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CHAPTER 11-12
AQUATIC INSECTS: HOLOMETABOLA – TRICHOPTERA, SUBORDERS INTEGRIPALPIA AND SPICIPALPIA

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CHAPTER 11-12
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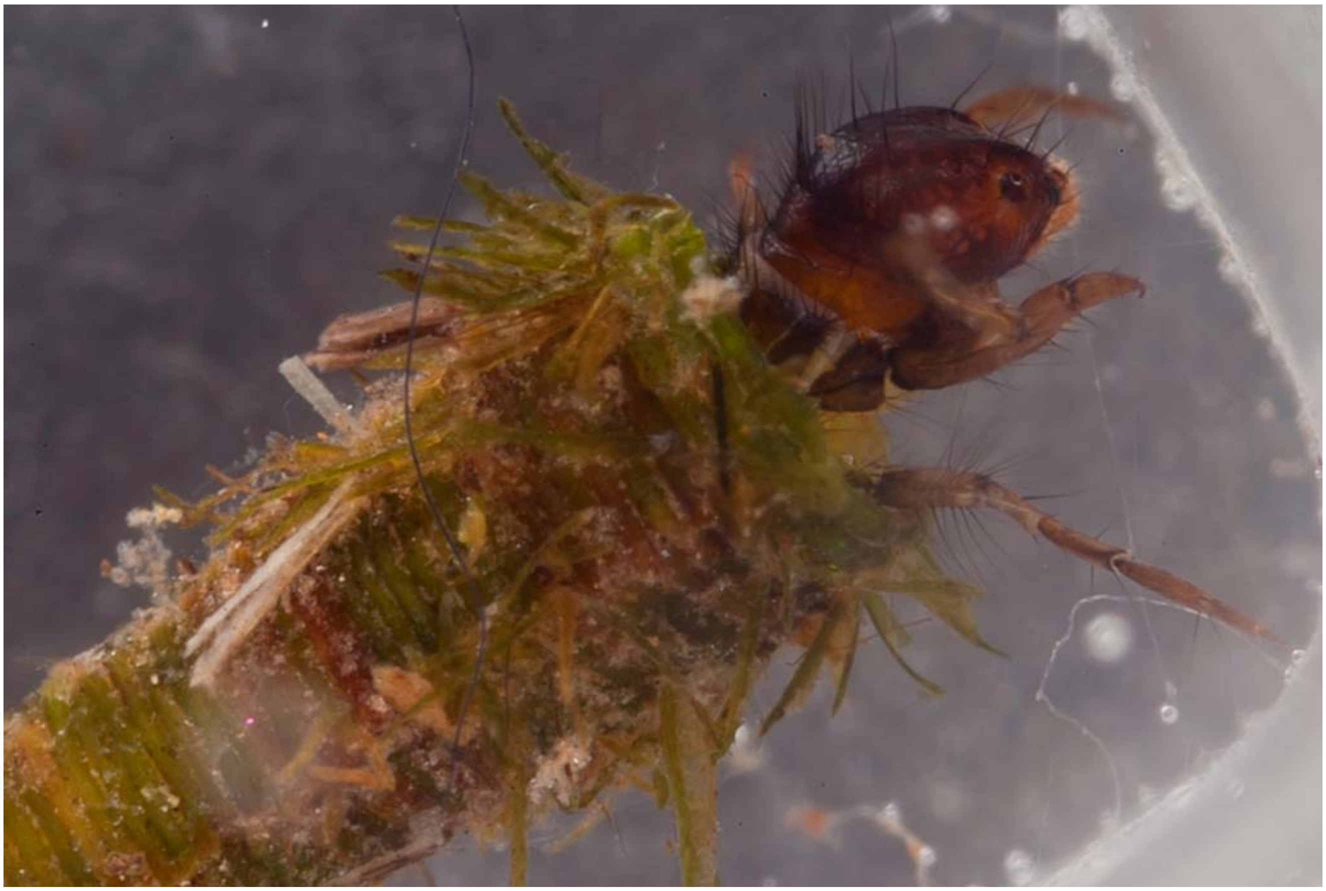

Figure 1. ***Adicrophleps hitchcocki*** (**Brachycentridae**), a larva that makes its case from mosses. Note the "furry" portion near the opening. Photo by D. N. Bennett, with permission.

SUBORDER INTEGRIPALPIA

Leptoceroidea

Odontoceridae – Mortarjoint Casemakers

This worldwide family lives in springs and small to medium streams and rivers, typically with slow flow; some are associated with waterfalls (Holzenthal *et al*. 2010c). Also known as the strong case-maker caddis, the larvae make very strong cases from bits of rock with more than usual amounts of the silk glue (Henricks 2011).

Although I never found ***Pseudogoera*** in my studies of stream insects among bryophytes in the mid Appalachians, ***P. singularis*** (Figure 2) is associated with mosses in waterfalls in the southern Appalachians, USA (Wallace & Ross 1971).

Figure 2. ***Pseudogoera singularis*** larva, a species that lives in mosses of waterfalls in the southern Appalachian Mountains. Photo by BIO Photography Group, through Creative Commons.

In the mid-Appalachian Mountain streams, I found two species of ***Psilotreta*** (Figure 3) among ***Hygroamblystegium fluviatile*** (Glime 1968). This genus has forewings of 6-17 mm (Parker & Wiggins 1987), representing one of the larger of the bryophyte dwellers.

Figure 3. ***Psilotreta*** larva, an inhabitant of ***Hygroamblystegium fluviatile*** in the Appalachian Mountains. Photo by Bob Henricks, with permission.

