mats of ***Platyhypnidium riparioides*** (Figure 39) (Takemon & Tanida 1992). This species is restricted to Honshu, Japan (Allen 1971).

Figure 92. ***Cincticostella nigra*** naiad. Photo from Shiiba Research Forest. Permission pending.

### *Drunella*

Allen and Edmunds (1962) did not report any bryophyte dwellers among the North American species of ***Drunella*** they examined. But Muttkowski and Smith (1929) did find ***Drunella*** twice among the mosses of strong rapids in Yellowstone National Park, USA. Hawkins (1984) found only 2% of two ***Drunella*** (Figure 93) species [***D. pelosa***, ***D. coloradensis*** (Figure 93)] among mosses in western Oregon, USA. But ***D. spinifera*** (Figure 94) was collected primarily (54%) in mats of ***Fontinalis*** (Figure 79). ***Drunella allegheniensis*** (see Figure 95) occurs among bryophytes in the Appalachian Mountain, USA, streams (Glime 1968). Gilpin and Brusven (1970) found ***D. grandis*** (Figure 96) among ***Fontinalis*** clumps in Idaho, USA, as well as in other habitats with protective cover. ***Drunella spinifera*** was common on ***Fontinalis***. And Barton (1980) found the latter species to be abundant on moss-covered stones in riffles and rapids of a stream in northeastern Alberta, Canada.

Figure 93. ***Drunella coloradensis*** naiad, a genus sometimes found among bryophytes. Photo by Bob Henricks, with permission.

Figure 94. ***Drunella spinifer*** naiad, a ***Fontinalis*** dweller. Photo by Joseph Fortier, through Creative Commons.

Figure 95. ***Drunella tuberculata***, a species very similar to ***Drunella allegheniensis***. Photo by Bob Henricks, with permission.

Figure 96. ***Drunella grandis*** naiad, a ***Fontinalis*** dweller. Photo by Bob Newell, with permission.

***Drunella grandis*** (Figure 97) was a characteristic species among clumps of the leafy liverwort ***Porella*** (Figure 98) in California, USA (Corona 2010). This species seems to be adapted to its bryological habitat by large dorsal projections on the head, thorax, and abdomen. These projections reduce the chance of being swept away by rapid current in the locations of the liverwort, hooking the mayfly on the branches (Hora 1930).

Figure 97. ***Drunella grandis*** naiad, a leafy liverwort dweller in California, USA. Photo by Bob Newell, with permission.

Figure 98. ***Porella pinnata***. This genus provides a home for ***Drunella grandis*** in California, USA. Photo by Des Callaghan, with permission.

### *Caudatella*

Although the records of the members of this genus inhabiting bryophytes are limited, Hawkins (1985) reported that four species of ***Caudatella*** had three of the four highest percentages of bryophytes in the gut among all the **Ephemerellidae** in Oregon, USA. The moss percentage in the diet of these species, which we must presume were associated with mosses, were ***C. histrix*** (Figure 99-Figure 100) (15% + 20% listed as ***C. cascadia***), ***C. edmundsi*** (Figure 101) (19%), and ***C. heterocaudata*** (15%).

Figure 99. ***Caudatella hystrix*** naiad, a mayfly for which mosses comprise 35% of the diet in Oregon, USA, streams and rivers. Photo by Bob Newell, with permission.

Figure 100. ***Caudatella hystrix*** adult. Naiads live in fast riffles in Idaho, USA, clinging to ***Fontinalis***. Photo by Bob Newell, with permission.

Figure 101. ***Caudatella edmundsi***, a naiad that sometimes occurs exclusively on ***Fontinalis***. Photo by Bob Newell, with permission.

