CHAPTER 11-6
AQUATIC INSECTS: HEMIMETABOLA – PLECOPTERA

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CHAPTER 11-6 AQUATIC INSECTS: HEMIMETABOLOUS INSECTS – PLECOPTERA

Figure 1. ***Taeniopteryx*** sp. naiad, a common inhabitant of stream bryophytes, especially in early stages. Photo by Bob Henricks, with permission.

PLECOPTERA – Stoneflies

Like the other **hemimetabolous** (incomplete metamorphosis with egg, naiad, and adult) aquatic orders, the **Plecoptera** (Figure 1) have an aquatic immature stage known as a **naiad**. They differ from the **Ephemeroptera** (Chapter 11-4) in that they consistently have only two tails (**caudal filaments**). Their gills occur in various locations but are not found in the middle of the abdomen. The gills are usually not extensive and are absent in many (Dodds & Hisaw 1924; Pennak 1953), so **Plecoptera** naiads require water with high oxygen levels (Needham 1901; Dodds & Hisaw 1924; Macan & Worthington 1951; Pennak 1953; Ward & Whipple 1959), making them good indicators of relatively clean water.

The naiads reach their greatest numbers in fast, cold mountain streams (Thorp & Covich 1991). Although most occur in streams, a few occur in cold, **oligotrophic** (low nutrient) lakes. The naiads must climb out of the water to emerge from their exoskeleton and become adults. The adults are short-lived, but live longer than mayflies, usually several days to two weeks (Thorp & Covich 1991). The naiads are largely night active and appear most often in the night-time drift (Elliott 1967).

Krno and Žiak (2012) found that the number of stoneflies in West Carpathian calcareous **submontane** (ecological zone pertaining to lower slopes of mountains) rivers increased with an increase in mosses, with several genera maintaining their highest density on mosses. **Plecoptera** can use bryophytes in a number of ways. The most obvious is their use as a substrate and shelter from the flowing water. They are especially common there as young instars when the bryophytes can protect these less able swimmers from the flowing water. Many are able to obtain food there, either by preying on smaller invertebrates, by using the collected **detritus** (dead organic matter and debris) and **periphyton** (attached algae and other microorganisms), or less often by eating the mosses themselves. When it is time to emerge, they can use the bryophytes to help them climb through the surface tension and sometimes even provide a surface on which to emerge from naiad to adult, spread their wings, and fly away (Figure 2). Finally, these adults may return to the mosses to lay their eggs (Figure 3).

Figure 2. ***Isoperla*** sp. emerging, using emergent vegetation for support and to pump fluids into its wings. Photo by Richard Bartz, through Creative Commons.

Figure 3. **Plecoptera** eggs, laid here on a rock. Photo by Wendy Brown <www.gunnisoninsects.org>, with permission.

But the presence of some stoneflies as major inhabitants among bryophytes may be the preference of both the stonefly and the bryophyte for the same habitat. Two of the most common families, **Leuctridae** and **Nemouridae**, prefer cooler upstream stations in a southern Ontario, Canada, stream (Harper 1973), a habitat type also very suitable for bryophytes. Both benefit from clean, cool water with rapid flow and a rocky substrate.

Predation Retreat or Restaurant?

Many of the stoneflies are carnivores on a microscale. Since they are small, living in water torrents, they need a food source that is close by. For many, bryophytes can provide that habitat, a place where they can move about, safe from the current, and find an abundance of yet smaller prey items. For them, it is a restaurant with an impressive menu, but it is also a retreat from larger predators. For the yet smaller insects – well, it might be easier to escape predators, but it might also be a trap where they are eaten.

Elliott (2003) used ***Baetis*** naiads as experimental prey items to determine the effect on stonefly interactions, including three known bryophyte dwellers [***Perlodes microcephalus*** (Figure 80), ***Isoperla grammatica*** (Figure 75), ***Dinocras cephalotes*** (Figure 42)]. They found that feeding was density dependent, with the number of ***Baetis*** being eaten dependent on the number provided (between 20 and 200). Handling time was not affected by predator density or presence of other predators. However, attack rate decreased as predator density decreased. As expected, prey consumption also decreased as predator density decreased, with the severity of competition with a paired species being similar to that with the same species.

Food Relationships

Gerson (1982) suggested that **Plecoptera** may feed on aquatic bryophytes, but Stern and Stern (1969) found that detritus was the most common food for stoneflies, and detritus is common among the mosses. Jones (1950) examined the gut contents of **Plecoptera** naiads in the River Rheidol. Four of the six species studied had mosses (***Fontinalis antipyretica***, Figure 4) in the gut: ***Chloroperla tripunctata*** (see Figure 15-Figure 16), ***Leuctra hippopus*** (Figure 5), ***Protonemura meyeri*** (Figure 20), ***Amphinemura sulcicollis*** (= *A. cinerea*; Figure 19). The highest number with mosses in the gut was 12 out of 100 for the species ***Protonemura meyeri***. But the question remains, were the mosses digested or just eaten for their adhering periphyton and detritus?

Figure 4. ***Fontinalis antipyretica***, food for a number of ***Plecoptera*** naiads. Photo by Kristian Peters, with permission.

Figure 5. ***Leuctra hippopus***, member of a genus that is common among stream bryophytes. Photo by Niels Sloth, with permission.

Small streams in the Tolvajärvi region of the Russian Karelia are characterized by higher nutrient and iron concentrations as well as a large amount of organic matter compared to the lake outlet. These small streams are dominated by the mosses ***Fontinalis*** (Figure 4) and ***Hygrohypnum*** (Figure 6) like the lake outlet habitats, but also the leafy liverworts ***Scapania*** sp. (Figure 7), ***Marsupella*** spp. (Figure 8), and ***Jungermannia*** sp. (Figure 9). The dominant moss inhabitants are stonefly **shredders** in the genera ***Nemurella*** (Figure 10-Figure 11), ***Nemoura*** (Figure 12-Figure 13), and ***Leuctra*** (Figure 5). Shredders typically eat leaf litter. Unfortunately, we have no data to indicate what they were shredding among the bryophytes.

Figure 6. ***Hygrohypnum alpinum***, habitat for stonefly shredders in the Russian Karelia. Photo by Michael Lüth, with permission.

Figure 7. ***Scapania undulata***, a common emergent liverwort in streams and home for a number of insects. Photo by David T. Holyoak, with permission.

Figure 8. ***Marsupella aquatica***, a stream insect habitat. Photo by Michael Lüth, with permission.

Figure 9. ***Jungermannia exertifolia*** ssp. ***cordifolia***, home for stream insects. Photo by Michael Lüth, with permission.

Figure 10. ***Nemurella pictetii*** naiad, a bryophyte inhabitant. Photo by Urmas Kruus, with permission.

Figure 11. ***Nemurella pictetii*** adult, a stonefly whose naiads live among bryophytes. Photo by Tim Faasen, with permission.

Typical Fauna

When I examined the bryophytes from the Appalachian Mountain streams in Pennsylvania, Maryland, and West Virginia, USA, I found that the stoneflies were mostly small members in the genera ***Nemoura*** (Figure 12-Figure 13), ***Allocapnia*** (Figure 14), and ***Leuctra*** (Figure 5). Berthélemy (1966) found the moss-dwelling species generally to be smaller than those living among stones. Stern and Stern (1969) likewise found that the bryophytes

served the smaller stoneflies, especially ***Nemoura*** (Figure 12), and acted as a nursery for the young of other Plecoptera.