Figure 4. ***Hygroamblystegium fluviatile***, home of ***Adicrophleps hitchcockii***. Photo by Michael Lüth, with permission.

Figure 5. ***Hygroamblystegium fluviatile*** leaf showing strong costa that seems to be used in making the cases of ***Adicrophleps hitchcockii***. Photo by Michael Lüth, with permission.

Limnephiloidea

Goeridae

This family occurs on all continents except Australia and South America (Holzenthal *et al*. 2007). Adults have a forewing length of 6-9 mm and are typically light brown (Figure 6) (Houghton 2012). The larvae (Figure 7) live in cool, flowing water and graze on **periphyton**. Their larval cases consist entirely of rock fragments, sometimes with larger rocks on each side of the case (Figure 8).

Figure 6. *Goera pilosa* adult, demonstrating the light brown wings typical of the family **Goeridae**. Photo from Biopix, through Creative Commons.

Figure 7. *Pseudogoera singularis* larva. Photo by BIO Photography Group, through Creative Commons.

Figure 8. *Goera calcarata* larva showing large rock fragments on sides of case. Photo by Bob Henricks, with permission.

Goerita is a small genus with only three species and is restricted to the Appalachian Mountains and Allegheny Plateau in eastern North America (Parker 1998). The larvae are **bryobionts**, living on rocks covered with mosses and liverworts where the rocks can be dry or covered by a film of water. The larvae do not eat the bryophytes, but instead feed on detritus and diatoms growing there.

Goerita semata lives on the undersides of rocks (Flint 1960), but in western North Carolina, Huryn and Wallace (1985) found the larvae among liverworts and mosses on vertical rock faces; fewer than 2% were found on other substrata. ***Goerita betteni*** lives in a similar habitat (Wiggins 1973). Huryn and Wallace (1985) suggested that the bryophytes may offer the larvae some protection from desiccation. Pupae typically occur on these same rocks with mosses and a thin film of water. Ultimately, females lay their eggs away from water on bare rock, mosses, and liverworts. Food of the larvae consists primarily of fine amorphous detritus (65%), and diatoms (32%), but diatom composition increases to an average of 64% in spring. Bryophyte clumps are typically good sources of both. Although the mechanisms of desiccation resistance are unknown in larvae of this species, it is likely that they are adapted behaviorally by living among the bryophytes.

In the River Rajcianka in Slovakia, ***Lithax niger*** (Figure 9) is a bryophyte dweller, living under water, but not in the wet emergent bryophytes (Krno 1990). This is a mountain species, occurring in the Alps and Balkans.

Figure 9. ***Lithax niger*** adult, a species whose larvae live among mosses in the River Rajcianka. Photo by Paul Frandsen, through public domain.

The larvae of ***Archithremma ulachensis*** move to a layer of ***Sphagnum*** (Figure 10) on the bank of a spring to pupate (Levanidova & Vshivkova 1984). These pupae are morphologically reduced, lacking long **setae** (hairs) and projections used to clean the silk disks that close the case. They also lack swimming legs. The larvae live in streams that have low water temperatures (3-5°C) in summer.

In a cool mountain stream of central Japan Tada and Satake (1994) found that ***Pseudostenophylax ondakensis*** (Figure 12) was significantly more abundant on mats of the moss ***Platyhypnidium riparioides*** (Figure 13) than in bare rock areas. Décamps (1967, 1968) found ***Rhadicoleptus spinifer*** (see Figure 14) to be abundant among mosses in the Pyrénées; at one station it comprised ~15% of the moss **Trichoptera** fauna (Décamps 1967).

Figure 10. ***Sphagnum cuspidatum***, a pupation site for ***Limnephilus peltus*** and ***Architremma ulachensis***. Photo by Bernd Haynold, through Creative Commons.

Limnephilidae – Northern Caddisflies

The **Limnephilidae** encompasses a wide variety of case-making caddisflies in a wide range of habitats. Their ingenuity in making these homes could challenge some of our most creative artists. This is one of the largest caddisfly families, with recent segregate families diminishing its numbers. Although it occurs worldwide, its records are concentrated in Europe and North America (Limnephilidae 2015). In North America it is often the dominant group in higher elevation streams. But these are mostly large caddisflies (15-35 mm) (Houghton 2012), making navigation difficult among bryophytes. ***Fontinalis*** (Figure 11), on the other hand, is a large enough moss with a streamer habit that permits these larger larvae to navigate (Glime 1968, 1994). Their dependence on terrestrial litter makes the larvae vulnerable to deforestation (Houghton 2012).

Figure 11. ***Fontinalis antipyretica***, home to many kinds of insects. Photo by Kristian Peters, with permission.

Figure 12. ***Pseudostenophylax ondakensis*** larva, a species that is significantly more abundant on the moss ***Platyhypnidium riparioides*** than on bare rock. Photo by Takao Nozaki, with permission.

Figure 13. ***Platyhypnidium riparioides***, home to ***Pseudostenophylax ondakensis*** in Japan. Photo by J. C. Schou, with permission.

Figure 14. ***Rhadicoleptus alpestris*** adult. ***Rhadicoleptus spinifer*** larvae are abundant among mosses in the Pyrénées. Photo by Niels Sloth, with permission.