In the St. Maries River of Idaho, USA, ***Caudatella hystrix*** (Figure 99-Figure 100) typically occurred in fast riffles where it would cling to ***Fontinalis*** (Figure 79) or the alga *Prasiola* (Maurer & Brusven 1983). These substrata did an effective job of concealing the naiads. ***Caudatella edmundsi*** (Figure 62, Figure 101) occurs in streams with lower mean summer temperatures at higher elevations and coincides with higher moss coverage (Jacobus *et al*. 2006; Hogue & Hawkins 2008). Hawkins (1984) found ***Caudatella edmundsi*** exclusively among ***Fontinalis*** in western Oregon, USA.

### *Attenella*

I am only aware of two species in this genus that live among the bryophytes. ***Attenella margarita*** (Figure 77) is a detritus shredder that also eats bryophytes and lives among them. In Appalachian Mountain streams, ***A. attenuata*** lives among the bryophytes, particularly ***Fontinalis dalecarlica*** (Figure 69), but its use of bryophytes for food is unknown (Glime 1968).

### *Torleya*

This is one of the many genera that have been split off from ***Ephemerella***. ***Torleya major*** is a bryophyte dweller in the River Rajcianka in Slovakia, where it lives below the surface but is not found among the emergent wet bryophytes (Krno 1990).

## Leptohyphidae – Little Stout Crawler Mayflies

This is a family of small mayflies (3-10 mm) that are clingers and sprawlers (Leptohyphidae 2015). They are widespread in North America, but most are not common among bryophytes. They do crawl about on plants.

***Tricorythodes*** (Figure 102) burrows among the stems and rhizoids of mosses (Armitage 1961). In North America Berner (1959) found it in streams with a perceptible current where it lived among mosses or other plant growth on large stones or amid fine sand and gravel. They eat mostly plants (Leptohyphidae 2015). These naiads rarely swim, but rather move by crawling (Berner 1959). Their gill covers protect the gills, keep them clean, and move water across them when the current is insufficient to provide the needed oxygen.

Figure 102. ***Tricorythodes*** sp. naiad, a genus that burrows among moss stems and rhizoids. Photo by Bob Henricks, with permission.

## Suborder Pisciforma

### Ameletidae – Combmouthed Minnow Mayflies

Unlike the **Leptophlebiidae**, the **Ameletidae** are fast swimmers. They are mostly limited to clean, cold water (Henricks 2011) of North America and Europe (Ameletidae 2015) where they feed by scraping algae (Zuellig *et al*. 2006). Some members of this univoltine family may be **parthenogenetic** (reproducing with an unfertilized egg). They range 7-21 mm in length (Zloty & Pritchard 1997).

***Ameletus*** (Figure 103) is not generally a moss dweller, preferring more open waters with a stream substrate free of silt (Schwiebert 2007). Nevertheless, mosses can play a role in its location. It is among the few mayflies able to tolerate acid water, permitting it to live downstream from a lake acidified by ***Sphagnum*** (Figure 51) (Bauernfeind & Moog 2000). ***Ameletus inopinatus*** (Figure 104) lives in such a habitat at higher altitudes. In my Appalachian Mountain streams it was an infrequent occupant of the bryophytes (Glime 1968).

Figure 103. ***Ameletus ludens*** naiad. Some members of this genus are able to tolerate the acidified outflow from ***Sphagnum*** lakes. Photo by Jason Neuswanger, with permission.

Figure 104. ***Ameletus inopinatus*** naiad, a species that is able to live in the *p*H extremes of outflow from ***Sphagnum*** fens and bogs at higher elevations. Photo by André Wagner, with permission.

### Baetidae – Blue-winged Olives

The **Baetidae** are distributed throughout the cooler (but not polar) parts of both the Northern and Southern Hemispheres (Hebert 2012). They are among the smallest mayflies, usually <10 mm, and mostly members of the open water column, hanging out on the stream bottom or darting into the flow (Baetidae 2013). They are strong swimmers, but feed mostly on algae. Nevertheless, the youngest naiads can be found sheltered among the bryophytes, out of the flow that is beyond their ability for controlled swimming at that early stage (Hynes 1961; Glime 1968). They leave the bryophytes when their swimming skills develop, but when it is time to emerge, the **Baetidae** may once again use the bryophytes to facilitate their break through the surface tension safely. And once above water, they may cling to bryophytes to escape their naiad skin (Figure 105).