Figure 12. ***Nemoura*** sp. naiad, a common bryophyte inhabitant in streams. Photo by Bob Henricks, with permission.

Figure 13. ***Nemoura*** cervical gills that enable the species to live in somewhat low oxygen. Photo by Bob Henricks, with permission.

Figure 14. ***Allocapnia*** naiad, common among stream bryophytes in its early (small) stages. Photo by Bob Henricks, with permission.

Frost (1942) found that the moss fauna differed between acid and alkaline waters of the River Liffey, Ireland. In the acid areas, ***Protonemura*** (Figure 20), ***Amphinemura*** (Figure 19), ***Leuctra*** (Figure 5), and ***Chloroperla*** (Figure 15-Figure 16) dominated the mosses, whereas in the alkaline waters only ***Isoperla*** (Figure 17) was common. This is consistent with my finding of **Nemouridae** and ***Leuctra*** among bryophytes in the acidic Appalachian Mountain, USA, streams (Glime 1968).

Figure 15. ***Chloroperla*** adult, a genus whose naiads are common in acid stream water. Photo by G. Bohne, through Creative Commons.

Figure 16. **Chloroperlidae** naiad, a group dominant among mosses in acid water. Photo by Bob Henricks, with permission.

Figure 17. ***Isoperla*** naiad, the only genus common among mosses in alkaline streams. Photo by Bob Henricks, with permission.

In a study of a cool mountain stream of central Japan, Tada and Satake (1994) found that the density of many **Plecoptera** was greater among bryophytes than in bare rock areas. These included ***Scopura*** sp. (**Scopuridae**; Figure 18) (also known from glaciers), ***Amphinemura*** (Figure 19), ***Protonemura*** (Figure 20), ***Isoperla towadensis*** (see Figure 21), and ***I. nipponica***.

Figure 18. ***Scopura longa***, a species whose naiads live on bryophytes in cold mountain streams in Japan. Photo by Shiro Kohshima, with permission.

Figure 19. ***Amphinemura sulcicollis*** adult; naiads of this genus are common among bryophytes in cool mountain streams of Japan. Photo by James K. Lindsey, with permission.

Figure 20. ***Protonemura meyeri*** naiad, member of a genus that is common among bryophytes in cool mountain streams in Japan. Photo by James K. Lindsey, with permission.

Figure 21. ***Isoperla carbonaria*** adult, member of a genus that occurs among stream mosses in Japan. Photo through Creative Commons.

Reproductive Use

Stoneflies can use bryophytes for emergence and egg laying. But in some cases the bryophytes are used in mating behavior. Some stoneflies have an interesting way to attract females. They wait on the shoreline of streams or lakes for the females to emerge from the water and escape their naiad skins. Then they drum their abdomens on such available objects as rocks, dry leaves, and mosses, presumably to attract females (Erman 1984). Mating takes place on the ground (Brinck 1949).

Life cycles are typically attuned to the climate, permitting the insects to overwinter or survive dry spells. These life cycle needs thus dictate part of the required niche. Hynes and Hynes (1975) reported that the life cycle of Australian species were less rigid than those of stoneflies in the Northern Hemisphere. Hence, they tend to have broader ecological niches.

Capniidae – Small Winter Stoneflies

This family of medium-sized stoneflies (usually 5-10 mm) is poorly represented among bryophytes, despite being one of the largest families with about 300 species (Capniidae 2014). In the mid-Appalachian Mountains I found only ***Allocapnia*** (Figure 22) represented among the stream bryophytes (Glime 1968). ***Allocapnia*** adults (Figure 23-Figure 24) emerge in winter (Ross & Ricker 1971). The males are wingless, and these stoneflies often can be seen on the snow (Figure 23), wandering as much as 100 m from their naiad stream. Even the females have reduced wings, poorly developed wing venation, and reduced **thoracic sclerites** (plates forming the outer cover of an arthropod thorax) associated with the flight muscles, so their dispersal ability may be more limited than in other genera. Nevertheless, they do have the ability to disperse downstream, with **gravid females** (females carrying eggs) occurring in the drift and riding on floating ice. And adults may disperse upstream by **planing** – climbing up trees and structures, then gliding to a new location.

Figure 22. ***Allocapnia pygmaea*** male naiad, member of a genus that spends young instars among mosses. Photo by Donald S. Chandler, with permission.

Figure 23. ***Allocapnia pygmaea*** male adult, a winter emerger. Photo by Donald S. Chandler, with permission.

Figure 24. ***Allocapnia pygmaea*** female adult, a winter emerger that can ride the ice downstream. Photo by Donald S. Chandler, with permission.

Bryophytes can be an important location for finding food for some members of the **Capniidae**. Production of ***Capnia vidua*** (Figure 25) naiads in the High Tatra of Slovakia is dependent on the detritus collected by the mosses, making the mosses a suitable habitat for them (Krno & Sporka 2003). This genus also contains members that emerge and flit about on the snow (Figure 26).

Figure 25. ***Capnia*** naiad, a frequent bryophyte dweller. Photo by Jason Neuswanger, with permission.

Figure 26. **Capniidae** adult on snow. Photo by Bob Armstrong, with permission.

Leuctridae - Rolled-winged Stoneflies

This is likewise a family of medium size (5-13 mm). They are long, narrow stoneflies of streams. Berthélemy (1966) suggested that ***Leuctra*** (Figure 5, Figure 30-Figure 31) might be a **muscicole** (living in association with mosses). The genus is known as the rolled-wing stoneflies because of the manner in which the wings curve around the adult body (Figure 27). However, a number of species are **apterous** (without wings) as adults.

Figure 27. ***Leuctra fusca*** adult showing rolled wings. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

The genus ***Leuctra***, along with the **Nemouridae**, are among the most common naiads among the European bryophytes (Carpenter 1927; Frost 1942; Illies 1952).

In the mid-Appalachian Mountain, USA, streams, ***Leuctra*** was a fairly common bryophyte inhabitant, occurring among ***Fontinalis dalecarlica*** (Figure 78), ***Hygroamblystegium fluviatile*** (Figure 89) – ***Platyhypnidium riparioides*** (Figure 62), and most abundant on the leafy liverwort ***Scapania undulata*** (Figure 7) (Glime 1968). These naiads are relatively small, and those on bryophytes tend to be the youngest, *i.e.* smallest, making species identification nearly impossible. In Toliver Run, Garrett Co., MD, USA, this genus reaches a peak in June, but reaches a secondary peak in December, suggesting the presence of two different species. Mackereth (1957) likewise reported seasonal peaks that differed among species in this genus. I also found one adult in my collections, suggesting that they may emerge among the bryophytes (Glime 1968).

Wulfhorst (1994) examined the relative abundance of **Leuctridae** in mosses and in **interstitial** (spaces between individual sand grains in the soil or aquatic sediments) spaces in the **hyporheic** zone (beneath the bed of a river or stream) of two streams in the Harz Mountains of West Germany. She found that the **Leuctridae** were more abundant among the mosses at most collection stations, but that they were also abundant in the interstitial spaces of the **hyporheic** zone at 10 and 20 cm depths (Figure 28).