The larvae of ***Chaetopterygopsis maclachlani*** (Figure 15) typically occur among clumps of ***Fontinalis*** (Figure 11) in the Vosges Mountains, eastern France, mostly in areas with slower or laminar flow (Lehrian *et al*. 2010). The mosses constitute ~65% of their diet, with the remainder being coarse leaf detritus (Dangles 2002). Dangles warned that some species, including this one, are able to shift their diet based on availability, causing misinterpretations based on the general feeding guild classification of these insects. Dangles (2002) considered ***Chaetopterygopsis maclachlani*** (Figure 15) to be a specialist on bryophytes; they furthermore build their cases from ***Fontinalis*** (Figure 62) (Malicky 1994). As adults they typically crawl, not fly, among the **riparian** (streambank) vegetation.

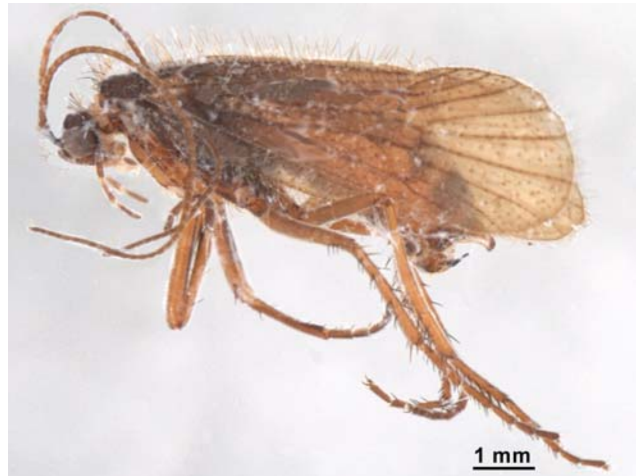

Figure 15. ***Chaetopterygopsis maclachlani*** adult, a species whose larvae live among ***Fontinalis*** and eat mosses as 65% of their diet. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Chaetopterygosis machlachlani is widespread in the Pyrenees to Baikal, specializing in ***Fontinalis*** and other streambed mosses (Báilint *et al*. 2011).

In the mid-Appalachian Mountain, USA, streams, the **Limnephilidae** are poorly represented among bryophytes (Glime 1968). Furthermore, those few that are present differ from any of the species I found in the literature as moss dwellers. Two species of ***Pycnopsyche*** [***P. luculenta***, ***P.*** cf. ***scabripennis*** (Figure 16)] were the most common, appearing in clumps of ***Fontinalis*** (Figure 62) (Glime 1968). This restriction is most likely due to the large size of the **Limnephilidae** larvae, especially when their bulky case is considered. They would have real difficulty moving about in ***Hygroamblystegium fluviatile*** (Figure 4-Figure 5) or ***Platyhypnidium riparioides*** (Figure 13).

Figure 16. ***Pycnopsyche scabripennis*** larva, a ***Fontinalis*** dweller. Photo by Tom Murray, through Creative Commons.

In an experimental study on ***Limnephilus rhombicus*** (Figure 17), Higler (1975) was able to keep the larvae alive on a diet of ***Fontinalis antipyretica*** (Figure 11) with dead birch and oak leaves. However, it appears that its natural diet is mostly living plants (Slack 1936), dead leaves (Slack 1936; Lepneva 1966) and sometimes Naididae (aquatic segmented worms). It is not typically a moss dweller, so the moss diet was most likely unnatural. But Slack (1936) did find that it ate ***Fontinalis*** in the field. On the other hand, when ***Potamophylax rotundipennis*** (Figure 18-Figure 19) was provided choices of birch, oak, and beech leaves and ***Fontinalis antipyretica***, it avoided the moss and beech leaves.

Figure 17. ***Limnephilus rhombicus*** larva, showing yet a third very different case, one using snail shells. Photo by Dragiša Savić, with permission.

Figure 18. ***Potamophylax*** larva and case. ***Potamophylax rotundipennis*** rejects ***Fontinalis antipyretica*** as a food choice. Photo by Michael Wiesner <www.waldzeit.ch>, with permission.

Although most of the **Limnephilidae** make large cases with large components of twigs and leaf fragments, some use bryophytes. ***Limnephilus externus*** (Figure 20-Figure 21) larvae are known to use the moss ***Leptodictyum riparium*** (Figure 22) to construct their barrel-shaped cases (Pritchard & Berté 1987). In experiments, this species was able to use wheat flakes, but not alder leaves, to make its case. In the same experiment, ***Nemotaulius hostilis*** (Figure 23) used alder, willow, and burreed but did not use wheat flakes or mosses. These same two insects are shredders that consume tracheophyte detritus, but the proportion of mosses in the diet increases as the larvae become older.

Figure 19. ***Potamophylax*** adult. Photo through Creative Commons.

Figure 20. Two ***Limnephilus externus*** larvae with the second grabbing the rear of the first. The two cases appear to be made of bits of grass and this camouflage most likely fools their predators because it confused my non-biologist reviewer! Photo by Wendy Brown <www.gunnisoninsects.org>, with permission.

Figure 21. ***Limnephilus externus*** larva. Photo by Wendy Brown <www.gunnisoninsects.org>, with permission.

Limnephilus peltus (Figure 24) doesn't spend much time among mosses as a larva, but when it is time to pupate, it burrows into mosses along fen streams where it spends its pupal life (Erman 1984). Unfortunately, if the stream dries out, the pupa is likely to die.

Figure 22. ***Leptodictyum riparium***, home of larvae of ***Limnephilus externus***. Photo by Jan-Peter Frahm, with permission.

Figure 23. ***Nemotaulius hostilis*** larva showing case made of leaf litter. Photo by Donald S. Chandler, with permission.

Figure 24. ***Limnephilus*** sp. larva, a genus that sometimes pupates in mosses of fens. Photo by Jason Neuswanger, with permission.