Figure 105. **Baetidae** newly emerged adults on wet moss. Photo by Jason Neuswanger, with permission.

Despite their open water nature, ***Baetis*** species are common among bryophytes in the River Rajcianka in Slavakia (Krno 1990). Those on submerged bryophytes include ***Baetis alpinus*** (Figure 106), ***B. fuscatus*** (Figure 107), ***B. lutheri***, ***B. muticus*** (Figure 108), ***B. rhodani*** (Figure 111), ***B. scambus***, ***B. vardarensis*** (Figure 109), and ***B. vernus*** (Figure 110). Among these, naiads of ***Baetis lutheri***, ***B. muticus***, ***B. rhodani***, and ***B. scambus*** are also able to move about among the wet emergent bryophytes.


Figure 106. ***Baetis alpinus*** naiad. Photo by Andrea Mogliotti <www.euroflyangler.com>, with permission.

Figure 107. ***Baetis fuscatus*** adult. Photo by Andrea Mogliotti <www.euroflyangler.com>, with permission.


Figure 108. ***Baetis muticus*** naiad, a species sensitive to low water *p*H. Photo by Andrea Mogliotti <www.euroflyangler.com>, with permission.

Figure 109. ***Baetis vardarensis*** naiad, a dweller of submerged bryophytes. Photo from Zoologische Staatssammlung Muenchen through Creative Commons.

Figure 110. ***Baetis vernus*** adult. Photo by Walter Pfliegler, with permission.

In a Welsh mountain stream Hynes (1961) found the very small (under 3 mm) members of ***Baetis*** (Figure 105-Figure 112) among mosses. I found a similar relationship of early instars among the mosses in Appalachian Mountain, USA, streams (Glime1968). Macan (1980) found that naiads of ***Baetis rhodani*** (Figure 111) in the River Lune, England, were common and abundant in the moss-covered area of the stream in winter. Naiads of four species of mayflies lived there spring to autumn, then overwintered in the egg. Hence, in the summer these other species appeared to displace ***Baetis rhodani*** from the mossy area. Wallace and Gurtz (1986) found that the biomass and production of ***Baetis*** were more than twice that of the weighted stream biomass and production. They suggested that part of this surge in biomass might be due to the large diatom count on mosses. Galdean (1994) further supported the importance of food among the mosses. On boulders where the velocity had increased in a stream, and the mosses on these boulders formed a felt that lacked detritus, ***Baetis rhodani*** was rare.

The mayfly ***Baetis*** (Figure 105-Figure 112) is well adapted to living where water levels fluctuate in streams. It can crawl to deeper water as the water level recedes, and it can relocate by entering the drift (Corrarino & Brusven 1983). When ***Baetis*** is in the drift, it swims to the surface, does a somersault, and hopefully is able to establish a hold on a substrate (Hughes 1966). Its streamlining makes it a good swimmer, and it is among the few insects that can swim against a current. It is positively phototactic and exits from its dark enclosures when there is the light.

In their experiments on effects of *p*H on mayflies, Willoughby and Mappin (1988) found that ***Baetis muticus*** (Figure 108) and ***Baetis rhodani*** (Figure 111) are directly sensitive to the low *p*H of the water, whereas ***Serratella ignita*** (Figure 1) was tolerant but absent in low *p*H water due to an inadequate food supply. Water acidity accounted for the absence of these ***Baetis*** species in the Upper Duddon, UK.

Figure 111. ***Baetis rhodani***, a species that is sensitive to low *p*H. Photo by J. C. Schou, with permission.

Figure 112. ***Baetis tricaudatus*** naiad, a common mayfly among ***Fontinalis neomexicana*** in Idaho, USA. Photo by Tom Murray, through Creative Commons.