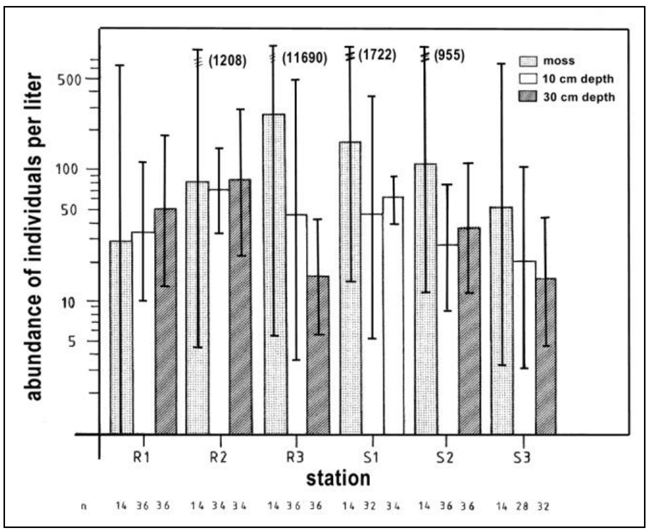

Figure 28. Mean abundance ± 95% CI of **Leuctridae** in moss clumps compared to depths of the hyporheic zone in two streams in the Harz Mountains, West Germany. Redrawn from Wulfhorst 1994.

Several species of ***Leuctra*** [***L. armata*** (Figure 29), ***L. autumnalis***, ***L. pusilla***] contribute to the production of Hincov Brook, High Tatra, Slovakia (Krno & Sporka 2003). Krno and Sporka concluded that these detritivorous stoneflies depend on the mosses to trap the coarse **benthic** (bottom) organic matter needed for their diet. The cold period produces higher productivity, attributable to reduction in feeding by brown trout.

In Radíkovský Brook in the Czech Republic, Jezberová (2003) found that substrate explains a large fraction of the data variability for **Ephemeroptera** and **Plecoptera**. Bryophytes play an important role for several species of ***Leuctra*** in that stream. Among these ***Leuctra albida*** and ***L. teriolensis*** highly prefer a bryophyte substratum.

Figure 29. ***Leuctra armata*** adult, a species whose naiads depend on mosses to trap detritus for their food. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Leuctra is herbivorous (Frison 1929). Jones (1949) found that ***Leuctra fusca*** (=*L. fusciventris*; Figure 30) and ***L. geniculata*** (Figure 31) had ***Fontinalis antipyretica*** (Figure 4) leaf fragments in about half the gut analyses from calcareous streams in South Wales. In the River Rheidol, UK, Jones (1950) found ***Fontinalis*** fragments in 8 of the 20 guts in which contents could be identified. Percival and Whitehead (1929) reported that several species of UK ***Leuctra*** had mosses in their guts. Dangles (2002) considered members of this genus to be generalist feeders, including bryophytes among their food choices.

Figure 30. ***Leuctra fusca***, a consumer of ***Fontinalis antipyretica*** in South Wales. Photo by Louis Boumans, through Creative Commons.

Figure 31. ***Leuctra geniculata*** naiad, a consumer of ***Fontinalis***. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

In the River Rajcianka, Slovakia, submerged bryophytes are home to ***Leuctra hippopus*** (Figure 5), ***L. inermis*** (Figure 32), and ***L. rauscheri*** (Krno 1990). Most are restricted to the submerged portions, but ***L. rauscheri*** is able to live above the water surface among emergent bryophytes.

Figure 32. ***Leuctra inermis*** adult, a species whose naiads live among bryophytes in River Rajcianka, Slovakia. Photo by James K. Lindsey, with permission.

Nemouridae – Spring Stoneflies

This is a family of small to medium stoneflies (5-20 mm). Wulfhorst (1994) examined the relative abundance of **Nemouridae** in mosses and in interstitial spaces in the hyporheic zone of two streams in the Harz Mountains of West Germany. She found that the **Nemouridae** were much more abundant among the mosses at all collection stations (Figure 33) than on other substrata. Furthermore, she found that most of them avoided 10 and 30 cm depths.

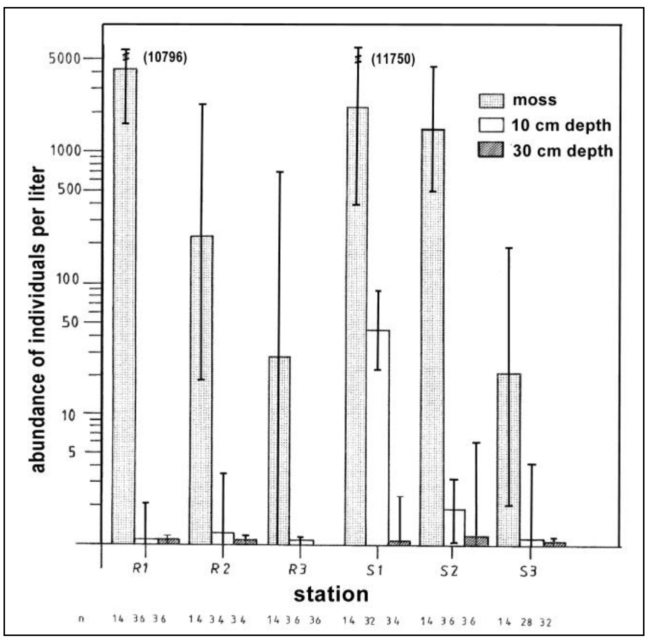

Figure 33. Mean abundance ± 95% CI of **Nemouridae** (***Amphinemura***/***Protonemura***) in moss clumps in two streams in the Harz Mountains, West Germany. Redrawn from Wulfhorst 1994.

In the Appalachian Mountain streams I studied, **Nemouridae** (Figure 34-Figure 37) were the most frequent and abundant of the Plecoptera, reaching their greatest numbers on turfs of ***Scapania undulata*** (Glime 1968, 1994). The species included ***Nemoura sinuata*** (Figure 34), ***Soyedina vallicularia***(?) (Figure 35-Figure 36), and ***Amphinemura nigritta*** (Figure 37). These occurred at all instar stages and most likely emerged to adulthood from the bryophyte mat.

Figure 34. ***Nemoura sinuata*** adult, a species that lives among bryophytes as naiads in Appalachian Mountain, USA, streams. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 35. ***Soyedina vallicularia*** naiad, a common inhabitant (or a similar species) among bryophytes in Appalachian Mountain, USA, streams. Photo courtesy of the State Hygienic Laboratory at the University of Iowa, with permission.

Figure 36. ***Soyedina vallicularia*** adults. Photo by R. E. DeWalt, through Creative Commons.

Figure 37. ***Amphinemura nigritta*** naiad, a common nemourid among Appalachian Mountain stream mosses. Photo by Tom Murray, through Creative Commons.

In subarctic Fennoscandia, some members of ***Nemoura***, such as ***N. viki***, deposit their eggs on damp mosses, although most are deposited in the water (Lillehammer 1986, 1988). ***Nemoura viki*** and ***N. arctica*** differ in their life cycles and in their preferred biotopes, effectively separating their niches. The temperature tolerance range of the eggs of ***N. arctica*** is wider. For the latter, temperature nevertheless has a profound effect on naiad development time. After 700 days at 4°C, the naiads still are not ready for emergence. On the other hand, at 16°C, the naiads can reach maturity in 120 days.