The habitat of larvae of the high altitude ***Drusus discolor*** (Figure 25) in the Pyrénées consisted of filamentous algae and the moss ***Bryum*** (Figure 26) (Décamps 1968). This caddisfly is one of the two most abundant caddisflies among mosses (Décamps 1967). In the River Rajcianka in Slovakia, ***Drusus annulatus*** (Figure 27) occurs not only among submerged bryophytes but also moving about among the wet bryophytes that emerge above the water level (Krno 1990).

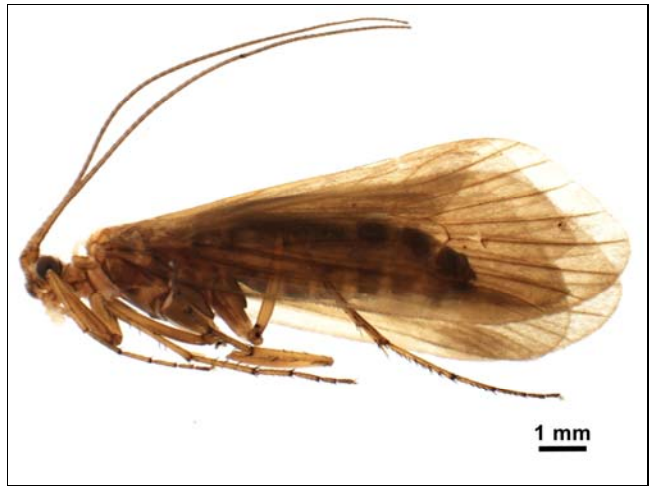

Figure 25. ***Drusus discolor*** adult, a species that lives among the moss ***Bryum*** in the Pyrénées. Photo from Biodiversity Institute of Ontario, through Creative Commons.

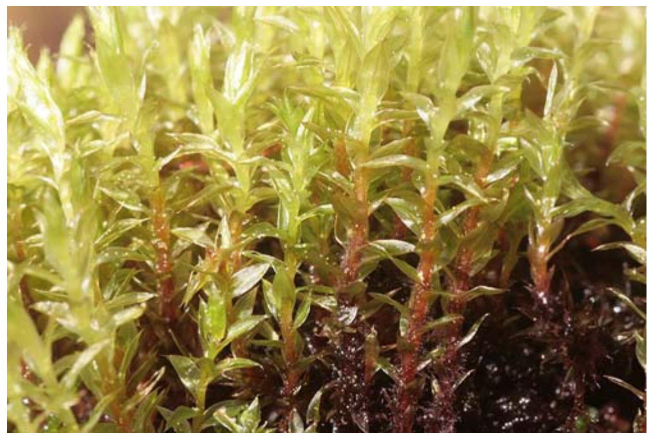

Figure 26. ***Bryum pseudotriquetrum***, home to several species of ***Drusus*** in Europe. Photo by Hermann Schachner, through Creative Commons.

Figure 27. ***Drusus annulatus*** adult, a species whose larvae can live above or below the water surface among bryophytes. Photo by James K. Lindsey, with permission.

Frenesia difficilis (Figure 28) lays its eggs out of the water, sometimes on mosses that overhang the water (Flint 1956). In this terrestrial location the eggs may freeze in winter. In the Massachusetts, USA, fish hatchery, Flint found no other relationship with mosses during the life cycle.

Figure 28. ***Fresnia difficilis*** male, a species that sometimes lays its eggs on mosses that overhang the water. Photo by Tom Murray, through Creative Commons.

The Arctic caddisfly ***Sphagnophylax meiops*** lives in Arctic pools in the tundra in the Northwest Territories of Canada (Wiggins & Winchester 1984) where the larvae take advantage of the surface water in the pool (Winchester *et al*. 1993). When the water recedes the larvae move to the organic materials accumulated above the permafrost to feed, grow, and metamorphose into pupae and adults. This caddisfly is flightless and has long bristles on its short wings.

Most **Trichoptera** spend their larval life in the water, but in the genus ***Enoicyla*** (**Limnephilidae**; Figure 29), the larvae are terrestrial and the adult female has only vestigial wings, limiting her travel and agility. Males, however, are capable fliers. Larvae may live far from water among the mosses around tree roots (Watson & Dallwitz 2003). Green (2012) noted at least 50 of these larvae climbing up logs, with several browsing a black slime mold. One can observe many larvae together on the surface of mosses and liverworts growing on a stream bank following rain.

Enoicyla pusilla (Figure 29) uses fine sand grains and other vegetable matter to make cases where it lives among the mosses (Watson & Dallwitz 2003). The larvae of ***Enoicyla***, despite being terrestrial, require 100% humidity (Green 2012). But when they become saturated, they climb upwards to dry, then drop back down when they need to get wet again (at 7% relative humidity). Their respiration is through the cuticle; they lack gills.

Figure 29. ***Enoicyla pusilla*** larvae, a terrestrial species that requires 100% humidity – a condition often found among mosses. Photo by Ernest van Asseldonk, through Creative Commons.

In his arguments to support that the **Trichoptera** (with hairs on wings) and **Lepidoptera** (with scales on wings) were closely related, Crampton (1920) used the common ability to use mosses in the caddisfly ***Enoicyla*** (**Limnephilidae**; Figure 29) and the larvae of moths in **Micropterygidae**.