Frost (1942) found that ***Baetis***, including the common ***B. rhodani*** (Figure 111), often makes its naiad home among mosses. In their study of colonization of ***Fontinalis neomexicana*** (Figure 79) in an Idaho stream, Maurer and Brusven (1983) found ***Baetis tricaudatus*** (Figure 112) to be common among the mosses.

The food of ***Baetis*** is typically diatoms, desmids, and filamentous algae (Butcher 1933; Percival & Whitehead 1929). But Brown (1961) found that detritus was the primary food of ***B. rhodani*** (Figure 111), a sometimes moss-dweller. Food of ***B. rhodani*** varied somewhat with habitat and season, also including algae. On the other hand, ***Baetis*** is frequent prey for fish. Frost (1942) found that 71% of the fish examined at Ballysmuttan and 59% at Straffan had ***Baetis*** in their guts. Such consumption is likely because of their frequent ventures into the open water.

Lee and Hershey (2000) found that ***Baetis*** (Figure 105-Figure 112) did not increase in numbers in fertilized reaches of the Kuparuk River in Alaska when the moss ***Hygrohypnum*** (Figure 43-Figure 44) increased in density. However, they grew larger in the fertilized zone, a fact Lee and Hershey attributed to greater abundance of epiphytic diatoms.

Wulfhorst (1994) compared naiads of ***Baetis*** (Figure 105-Figure 112) on mosses and in the **interstitial** spaces (spaces between individual sand grains in the soil or aquatic sediments) in the **hyporheic** zone (region beneath and alongside a stream bed) of two streams in the Harz Mountains, West Germany. There the mosses were home to many more of these mayflies than the interstitial spaces of the stream bed (Figure 113). On the other hand, Arnold and Macan (1969) found that ***Baetis***, in addition to inhabiting mosses, occurred on unstable bare stones on the stream bottom.

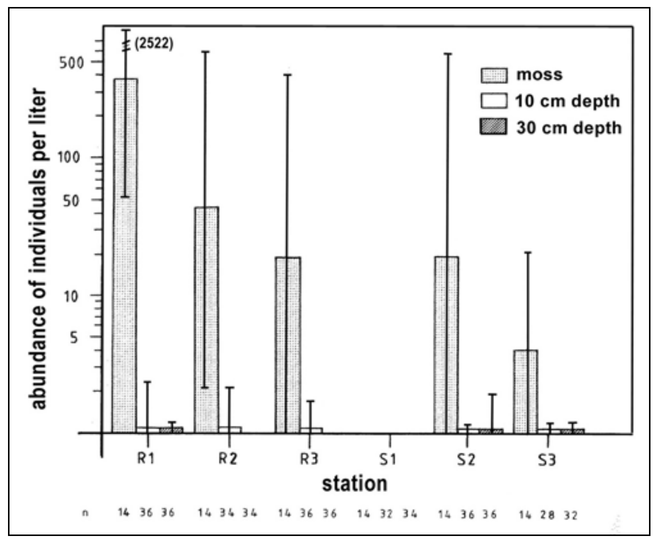


Figure 113. Mean abundance ± 95% CI of ***Baetis*** naiads in moss clumps in two streams in the Harz Mountains, West Germany. Redrawn from Wulfhorst 1994.

In the Arctic, conditions that favor mosses do not always favor the insects. Cold temperatures require life cycles that protect them in the winter. Among those species known to occupy mosses elsewhere, Giberson *et al.* (2007) found ***Ephemerella aurivillii*** (Figure 45) and ***Baetis tricaudatus*** (Figure 112) in the Arctic streams of Nunavut, Canada. The **Baetidae** was the most common family there. ***Baetis bundyae*** (Figure 114) naiads hatched within 2-3 weeks of ice-out and completed their development in 2.5-4 weeks. Giberson *et al.* considered the female-biased sex ratio to be an indication they might experience parthenogenesis. The Arctic **Baetidae** species are able to survive by having freeze-tolerant eggs, good dispersal, and a female-biased sex ratio that promotes greater reproduction.