Wu (1923) reported that ***Nemoura*** (Figure 12) was a herbivore, eating mostly desmids and diatoms; he never found animal tissue in the diet. On the other hand, Chapman and Demory (1963) found that ***Nemoura*** in two Oregon, USA, streams consumed mostly detritus. Leberfinger and Bohman (2010) found that ***Nemoura*** sp. chose algae and shrubby cinquefoil when offered leaves of birch, Swedish whitebeam, shrubby cinquefoil, dead and fresh grass, moss, and algae. The least consumed food was dead grass, despite its being the most abundant food in the stream. Even though the fresh food had the highest carbon to nitrogen content, it was the dead leaves of the shrubby cinquefoil that was the food of choice, suggesting that perhaps fungal or bacterial decomposer organisms might have been important in the diet. A word of caution – the genus ***Nemoura*** has since been divided into multiple genera, so these generic designations may be misleading; The designation by Leberfinger and Bohman (2010) is recent and is most likely reflective of modern nomenclature.

Nemoura flexuosa (Figure 38), ***N. marginata***, and ***N. monticola*** all live among bryophytes in the River Rajcianka, Slovakia (Krno 1990). ***Nemoura monticola*** seems to be restricted to submerged bryophytes, whereas the other two species are able to move about within the wet bryophyte clumps above that water line.

Figure 38. ***Nemoura flexuosa*** naiad, a bryophyte dweller in Europe. Photo by Niels Sloth, with permission.

Nemoura cinerea (Figure 39-Figure 40) survives low oxygen levels better than ***Diura bicaudata*** (**Perlodidae**; Figure 41) and ***Dinocras cephalotes*** (**Perlidae**; Figure 42) (Benedetto 1970), perhaps explaining the ability of ***N. cinerea*** to live among mosses with heavy sedimentation. Furthermore, ***N. cinerea*** was the only species among the four tested that did not display undulations as oxygen levels became low (Benedetto 1970). ***Amphinemura*** has a cluster of pompon-like gills in each side of the neck (Figure 43). But ***N. cinerea***, like all ***Nemoura*** species, lacks this group of gills and does not have the ability to acclimate and change its low oxygen response to temperature (Nagell & Fagerstrom 1978).

Figure 39. ***Nemoura cinerea*** mating, a species whose naiads are unable to acclimate to low oxygen but that is a better survivor in these conditions than ***Diura bicaudata*** and ***Dinocras cephalotes***. Photo by James K. Lindsey, with permission.

Figure 40. ***Nemoura cinerea*** naiad, lacking cervical gills. Photo by James K. Lindsey, with permission.

Figure 41. ***Diura bicaudata*** adult, a species that is not able to survive well in low oxygen. Photo by Pentti Ketola, through free usage.

Figure 42. ***Dinocras cephalotes*** naiad, a species that does not survive low oxygen levels, a factor that may keep it out of some bryophyte clumps. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

Figure 43. ***Amphinemura*** cervical gills, adapting it to low oxygen levels. Photo by Bob Henricks, with permission.

Nemouridae (Figure 39-Figure 43) are very tolerant of low temperatures, achieving a growth rate of 1.6% per day at a mean water temperature of only 0.6°C in a subalpine lake in the Jotunheimen Mountains of southern Norway (Brittain 1983). This is also a typical stream temperature in northern Appalachian Mountain streams of New Hampshire in winter (Glime, unpubl data).

Krno (1990) reported several species of ***Protonemura*** on submerged bryophytes in the River Rajcianka, Slavakia: ***Protonemura auberti***, ***P. autumnalis***, ***P. hrabei*** (Figure 44), ***P. intricata*** (Figure 45), ***P. praecox*** (Figure 46-Figure 48). Of these, ***Protonemura auberti***, ***P. autumnalis***, ***P. hrabei***, and ***P. intricata*** also occurred on emergent wet bryophytes. Krno and Žiak (2012) reported that ***Protonemura*** was one of the taxa that was greatest on bryophytes in calcareous submontane rivers of the West Carpathians. ***Protonemura*** is likewise abundant among mosses in the Pyrénées (Berthélemy 1966), causing Berthélemy to consider ***P. pyrenaica*** to be a **muscicole** (living in association with mosses).

Figure 44. ***Protonemura hrabei*** naiad, a Slovakian moss dweller. Photo by J. C. Schou, with permission.

Figure 45. ***Protonemura intricata*** adult, a species whose naiads live among bryophytes. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 46. ***Protonemura praecox*** emergent female adult before wings are inflated. Photo by Walter Pfliegler, with permission.

Figure 47. ***Protonemura praecox*** emergent female adult attempting to inflate her wings. Photo by Walter Pfliegler, with permission.

Figure 48. ***Protonemura praecox*** female adult with fully inflated wings. Photo by Walter Pfliegler, with permission.

Protonemura meyeri (Figure 20) is common on ***Fontinalis*** (Figure 4) and other mosses in Europe (Hynes 1941; Costello 1988). This is a species that not only lives among bryophytes below the water surface, but also is able to go above the water level in the protective moisture of the bryophytes (Krno 1990). Frost (1942) concluded that ***P. meyeri*** lives among mosses throughout its entire naiad life. Not only did Hynes (1941) find that moss is the primary habitat for ***P. meyeri***, but Frost (1942) found that in the River Liffey it feeds almost entirely on mosses. However, Jones (1950) found ***Fontinalis*** in the guts of only 12 out of 32 ***Protonemura meyeri*** and in 2 out of 43 ***Amphinemura sulcicollis*** (Figure 19) in the River Rheidol, UK. Availability of moss vs other food choices influence which the stoneflies will eat.

On the other hand, Dangle (2002) considered ***Protonemura*** to be a generalist, including mosses among its food selections. But Dangle also cautioned against making generalizations from one species to another within a genus, even when the mouth parts were essentially the same. Krno and Sporka (2003) found that mosses were important for ***P. montana*** and ***P. nimborum*** because of the coarse benthic organic matter that accumulated there, providing both a stable habitat and a detrital food source.

Kamler (1967) found large numbers of ***Protonemura nitida*** among mosses in the early naiad stages. Bottová and Derka (2013) found that ***P. nitida*** was a significant contributor to the biomass in a **karstic** (limestone terrain characterized by sinks, ravines, and underground streams) spring in the West Carpathians. Its numbers reached 13,585 per m^2 in moss there, making them the most abundant stonefly. Steiner (1991) was surprised to find that when the surface film in ***Fontinalis antipyretica*** (Figure 4) was removed, small ***P. nitida*** fed on the leaf interior, but larger naiads tore the leaves, becoming moss shredders.

In the calcareous submontane rivers of the West Carpathians, ***Amphinemura*** was in its greatest abundance on mosses (Krno & Žiak 2012). Percival and Whitehead (1929) found ***Amphinemura sulcicollis*** (Figure 19) would occupy both thick and loose mosses, but it is much more abundant in the tracheophyte *Potamogeton* (Figure 49). Butcher *et al*. (1937) commented that it is probable that all the naiads belonged to this species, alluding to the difficulty in identifying the young instars. Frost (1942) found only two individuals of this species among the mosses in the alkaline station, but over 2000 at the acid water station. In their experiments, Willoughby and Mappin (1988) found that the tolerance of low *p*H by ***Amphinemura sulcicollis*** from acidic streams in the watershed of the River Duddon was similar to that of the mayfly ***Serratella ignita*** (Figure 1). It is interesting that ***A. sulcicollis*** slightly increases the percentage of detritus in its diet as it grows rather than increasing the moss component, as is common among other stoneflies and mayflies (López-Rodríguez *et al*. 2008). Nevertheless, mosses appear to be important components of the habitat for ***A. sulcicollis*** as evidenced by its presence in thirteen localities on the Isle of Man where mosses or overhanging grass were present (Hynes 1952). In North America, ***A. nigritta*** (Figure 50) occurs among bryophytes in the mid-Appalachian Mountain streams, inhabiting all the major bryophytes there: ***Fontinalis dalecarlica*** (Figure 78), ***Hygroamblystegium fluviatile*** (Figure 89) – ***Platyhypnidium riparioides*** (Figure 62), and ***Scapania undulata*** (Figure 7) (Glime 1968).