The caddisflies living in peatlands are typically generalist taxa with wide habitat requirements (Flannagan & Macdonald 1987). But a few are **tyrphobionts** (living only in peat bogs and mires). The larvae of ***Phanocelia canadensis*** (Figure 30-Figure 31) are elusive. The second report of the larvae by Colburn and Clapp in 2006 was from kettle hole wetlands in Massachusetts, USA. Colburn and Clapp attribute the limited reports of larvae of this species to its limited habitat requirements. It lives in ***Sphagnum*** (Figure 10) habitats with low *p*H and makes its case from ***Sphagnum*** (Figure 30) [The picture below (Figure 31) indicates other mosses are used as well.] Larvae remain closely associated with the moss during development. They become dormant in summer, remaining in unsealed cases that are firmly attached to the moss. In autumn they seal the ends of the case and develop into pupae. Even fossil records support their preference for ***Sphagnum*** (Figure 10) bogs. The larva was originally described from floating ***Sphagnum*** at the edge of acidic ponds in a spruce-***Sphagnum*** bog in New Brunswick, Canada (Fairchild & Wiggins 1989). It appears that adult habitats are much broader, perhaps misleading its collectors (Colburn & Clapp 2006).

Figure 30. ***Phanocelia canadensis*** larva showing its case made with ***Sphagnum***. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 31. ***Phanocelia canadensis*** larva showing case made with at least some non-***Sphagnum*** mosses. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Leberfinger and Bohman (2010) gave larvae of ***Limnephilus bipunctatus*** (Figure 32) choices of food that included grasses, mosses, algae, and leaves. The larvae preferred leaves of the shrubby cinquefoil. Although they ate little of the mosses, grass was the least preferred food.

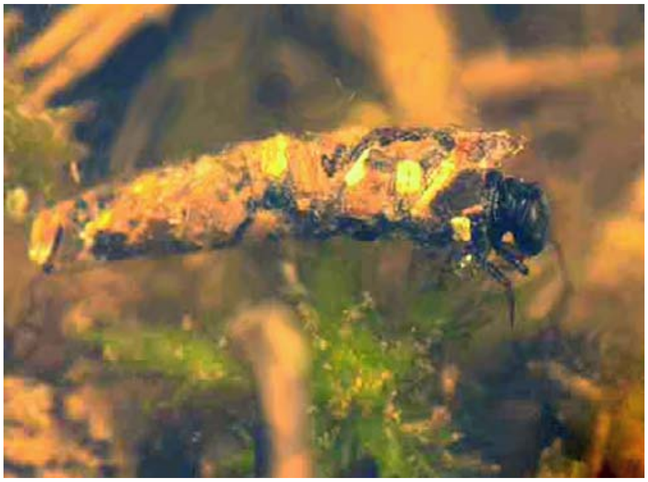

Figure 32. ***Limnephilus bipunctatus*** larva in case, a species that includes mosses in its diet. Photo by James K. Lindsey, with permission.

Philocasca is not a genus one often reads about in moss habitats. Nevertheless, mosses appear to be suitable sites for pupation. In describing the new species ***Philocasca rivularis*** (see Figure 33) Wiggins and Anderson (1968) state that pupae attach to the undersides of moss clumps along stream banks. Mutch and Pritchard (1984) found that instar V larvae of ***P. alba*** (Figure 34) in a Rocky Mountain stream had mostly moss (***Hygrohypnum luridum*** – Figure 35) in the gut in spring and summer, but had leaf fragments in the gut in autumn. Furthermore, when fed detritus supplemented with moss these larvae grew significantly better than when fed detritus alone, suggesting that the moss was an important nutrient source.

Figure 33. ***Philocasca thor*** adult. ***Philocasca rivularis*** pupates on undersides of moss clumps on streambanks. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 34. ***Philocasca alba*** adult, a species whose larvae feed on the moss ***Hygrohypnum luridum*** in a Rocky Mountain, USA, stream in spring and summer. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 35. ***Hygrohypnum luridum***, a species that typically occurs both in the water and above it. Photo by Dale Vitt, with permission.

Onocosmoecus unicolor (Figure 36-Figure 37) is a large shredder that includes mosses in its varied diet (National Park Service 2014).

Figure 36. ***Onocosmoecus unicolor*** larva, a moss consumer. Photo by Jason Neuswanger, with permission.

Figure 37. ***Onocosmoecus unicolor*** adult. Photo by Bob Newell, with permission.

Chyranda centralis (Figure 38) is a caddisfly of small spring streams among leaf accumulations. Its food includes leaves, bark, and may even include mosses (National Park Service 2014).

Figure 38 ***Chyranda*** larva of small spring streams; it may sometimes eat mosses. Photo from California Department of Fish and Wildlife, through public domain.

Mosses provide vertical zonation possibilities for the caddisflies. Krno (1990) addressed these vertical zones in the River Rajcianka in Slovakia. There, the limnephilids ***Allogamus auricollis*** (Figure 39-Figure 40) (a shredder), ***A. uncatus***, and ***Drusus annulatus*** (Figure 41) occurred among the submerged mosses, but above water only ***Allogamus auricollis*** and ***Drusus annulatus*** occurred among emergent wet mosses. On the other hand ***Parachiona picicornis*** (Figure 42) was only found above water among the wet mosses.

Figure 39. ***Allogamus auricollis*** larva, a species that traverses among mosses both below and above the water surface. The larva is seen here breaking the surface tension. Photo through Creative Commons.

Figure 40. ***Allogamus auricollis*** larvae. Photo by Wolfram Graf, with permission.

Figure 41. ***Drusus annulatus*** adult, a species whose larvae live among submerged mosses and will venture above the water among wet mosses. Photo by James K. Lindsey, with permission.