Figure 114. ***Baetis bundyae*** naiad, a species with a female-biased sex ratio that is possibly parthenogenetic. Photo by Donna Giberson, with permission.

When we enter the Southern Hemisphere, the fauna changes, but major groups tend to remain the same. In Africa, baetid ***Acanthiops elgonensis*** (=*Afroptilum erepenscan*) attaches to mosses, barely covered by water, in the spray of water falls (Gillies 1990).

## Siphlonuridae - Primitive Minnow Mayfly

This family generally occurs in slow water. In St. Maries River in Idaho, USA, Gilpin and Brusven (1970) found ***Siphlonurus occidentalis*** (Figure 115) typically clinging to ***Fontinalis*** (Figure 47) growing at the stream margins.

Figure 115. ***Siphlonurus occidentalis*** naiad. Photo by Bob Newell, with permission.

## Heptageniidae – Clinger Mayflies

This family is widespread in the Holarctic, Oriental, and Afrotropical regions, as well as Central American Tropics and extreme northern South America (Heptageniidae 2014). Most of them occur in very fast flow where they anchor themselves on rocks by using their collective gills as a suction cup.

Because of this suction cup arrangement, bryophytes are not friends to the **Heptageniidae**. For example, when mosses increased in growth downstream from impoundments, the **Heptageniidae** diminished or were eliminated completely (Brittain & Saltveit 1989). Bottová and Derka (2013) reported that ***Rithrogena semicolorata*** avoided mosses in a karstic spring in the West Carpathians, despite its high coverage of mosses. But in the moderately eutrophic River Rajcianka in Slovakia ***Rithrogena ferruginea*** did occur among the bryophytes, despite the family's adaptations for smooth rock surfaces.

This is a family of flattened mayflies adapted to living on rock surfaces, typically with gills arranged along the abdominal segments to form a suction cup. Nevertheless, Jones (1949, 1950) found all of the guts with identifiable contents from 22 ***Ecdyonurus venosus*** naiads (Figure 116) contained the moss ***Fontinalis antipyretica*** (Figure 47). Winterbourn *et al*. (1986) likewise found that this species ate mosses in two British river systems. In the St. Maries River of Idaho, USA, ***Cinygmula*** sp. (Figure 117) occasionally occurred in clusters among ***Fontinalis*** (Gilpin & Brusven 1970). Among bryophytes in mid-Appalachian Mountain, USA, streams, I only found ***Epeorus*** (Figure 118-Figure 119) representing this family (Glime 1968).

Figure 116. ***Ecdyonurus venosus*** naiad, a mayfly that eats ***Fontinalis antipyretica***. Photo by Guillaume Doucet <http://guillaume.doucet.free.fr/>, with permission.

Figure 117. ***Cinygmula subaequalis*** naiad, member of a genus with moss-dwelling members. Photo by Donald S. Chandler, with permission.

Figure 118. ***Epeorus*** sp. naiad showing flattened body and legs. Photo by Tom Murray, through Creative Commons.

Figure 119. ***Epeorus*** sp. naiad showing ventral arrangement of gills into a suction cup. Photo from NABS through NSF funding public domain.

### Isonychiidae

The **Isonychiidae** are mostly North American, with scattered records in Asia (Isonychiidae 2015). These active swimmers are 8-17 mm long and occupy rapid currents (Waterbugkey 2015). They filter algae and diatoms from the water by using the long hairs on their forelegs, but they also eat smaller insects.

In the Appalachian Mountain streams I (Glime 1968) found ***Isonychia*** (Figure 120-Figure 121) occasionally among the bryophytes.

Figure 120. ***Isonychia bicolor*** naiad, member of a genus that sometimes occurs among bryophytes. Photo by Jason Neuswanger, with permission.

Figure 121. ***Isonychia bicolor*** naiad, showing fibrillate gills with gill covers. Photo by Jason Neuswanger, with permission.