Figure 49. ***Potamogeton gramineus***, a genus that is a common home for ***Amphinemura sulcicollis***, also a moss dweller. Photo by Kristian Peters, with permission.

Figure 50. ***Amphinemura nigritta*** naiad, a common bryophyte inhabitant in Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

In streamside mosses like ***Cratoneuron*** (Figure 51), the stonefly ***Nemurella pictetii*** (Figure 10-Figure 11) may reach 16,500 individuals per square meter in a Danish spring (Lindegaard *et al*. 1975), and Thorup (1963) considered it to prefer mosses as a substrate. This species not only occurs in springs, but is among the few moss dwellers that are also common in lakes (Kamler 1967). Its adaptability to climate changes and habitat differences is seen in its ability to have both **bi**- and **trimodal** emergence patterns (having 2 and 3 peaks, respectively), coupled with partial **bivoltinism** (two broods per year), in Central Europe (Wolf & Zwick 1989), representing the only confirmed multivoltinism in a stonefly. Its emergence threshold temperature of 8°C prevents it from emerging when freezing danger is still likely. Rather than relying on seasonal life cycle cues, this species seems to be regulated by temperature, registered as accumulated degree days and an emergence temperature threshold.

Figure 51. ***Cratoneuron filicinum*** where ***Nemurella pictetii*** lives on springs and streamside. Photo by Michael Lüth, with permission.

Zapada cinctipes (=*Nemoura cinctipes*; Figure 52) was most abundant in the upper reaches of Trout Creek, Utah, USA, where the substrate was densely covered with the moss ***Hygrohypnum bestii*** (Figure 53) (Hales & Gaufin 1971). ***Zapada columbiana*** (Figure 54), a native of subalpine streams in Calgary, Canada, has a three-year life cycle (Mutch & Pritchard 1984, 1986). The naiads live primarily on boulders and cobble among mosses (Clifford 2014). Despite their long life cycle, they only grow during the ice-free season (Mutch & Pritchard 1986). The females do not move upstream to lay eggs (Mutch & Pritchard 1984). Of the six females examined, their egg production ranged 800-1200 eggs each (Mutch & Pritchard 1986). These eggs hatch before winter so that the young naiads spend the first winter living among the mosses. Nevertheless, the eggs of these stoneflies develop best at lower temperatures.

Figure 52. ***Zapada cinctipes*** naiad, a species common where ***Hygrohypnum bestii*** is present in Trout Creek, Utah, USA. Photo by Bob Armstrong, with permission.

Figure 53. ***Hygrohypnum bestii***, home of the stonefly ***Zapada cinctipes***. Photo by Robin Bovey, with permission through Dale Vitt.

Figure 54. ***Zapada columbiana*** adult on snow. Photo by Bob Newell, with permission.

Although ***Zapada columbiana*** (Figure 54) lives for three years in the rocky streams of the Alberta, Canada, Rocky Mountains, some naiads may complete their life cycle in two years (Mutch & Pritchard 1984). Important to these naiads is the food available to them. Mutch and Pritchard found that at any time during their growth season (June to November) at least 50% of them were living among the mosses covering the boulders or cobble in riffles. Furthermore, mosses are the predominant food in the gut for these shredders, but during winter highly conditioned conifer detritus becomes the predominant component. In experiments these naiads grow better on a moss diet than on the leaves of the willow *Salix glauca*.

Notonemouridae

This New Zealand/southern Africa family is another stonefly addition to the moss fauna and is not known from the Northern Hemisphere. All the genera are endemic to New Zealand except ***Notonemoura*** (McLellan 1991). They are typical of cool, high elevation lakes and rivers (Notonemouridae 2015), but some have terrestrial naiads and others have naiads that spend their early instars in the water and later instars on land, and some live in lowlands (McLellan 1991). They are herbivores and detritivores. Their enlarged hind femora helps them to climb vertical surfaces against flowing water (Notonemouridae 2015). The females lay their sticky eggs in the crevices of logs and rocks. These are small stoneflies (5-8 mm) and are mostly leaf shredders (Picker *et al*. 2004).

Notonemoura latipennis occurs in bog pools and bog outlet streams (McLellan 1991). ***Spaniocercoides hudsoni*** (see Figure 55) naiads live in ***Sphagnum*** bogs (Figure 56-Figure 57) (McLellan 2005). ***Spaniocerca zelandica*** naiads live in streams under stones or fallen logs or hidden among mosses or leaf litter (Winterbourn 1968).

Figure 55. ***Spaniocercoides philpotti*** naiad, member of a genus that lives in bogs and in streams among mosses. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Chloroperlidae – Green Stoneflies

Members of this family are medium in size (10-20 mm) and typically green as adults (Figure 58). ***Chloroperla tripunctata*** (see Figure 59) occasionally eats fragments of ***Fontinalis*** (Figure 4), but Jones (1950) reported only 3 specimens out of 113 with this moss in their guts in the River Rheidol, UK.

Figure 56. Bog in Fiordland, NZ. Photo through Creative Commons.

Figure 57. ***Sphagnum crispum***, a common ***Sphagnum*** species in New Zealand. Photo by Janice Glime.

Figure 58. **Chloroperlidae** exuviae (shed exoskeletons) and adults showing the green color of the adults. Photo by Jason Neuswanger, with permission.

Figure 59. **Chloroperlidae** naiad, a family where some members occasionally eat ***Fontinalis***. Photo by Bob Henricks, with permission.

In the High Tatra of Slovakia, ***Siphonoperla neglecta*** (Figure 60) depends on mosses that trap the coarse benthic detritus that serves as their food (Krno & Sporka 2003). The moss helps them to avoid predation by the brown trout until the cold season when the trout cease feeding actively.

Figure 60. ***Siphonoperla torrentium*** mating; ***Siphonoperla neglecta*** escapes brown trout predation by hiding among mosses. Photo by James K. Lindsey, with permission.

Taeniopterygidae – Winter Stoneflies

The Taeniopterygidae are among the small to medium (10-20 mm) bryophyte-dwelling stoneflies. These shredders and detritivores prefer cold, clear running water of large streams and rivers (Entz 2006). They emerge in winter and are not among the bryophytes year-round because they are very sensitive to warm temperatures and require high oxygen levels.

The genus ***Taeniopteryx*** (Figure 61) commonly develops among mosses (Berthélemy 1966). It is common in some mid-Appalachian Mountain streams among ***Hygroamblystegium fluviatile*** (Figure 89) – ***Platyhypnidium riparioides*** (Figure 62) clumps, seemingly either abundant or absent. (Glime 1968). This species disappears from the bryophytes as it grows and is never present in older stages. Krno and Žiak (2012) reported that ***Taeniopteryx auberti*** is one of the taxa that reaches its greatest abundance on mosses in calcareous submontane rivers of the West Carpathians. Tiny naiads of ***Taeniopteryx nebulosa*** (Figure 61) are common among ***Platyhypnidium riparioides*** in Britain (Langford & Bray 1969). Hubault (1927) considered ***Taeniopteryx hubaulti*** to be a strong muscicole.