Figure 42. ***Parachiona picicornis*** adult, a species whose larvae live among submerged mosses but will not venture above the water among wet mosses. Photo by James K. Lindsey, with permission.

Chaetopterygopsis maclachlani larvae in the Carpathians are "specialized" on the aquatic moss ***Fontinalis*** (Figure 62) in mountain streams (Bálint *et al*. 2011).

Figure 43. ***Chaetopterygopsis machlachlani*** larva, a ***Fontinalis*** dweller. Photo by Michael Balke, through Creative Commons.

Lepidostomatidae – Bizarre Caddisflies

This family is widespread in the Northern Hemisphere, extending southward to Panama, New Guinea, and the Afrotropical region (Holzenthal *et al*. 2010a). Hilsenhoff (1975), in reporting on Wisconsin, USA, **Lepidostomatidae**, considered the larvae of this family to inhabit a wide range of clean streams. The larvae live among rocks, debris, and mosses on rocks and eat mostly detritus (BugGuide 2005). In North America the larvae inhabit springs, streams, and large slow-moving rivers where they eat detritus. They build a log cabin style of case from stem and leaf pieces or sand grains.

I did find ***Lepidostoma americana*** in clumps of ***Hygroamblystegium fluviatile*** (Figure 4-Figure 5) in the Appalachian Mountain streams (Glime 1968). Some older cases of ***Lepidostoma*** sp. contained fragments of the liverwort ***Scapania undulata*** (Figure 74) in them near the opening. ***Lepidostoma hirtum*** (Figure 44-Figure 45) is common among mosses at both Ballysmuttan and Straffan in the UK (Frost 1942). Its diet consists of algae, mosses, and tracheophytes (Rousseau *et al*. (1921). The moss not only provides a suitable location to find its food, but provides it protection from trout and other fish that are its predators.

Figure 44. ***Lepidostoma hirtum*** larva, an inhabitant of bryophytes that also eats them. Photo by Urmas Kruus, with permission.

Figure 45. ***Lepidostoma hirtum*** larva head. Photo by Urmas Kruus, with permission.

Crunoecia irrorata (Figure 46) prefers moss cushions and fallen leaves (Köcherfliegen 2015). In UK streams, this species had mosses in the gut (Percival & Whitehead 1929).

Oeconesidae

This is a small family from Tasmania (1 species) and New Zealand (Holzenthal *et al*. 2007), but of a relatively large size (adults 30-38 mm) (Oeconesidae 2013). Larvae live in small, forested streams, make cases from plant and rock material, and feed on plant debris (Holzenthal *et al*. 2007).

Figure 46. ***Crunoecia irrorata*** larva, a moss consumer. Photo by Niels Sloth, with permission.

In New Zealand, both ***Oeconesus maori*** (see Figure 47) and ***Zelandopsyche ingens*** (Figure 48) occasionally ingest bryophytes (Suren 1988). Suren and Winterbourn (1991) determined that of the 14 taxa that had bryophyte fragments in their guts, only ***Zelandopsyche ingens*** and ***Oeconesus similis*** consumed them regularly.

Figure 47. ***Oeconesus*** larva, a bryophyte dweller and bryophyte consumer in New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 48. ***Zelandopsyche*** larva and case, a bryophyte dweller and regular bryophyte consumer. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Uenoidae

This family lives mostly in cool, fast-flowing headwaters and is distributed in North America, southern Europe, and eastern Asia (Holzenthal *et al*. 2007). Their cases may be constructed either of coarse pebbles, as in ***Neophylax*** (Figure 53-Figure 55), or of fine sand, flattened, and shaped like the shell of a limpet, as in ***Thremma*** (Figure 49). Larvae eat diatoms and fine particulate matter that they scrape from rocks. These larvae are among the smaller caddisflies, being up to 15 mm (Wiggins 2004), although for moss dwellers they would be in the medium to large category.

Figure 49. ***Thremma gallicum*** larva showing limpet type of case. Photo from Guillaume Doucet, with permission.

Thremma sp. (Figure 49) in the trout streams of Yellowstone National Park, USA, occurs among mosses and the alga *Cladophora* in strong rapids (Muttkowski & Smith 1929). Each of these caddisflies collected from the mosses had mosses in the gut, averaging 70% of the contents. The alga ***Epithemia*** (Figure 50), most likely living among the mosses, comprised the remaining 30%. Brown (2007) found significant numbers of ***Neothremma alicia*** (Figure 51-Figure 52) in small, mossy streams in the headwaters of the East River, Colorado, USA.

Figure 50. ***Epithemia***, a diatom genus that is a common food source for the caddisfly ***Thremma***. Photo by Kristian Peters, with permission.

Figure 51. ***Neothremma alicia*** larva with case, a moss dweller in small, headwater streams. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 52. ***Neothremma alicia*** larva outside its case. Photo from Biodiversity Institute of Ontario, through Creative Commons.

In the Appalachian Mountain stream bryophytes, the **Uenoidae** were represented by a completely different genus from the ones I found in publications, the only one being ***Neophylax***, a genus that sometimes reached large numbers among the **Trichoptera**, but usually was absent (Glime 1968). Nevertheless, three species were represented: ***N. concinnus*** (Figure 53), ***N. consimilis*** (Figure 54), ***N. oligius*** (Figure 55). These were usually in the mat-forming bryophytes, a location permitted by their smaller size.

Figure 53. ***Neophylax concinnus*** larva, a moss dweller in mid-Appalachian Mountain streams. Photo by Bob Henricks, with permission.