### Oligoneuriidae – Brushleg Mayflies

This is mostly a river family, but occasionally they are associated with bryophytes. In the Sierra Nevada Mountains in southern Spain, young naiads of ***Oligoneuriella marichuae*** (Figure 122) require physical support and a way to capture food in the absence of a well developed filtering device (Alba-Tercedor 1990). For this they use roots, filamentous algae, and mosses. After they grow, they are able to move into the current.

Figure 122. ***Oligoneuriella rhenana*** naiad, a congener of ***O. marichuae*** that lives among mosses. Photo by Guillaume Doucet <www.guillaume.doucet.free.fr>, with permission.

## Suborder Carapacea

### Baetiscidae – Armored Mayflies

This small family of North American mayflies has a distinctive morphology (Figure 123) – the **notum** (Figure 124) covers the thorax and part of the abdomen (Edmunds 1960). These mayflies are medium sized (4-14 mm long) and live in pools or flowing water of sandy streams (Baetiscidae 2015b). Hence their occurrences among bryophytes are rare. Their feeding strategies are gatherers and scrapers (Baetiscidae 2015a). When they swim, they tuck their legs under the body and move by undulating the abdomen and caudal filaments (Baetiscidae 2015b).

I am delighted to report this unusual-looking family as having at least occasional moss dwellers. In fact, both ***Baetisca obesa*** (Figure 123) and ***B. rogersi*** (Figure 124) are moss dwellers. Berner (1955, 1956) found ***B. obesa*** among mosses that grew on submersed parts of trees in slow streams in North America. Later, Pescador (1973) found ***B. rogersi*** early instars in thick mats of the moss ***Leptodictyum riparium*** (Figure 125), likewise in slow water. In Appalachian Mountain, USA, streams, I found ***B. callosa*** and ***B. carolina*** among bryophytes, but infrequently (Glime 1968).

Figure 123. ***Baetisca obesa*** naiad, a species that lives on mosses in slow water. Photo by Jason Neuswanger, with permission.

Figure 124. ***Baetisca rogersi*** naiad, whose early instars occur in thick mats of the moss ***Leptodictyum riparium***. Note the large **notum** that covers the thorax and part of the abdomen. This one has a large spine on each side. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 125. ***Leptodictyum riparium*** in shallow root pit. Photo by Betsy St. Pierre, with permission.


## Summary

The **Collembola** are no longer considered insects and are now placed in the class **Entognatha**. Few live in the water and small numbers may mean they have fallen in. But some can occur in large numbers on the water surface, wet bryophytes of bogs, fens, and streambanks, and emergent bryophytes. They possess a **furcula** that propels them forward like a spring. The **collophore** facilitates respiration and absorption of water. Antennae recognize light intensity, wind direction, and heat.

The **Isotomidae** is the most frequent aquatic family, especially ***isotomurus palustris***. This species is **viviparous**.

The **Hemimetabola** have **incomplete metamorphosis** with egg, nymph or naiad, and adult. Naiads typically have gills.

**Ephemeroptera** (mayflies) live only about one day as adults, emerging, mating, and dying, but not eating. Mating is accomplished in swarms. All the immatures (***naiads***) are aquatic. Some are **univoltine** (one brood per year) and some are **bivoltine** (two broods per year).

Most mayflies have high oxygen requirements. Mayfly naiads have gills, and those with gill covers are able to increase movement of water and oxygen across the gills by beating the gill covers. Some use body undulations to increase contact with oxygenated water.

The most common mayfly family among bryophytes is the **Ephemerellidae**. This is the family that most commonly eats bryophytes, and consumption of mosses increases as the naiads age. However it is not clear if they eat the mosses to assimilate them or if they only assimilate the attached algae and bacteria. ***Baetis*** (**Baetidae**) seems to use bryophytes as a nursery and a stopping point when they enter the drift, a usage common among a number of other families.



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