Figure 61. ***Taeniopteryx nebulosa*** naiad, member of a genus that is common among ***Platyhypnidium riparioides*** in the UK. Photo by Niels Sloth, with permission.

Figure 62. ***Platyhypnidium riparioides***, home of ***Taeniopteryx nebulosa***. Photo by Michael Lüth, with permission.

Brachyptera risi (Figure 63) in a Dartmoor stream was confined to mosses on the sides of boulders in the stream (Elliott 1967). Costello (1988) found it both widespread and abundant among mosses in Irish streams. Langford and Bray (1969) found larger nymphs of this species throughout the year on the mosses ***Platyhypnidium riparioides*** (Figure 62) and ***Fontinalis antipyretica*** (Figure 4), two species that usually did not occur together, in British lowland streams. Dangles (2002) reported ***Brachyptera seticornis*** as specializing on algae and bryophytes for its food.

Figure 63. ***Brachyptera risi*** naiad, a species confined to mosses in a Dartmoor stream. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

Perlidae – Common Stoneflies

The **Perlidae** are larger than members of the previous families, reaching 20-50 mm as adults. Although their distribution is nearly worldwide, they are most abundant in eastern North America (Perlidae 2013). Although they typically occur in cool, clear medium-sized to large streams, they can occur in quiet waters. When water is not moving over their bodies, they undulate the body to increase oxygen exchange. They are predators that engulf their prey.

Krno and Žiak (2012) reported that the perlid genus ***Dinocras*** reached its greatest abundance among mosses, compared to other substrata, in calcareous submontane rivers of the West Carpathians. Berthélemy (1966) considered ***Dinocras*** to be a muscicole, suggesting that the mosses help to stabilize the habitat for ***Dinocras cephalotes*** (=*Perla cephalotes*) (Figure 42). ***Dinocras cephalotes*** is one of the largest stoneflies in the Shropshire Hill Stream, UK, and is found mostly in streams and rivers where mosses cover stable stones (Arnold & Macan 1969). Hynes (1941) similarly found that it was much more common where the substrate was stable and moss-covered. And ***Dinocras cephalotes*** occasionally ingests mosses, including ***Fontinalis antipyretica*** (Figure 4) (Percival & Whitehead 1929; Jones 1949). But more importantly, at least in North Wales, the ***D. cephalotes*** hung out near where the triclads (flatworms) were abundant, forcing the triclads to live exclusively in dense patches of moss (Wright 1975).

In trout streams of Yellowstone National Park, USA, one could find ***Hesperoperla pacifica*** (Figure 64) among mosses and the green alga *Cladophora* (Figure 65) (Muttkowski & Smith 1929). This medium-sized species is a carnivore, but Muttkowski and Smith did find mosses in many of the guts, perhaps taken along with a grab for an insect prey.

Figure 64. ***Hesperoperla pacifica*** naiad, a moss inhabitant in trout streams in Yellowstone. Photo by Arlen Thomason, with permission.

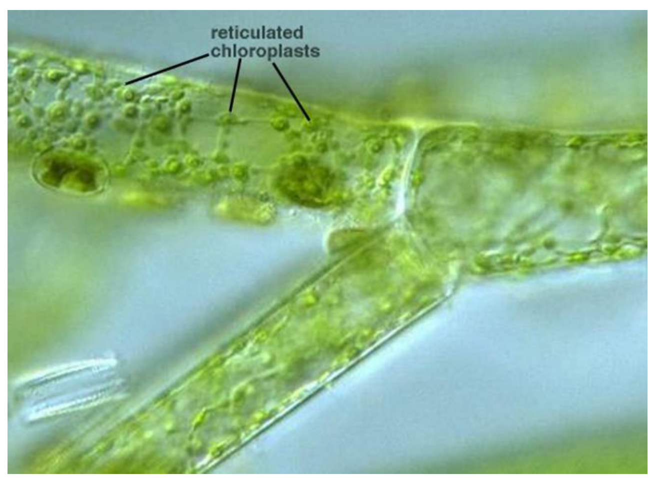

Figure 65. *Cladophora*, habitat, along with mosses, for ***Hesperoperla pacifica***. Photo by Yuuji Tsukii, with permission.

In the eastern USA, one can find a different array of **Perlidae** among the stream bryophytes. In the Appalachian Mountains, I found ***Acroneuria*** (Figure 66), ***Agnetina capitata*** (Figure 67), ***Perlesta placida*** (Figure 68-Figure 69), and ***Paragnetina*** (Figure 70) (Glime 1968). ***Acroneuria carolinensis*** (Figure 66) in Panther Creek, West Virginia, USA, clings to mosses, sand, rocks, and stems of *Rhododendron* (Schmidt & Tarter 1985). I often found this genus among the bryophytes in Appalachian Mountain streams (Glime 1968).

Figure 66. ***Acroneuria carolinensis*** naiad, a species that clings to mosses and other things in its native streams. Photo by Bob Henricks, with permission.

Figure 67. ***Agnetina capitata*** naiad, a species that sometimes occurs among ***Fontinalis*** species. Photo by Donald S. Chandler, with permission.

Figure 68. ***Perlesta placida*** adult, a species whose naiads sometimes occur among bryophytes in the Appalachian Mountains. Photo by Jason Neuswanger, with permission.

Figure 69. ***Perlesta nelsoni*** naiad, a New Hampshire, USA, species in a genus that sometimes occurs among stream bryophytes. Photo by Donald S. Chandler, with permission.

Figure 70. ***Paragnetina immarginata*** naiad, member of a genus that sometimes occurs among bryophytes in Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Perlodidae – Springflies & Yellow Stones

Like the **Perlidae**, the **Perlodidae** tend to be somewhat larger than the previous families (10-50 mm). The adults hatch in April to June and the eggs provide **diapause** (period of suspended development; physiological dormancy) during the warmer months, making the naiads absent from their native streams at that time because they have only one generation per year (Perlodidae 2014). Like the **Perlidae**, they are mostly engulfing predators, but some are scrapers and collector-gatherers. In addition to their diet of small invertebrates, at least some eat plant material, especially when they are young.

This is not a common family among moss dwellers, but in their study of an Idaho, USA, stream, Maurer and Brusven (1983) found a species of ***Cultus*** (Figure 71) to be common in clumps of ***Fontinalis neomexicana*** (Figure 72) as well as on the mineral substrate. Naiads climb out of the water and emerge on nearby rocks and vegetation (Figure 73).

Figure 71. ***Cultus verticalis*** naiad, from a genus that is common among ***Fontinalis neomexicana*** in Idaho, USA, streams. Bryophytes may also provide emergence sites. Photo by Tom Murray, through Creative Commons.

Figure 72. ***Fontinalis neomexicana*** in a dry streambed; home of ***Cultus verticalis*** naiads. Photo by Janice Glime.

Figure 73. **Perlodidae** emerged on rock at edge of stream. Photo by Janice Glime.