Figure 54. ***Neophylax consimilis*** larva, a moss dweller in mid-Appalachian Mountain streams. Photo by Bob Henricks, with permission.

Figure 55. ***Neophylax oligius*** larva, a moss dweller in mid-Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

Phryganeoidea

Brachycentridae – Humpless Casemaker Caddisflies

The **Brachycentridae** are a Northern Hemisphere family (Holzenthal *et al*. 2010b). They eat algae and plankton (Neuswanger 2015b), but some also ingest bryophytes (Muttkowski & Smith 1929). These caddisflies build cases that resemble log cabins or cylinders made of tiny plant fragments (Holzenthal *et al*. 2010b), including bryophytes in some genera (Glime 1968). Often they are found among mosses (Bouchard 2004). When they emerge, they do so on the surface, which sometimes subjects them to 3-7 m of drifting (Neuswanger 2015b). Females may dive to lay eggs or land with spread wings on the surface to accomplish the task.

Brachycentrus

Larvae of ***Brachycentrus*** (Figure 56-Figure 59) species actually attach to the mosses (Armitage 1961; Glime 1968). ***Brachycentrus*** was one of only two genera of caddisflies that Muttkowski and Smith (1929) found among mosses in the trout streams of Yellowstone National Park, USA. Needham and Christenson (1927) reported ***Brachycentrus*** from mosses in streams of northern Utah, USA. In Europe, Krno (1990) found ***Brachycentrus montanus*** (Figure 56) among mosses in the River Rajcianka, Slavakia. In the Appalachian Mountains, ***B.*** cf. ***numerosus*** (Figure 56) occurred in clumps of the moss ***Hygroamblystegium fluviatile*** (Figure 4-Figure 5) (Glime 1968).

Figure 56. ***Brachycentrus numerosus*** larva, a species like one that is common among ***Hygroamblystegium fluviatile*** in the Appalachian Mountain streams. Photo by Tom Murray, through Creative Commons.

Figure 57. ***Brachycentrus montanus*** adult, a species that lives among stream mosses. Photo by James K. Lindsey, with permission.

Gallepp (1977) considered ***Brachycentrus*** – ***B. americanus*** (Figure 58), ***B. occidentalis*** (Figure 59) – to be filter feeders, but Muttkowski and Smith (1929) found that mosses were among the food items in the gut, with one individual having 90% moss. Others had only algae and a few had aquatic insects.

Figure 58. ***Brachycentrus americanus*** larva, a moss consumer. Photo by Donald S. Chandler, with permission.

Figure 59. ***Brachycentrus occidentalis*** larvae, a moss consumer species. Photo by Arlen Thomason, with permission.

Gallepp (1977) found that two species of ***Brachycentrus*** were more responsive to temperature and food availability than to the flow rate. Although case-building decreased with increasing temperature over the range of 4-17°C, ***B. occidentalis*** (Figure 59) grew faster as the temperature increased in the range of 4-27°C.

Micrasema

The larvae of the grazer genus ***Micrasema*** (Figure 60) (Gallepp 1977) are common among mosses (Glime 1968, 1994; Tada & Satake 1994). In the mid-Appalachian Mountain streams I was able to distinguish three different morphotypes (species?) among the bryophytes (Glime 1968). In fact, this genus seems to be almost restricted to that habitat (Hilsenhoff 1975). Tada and Satake (1994) found a species in this genus to be the most abundant insect taxon on mats of ***Platyhypnidium riparioides*** (Figure 13) in a cool mountain stream in central Japan. Among the bryophyte mats its density exceeded 100,000 individuals per square meter in November, an abundance that was 2.8-16.3 times as high as that on the bare rock bottom. At least one species of ***Micrasema*** (Figure 60) constructs a "log cabin" out of moss stems and leaves (Glime 1968).

Figure 60. ***Micrasema charonis*** larva, a common moss-dweller that often makes its case from mosses. Photo by Bob Henricks, with permission.

Chapman and Demory (1963) found that in two streams in Oregon, USA, this genus occurred only among mosses and liverworts where there was little detritus. They graze on periphytic algae during the first instar, but in later instars they are likely to be herbivore-chewers (shredders) on mosses and other small photosynthetic material (Chapman & Demory 1963; Aquatic Insects). In fact, Chapman and Demory (1963) found that ***Platyhypnidium riparioides*** (Figure 13) was the most frequent food, but both mosses and liverworts were eaten. Diatoms were also present in the gut, but they might have been eaten inadvertently along with the bryophytes. And in the Pyrénées ***Micrasema morosum*** behaves as a shredder and eats mosses (and periphyton) as well (Décamps & Lafont 1974).

In the Pyrénées Décamps (1968) found that ***Micrasema morosum*** was abundant in the mosses ***Cratoneuron commutatum*** (Figure 61) and ***Bryum*** (Figure 26) and was the most abundant bryophyte-inhabiting caddisfly. At one station ***M. morosum*** comprised 56% of the Trichoptera fauna among mosses and at another it comprised 87.8% (Décamps 1967). ***Micrasema vestitum*** was abundant in ***Fontinalis squamosa*** (Figure 62) and in one location it comprised 69% of the **Trichoptera** fauna among the mosses**.**

Figure 61. ***Cratoneuron commutatum***, home to several species of ***Micrasema***. Photo through Creative Commons.

Figure 62. ***Fontinalis squamosa***, home to several species of *Micrasema* larvae. Photo by David T. Holyoak, with permission.