Krno and Žiak (2012) reported that ***Isoperla*** is one of the taxa that is at its greatest abundance on mosses in calcareous submontane rivers of the West Carpathians. ***Isoperla petersoni*** is abundant in the upper 100 m of a Utah stream where the moss ***Hygrohypnum bestii*** (Figure 74) provides heavy cover on the substrate (Hales & Gaufin 1971). ***Isoperla grammatica*** (Figure 75) seems to be more common elsewhere than among mosses, but in her study of the River Liffey, Ireland, Frost (1942) found it to be the dominant moss-dwelling stonefly in the alkaline station of her study. Percival and Whitehead (1929) likewise found it to form denser populations among mosses than among stones. Langford and Bray (1969) reported it to have its largest numbers among the moss ***Platyhypnidium riparioides*** (Figure 62) in Britain, citing Brinck's (1949) comment that it has the widest ecological amplitude of all Swedish **Plecoptera**. This is a species that is common among submerged bryophytes in the River Rajcianka, Slovakia, but unlike some stoneflies, it is absent among the wet emergent mosses (Krno 1990). The same relationship of confinement to submersed bryophytes is true for ***Isoperla oxylepis*** and ***I. sudetica***. Krno and Sporka (2003) found that ***Isoperla sudetica*** in the High Tatra of Slovakia depends on the detritus collected by mosses. This stonefly is most productive in winter when the brown trout is not actively feeding.

Figure 74. ***Hygrohypnum bestii***, home to ***Isoperla petersoni*** in a Utah, USA, stream. Photo by Robin Bovey, with permission.

Figure 75. ***Isoperla grammatica*** naiad, a stonefly whose preference for mosses varies among streams. Photo by Urmas Kruus, with permission.

In the Nearctic, Nelson and Kondratieff (1983) found ***Isoperla major*** only at the source of a stream where naiads hid under large, moss-covered cobble. In Appalachian Mountain streams, ***Diploperla duplicata*** (Figure 76) and ***Isoperla bilineata*** (Figure 77) both occur among mosses (Glime 1968). The former is the most common, occurring among all the major bryophytes [***Fontinalis dalecarlica*** (Figure 78), ***Hygroamblystegium fluviatile*** (Figure 89) – ***Platyhypnidium riparioides*** (Figure 62), ***Scapania undulata*** (Figure 7)]. What is surprising here is that these are mature naiads, not the tiny young ones.

Figure 76. ***Diploperla duplicata*** naiad, a common bryophyte inhabitant in Appalachian Mountain streams. Photo by Bob Henricks, with permission.

Figure 77. ***Isoperla bilineata*** naiad, a common bryophyte inhabitant in Appalachian Mountain streams. Photo by Royce Bitzer (<Iowa State Entomology Image Gallery>, with permission.

Figure 78. ***Fontinalis dalecarlica*** habitat Highlands, NC. Photo by Janice Glime.

In the Sturgeon River, northern Michigan, USA, ***Isoperla signata*** (Figure 79) had similar growth above and below a hydroelectric power plant, but the naiads were six times as abundant below the power plant (46 m^{-2} vs 7 m^{-2}) (Mundahl & Kraft 1988). Mundahl and Kraft suggested that the greater abundance below the dam may be from the rich growth of ***Fontinalis*** below the dam. These mosses were able to trap the detritus released from the dam and thus provide both cover and food for the stoneflies.

Figure 79. ***Isoperla signata*** naiad, a species that thrives on detritus collected by ***Fontinalis***. Photo by Royce Bitzer <Iowa State Entomology Image Gallery>, with permission.

In the High Tatra, Slovakia, ***Diura bicaudata*** (Figure 41) is dependent on detritus that collects among mosses (Krno & Sporka 2003). This species is common in both stream mosses and in lakes (Kamlet 1967).

In Estonia ***Perlodes microcephalus*** (Figure 80) occurs in stony and gravelly bottoms where ***Fontinalis*** (Figure 4) grows (Timm 2000). ***Perlodes intricatus*** in the High Tatra of Slovakia depends on the detritus that accumulates among mosses in streams (Krno & Sporka 2003). The mosses also provide them with shelter from the predatory brown trout.

Figure 80. ***Perlodes microcephalus*** naiad, a species that hangs out near ***Fontinalis*** in stony streams of Estonia. Photo by Niels Sloth, with permission.

Susulus venustus from California, USA, is one of the species that drums on mosses and other substrates to attract females (Bottorff *et al*. 1989). The male drumming call is 1-3 groups of bi-beats and is a unique pattern among the **Perlodidae**. After mating, the females fly to the dark detritus and moss substrate, then walk into the shallow water where they release their eggs.

Peltoperlidae – Roachflies

This family (~8-20 mm) did not appear in any of the published studies I found. This is understandable because their preferred habitat is flowing streams characterized by sediments, vascular plants, and detritus (Peltoperlidae 2014). However, I did find ***Peltoperla*** (Figure 81) occasionally among all the major bryophytes [***Fontinalis dalecarlica*** (Figure 78), ***Hygroamblystegium fluviatile*** (Figure 89) – ***Platyhypnidium riparioides*** (Figure 62), and ***Scapania undulata*** (Figure 7)] I studied in the Appalachian Mountain, USA, streams (Glime 1968). It typically preferred the mat habit.

Figure 81. ***Peltoperla*** naiad, an occasional dweller among bryophytes in streams in the Appalachian Mountains, USA. Photo by Bob Henricks, with permission.

Gripopterygidae

This family has become terrestrialized to the degree that the naiads usually live among damp substrata on land (McLellan 1977). But the naiads of ***Zelandoperla fenestrata*** (10-14 mm; see Figure 82) are widely distributed, especially among mosses, in stony streams in the mountains of New Zealand (Winterbourn & Gregson 1981). This species is most abundant among the ***Fissidens rigidulus*** (Figure 83) in the torrential water mid stream (Cowie & Winterbourn 1979). These naiads feed on the diatoms and detritus collected there.

Figure 82. ***Zelandoperla pennulata*** from the Takitimu Mountains, N. Z. Photo by Brian Patrick, with permission.

Figure 83. ***Fissidens rigidulus***, home to ***Zelandoperla fenestrata*** in New Zealand. Photo by Bill & Nancy Malcolm, with permission.

Cardioperla nigrifrons occurs in large numbers among surface mosses in a fast waterfall (45° angle) in Tasmania (Dean & Cartwright 1992).

South American Plecoptera, like those from New Zealand and Tasmania, are often different from the ones found in the Northern Hemisphere. ***Alfonsoperla flinti*** occurs among mosses in high waterfalls in Chile (McLellan & Zwick 2007). Illies (1963) found this species among mosses on the stream beds.

Zelandobius (Figure 84-Figure 85) is one of the common small stoneflies in New Zealand, starting its life at about 0.6 mm length, with adults 7-11 mm (Death 1990). It is amphibious and is able to climb out of the water and move about among the emergent wet mosses of streams (Auckland Council 2011).

Figure 84. ***Zelandobius*** sp. naiad, a genus that can climb out of the water to explore among emergent mosses. Photo from Landcare Research, through Creative Commons.

Figure 85. ***Zelandobius illiesi*** naiad, a genus that can climb out of the water to explore among emergent mosses. Photo from Landcare Research, through Creative Commons.

Pteronarcyidae – Giant Stoneflies

This family has the largest members (15-70 mm) among the **Plecoptera**, hence the common name. The largest stonefly I have encountered among mosses is ***Pteronarcys biloba*** (Figure 86) (Glime 1968, 1994). The large size of older individuals seems to preclude their habitation among smaller mosses like ***Platyhypnidium riparioides*** (Figure 62) and ***Hygroamblystegium fluviatile*** (Figure 89). But within the larger spaces among branches of ***Fontinalis*** species (Figure 4) the genus is able to move about more freely. One feature that may contribute to its ability to hide deep within the streaming ***Fontinalis*** away from the rapid current is its possession of numerous thoracic tufts of gills that resemble pompoms (Figure 88). These gill tufts facilitate obtaining oxygen and permit the stoneflies to live deep within the clump, out of the rapid flow that brings oxygen to surface dwellers. On the other hand, small individuals (early instars) of ***Pteronarcys proteus*** (Figure 87-Figure 88) are able to live among the smaller spaces of ***Hygroamblystegium fluviatile*** (Figure 89).

Figure 86. ***Pteronarcys biloba*** naiad, a ***Fontinalis*** dweller in the Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Figure 87. ***Pteronarcys proteus*** naiad, an occasional occupant of ***Hygroamblystegium fluviatile*** in the Appalachian Mountains. Photo by Jason Neuswanger, with permission.

Figure 88. ***Pteronarcys proteus*** naiad, an occasional moss dweller, showing well-developed thoracic gills. Photo by Jason Neuswanger, with permission.

Muttkowski and Smith (1929) found mosses, along with diatoms (especially ***Epithemia***, Figure 90) in the guts of five out of six ***Pteronarcys californica*** (Figure 91) examined from among mosses in strong rapids of trout streams in Yellowstone National Park, USA. The researchers were surprised that this large stonefly was a vegetarian, with only 4% of its diet consisting of animals; instead the guts contained over 50% detritus.

Figure 89. ***Hygroamblystegium fluviatile*** in the Appalachian Mountains, USA, a moss that provides spaces too small for ***Pteronarcys biloba***, but houses smaller individuals of ***P. proteus***. Photo by Janice Glime.

Figure 90. ***Epithemia*** on a filamentous alga. Photo by Jason Oyadomari, with permission.

Figure 91. ***Pteronarcys californica*** naiad, a bryophyte consumer. Photo by Bob Henricks, with permission.

Several researchers have attempted to explain these diet preferences. ***Pteronarcys pictetii*** (Figure 92) and ***P. californica*** (Figure 91) have a diet that is 50-80% detritus during most of the year (Martin *et al*. 1981). Lechleitner and Kondratieff (1983) found that ***P. californica*** naiads switch from a diet of 40% algae in October to one with more mosses and blackflies in December. However they increase their moss intake when their normal food is insufficient. Martin and coworkers (1981) found that the midgut **proteolytic** (breaking down of proteins into simpler compounds) activity of the naiads is very high, similar to that in other aquatic detritivores. But the conditions differ from those of detritus-feeding **Diptera** and lack the digestive systems that are adapted for digesting proteins that are bound to **polyphenols** (compounds such as tannic acid composed of multiple phenol structures and that have toxic, metabolic, and other biological properties). They furthermore are poorly adapted for digesting the major **polysaccharides** (carbohydrate such as starch, cellulose, or glycogen whose molecules consist of a number of sugar molecules bonded together) present in detritus. Polysaccharide digestion is presumed to be restricted to α-1,4-glucans, the primary storage polysaccharide of higher plants, algae, and presumably bryophytes. But there seemed to be little enzymatic activity on the major structural polysaccharides of higher plants, suggesting that organisms that accompany the food items may help in the digestion.

Figure 92. ***Pteronarcys pictetii*** naiad, a detritus feeder. Photo from <Plecoptera.SpeciesFile.org> through Creative Commons.

Pteronarcella badia (Figure 93) is generally a detritus feeder in its early stages, but in later instars the naiads make mosses a substantial portion of their diet (Fuller & Stewart 1979). The other eight stonefly species examined from several Colorado, USA, rivers ate predominantly animals – **Chironomidae** (Figure 94), **Simuliidae** (Figure 95), and **Ephemeroptera** (see Chapter 11-4). Even though diets shifted for these other species as they developed, only ***Pteronarcella badia*** shifted to mosses (Fuller & Stewart 1977).

Figure 93. ***Pteronarcella badia*** naiad, a species that switches to feeding on mosses as it gets older. Photo by Arlo Pelegrin, with permission.

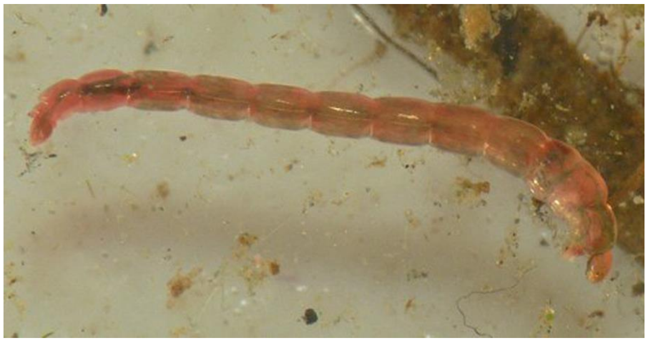

Figure 94. **Chironomidae** larva, a typical part of stonefly diet. Photo by Bob Armstrong.

Figure 95. **Simuliidae** larvae on rock, common food for stoneflies. Photo by Jason Neuswanger, with permission.

Hassage *et al*. (1988) examined feeding behavior in the shredder species ***Pteronarcella badia*** and found that in small groups (1-4) the naiads distributed themselves in proportion to the available surface area. However, when the group was increased to 14, they formed aggregations that often involved body contact. Addition of the predator ***Claassenia sabulosa*** (Figure 96) cause them to exhibit a random distribution. It would be interesting to see if this behavior differs on rocks vs bryophytes.

Figure 96. ***Claassenia sabulosa*** naiad, a predator on ***Pteronarcys badia***. Photo by Bob Henricks, with permission.

Summary

The **Plecoptera** (stoneflies) are **hemimetabolous**, having eggs, naiads, and adults. Some have gills and others are gill-less, requiring high oxygen concentrations. This requirement for oxygen makes them more common in cold, rapid streams. The naiads are mostly night active. Many of the smaller **Plecoptera** are moss dwellers, especially in young stages, where they eat mostly **detritus** and **periphyton**, but some eat bryophytes.

The stoneflies use the bryophytes for depositing eggs, escaping the drift, protection and food source during early instars, and emergence. Adults of some use the bryophytes as a substrate for attracting females – the males drum their abdomens on the mosses. Some stoneflies, however, emerge in the winter, often climbing out of the water on emergent bryophytes, and can be seen on the snow.

The **Nemouridae** and **Leuctridae** are the most common families among bryophytes, although in some locations the **Taeniopterygidae** are abundant. The **Notonemouridae** is a somewhat terrestrialized moss-dwelling family restricted to the Southern Hemisphere. In New Zealand one can find **Gripopterygidae** among stream mosses, although this stonefly family is mostly terrestrialized. Large stoneflies like the **Pteronarcyidae** are usually absent in the small spaces of most bryophytes, but they are able to maneuver among the larger branches of ***Fontinalis***. Other families that include regular moss dwellers are **Capniidae**, **Chloroperlidae**, **Perlidae**, **Perlodidae**, and **Peltoperlidae**.

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