Décamps and Lafont (1974) demonstrated the change in moss substrate for ***Micrasema morosum*** as altitude changes in the Pyrénées. At 1940 m asl the dominant bryophytes were ***Brachythecium rivulare*** (Figure 63), ***Cratoneuron commutatum*** (Figure 61), and ***Hygrohypnum molle*** (Figure 64). At 1590 m asl dominance shifted to ***Fontinalis squamosa*** (Figure 62), ***Fissidens polyphyllus*** (Figure 65), and ***Platyhypnidium riparioides*** (Figure 13). At 1360 m asl ***Fissidens grandifrons*** (Figure 66) appeared and ***Platyhypnidium riparioides*** (Figure 13) remained in the stream flora. At

550 m asl the dominant mosses were ***Brachythecium rivulare***, ***Fissidens grandifrons***, ***Platyhypnidium riparioides***, and ***Chiloscyphus polyanthos*** (Figure 67), with a change in the ***Micrasema*** species to ***M. morosum***, ***M. longulum***, ***M. moestum***, ***M. difficile***, and ***M. minimum***. At the lowest location of 430 m, asl ***Brachythecium rivulare***, ***Cinclidotus fontinaloides*** (Figure 68), ***Fontinalis antipyretica*** (Figure 11), ***Platyhypnidium riparioides***, and ***Cratoneuron filicinum*** (Figure 69) with ***Micrasema morosum*** once again the predominant species. The food of these ***Micrasema*** species consisted of fragments of mosses and periphytic algae, with some food unidentifiable.

Figure 63. ***Brachythecium rivulare***, home to several species of ***Micrasema*** larvae. Photo by David T. Holyoak, with permission.

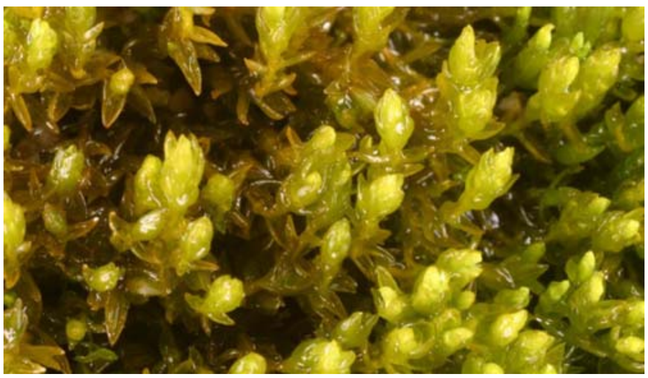

Figure 64. ***Hygrohypnum molle***, home to several species of ***Micrasema*** larvae. Photo by Jan-Peter Frahm, with permission.

Figure 65. ***Fissidens polyphyllus***, home for several species of ***Micrasema***. Photo by David T. Holyoak, with permission.

Figure 66. ***Fissidens grandifrons***, home to larvae of several ***Micrasema*** species. Photo by Scot Loring, through Creative Commons.

Figure 67. ***Chiloscyphus polyanthos***, home to lower elevation species of ***Micrasema*** larvae in the Pyrénées. Photo by Barry Stewart., with permission

Figure 68. ***Cinclidotus fontinaloides***, home to lower elevation species of ***Micrasema*** larvae in the Pyrénées. Photo by David T. Holyoak, with permission.

Figure 69. ***Cratoneuron filicinum*** in Europe, home for many immature insects. Photo by Michael Lüth, with permission.

In Japan, ***Micrasema uenoi*** (Figure 70) feeds on the leaves of ***Platyhypnidium riparioides*** (Figure 13) and the first instar larvae make their cases of its leaves (Kato 1995). The first two instars live in greater numbers among mosses than on cobble, but by third to fifth instars the numbers are about equal. When artificial mosses (glass wool) and cleaned mosses were introduced, these larvae reached normal densities in 15-30 days. Surprisingly, the density on the glass wool was 2-3 times that among the mosses, but it subsequently decreased quickly. Gut contents of those third to fifth instars on bryophytes was 80% moss; those on the glass wool contained litter and detritus instead. The larvae move about a lot between the pebbles and the mosses. Eggs were apparently absent on the mosses, suggesting that the hatchlings move there.

Figure 70. ***Micrasema uenoi*** adult, a species whose larvae feed on leaves of ***Platyhypnidium riparioides*** in Japan. Photo by Takao Nozaki, with permission.

D. N. Bennett (pers. comm. 6 August 2013, 12 August 2014) observed ***Micrasema wataga*** (Figure 71-Figure 72) larvae eating moss (possibly ***Hygrohypnum montanum***) leaves (Figure 71) in the Blue Ridge Mountains of Virginia, USA. They made their cases of the same moss, starting with a tiny cone of minute sand grains. The mosses closest to this cone part, hence the oldest, were no longer green, but those near the opening were still green. This can be a possible source of dispersal of fragments that break away from the unfinished cases. But a later observation showed that the mosses in the case actually sprouted there (Figure 72)! This case was apparently occupied by a pupa, ceasing the activity that could break off these sprouts before they attained sufficient size to exist on their own.

Figure 71. ***Micrasema wataga*** eating moss (***Hygrohypnum montanum***?). Photo by D. N. Bennett, with permission.

Figure 72. ***Micrasema wataga*** case with moss sprouts. A pupa is hiding inside. Photo by D. N. Bennett, with permission.

Adicrophleps hitchcockii

This interesting larva makes its case from bryophytes. It was relatively common among ***Hygroamblystegium fluviatile*** (Figure 4-Figure 5) in Appalachian Mountain streams (Glime 1968). It appeared to have used costae from this moss in the construction of its cases.

D. N. Bennett likewise collected larvae of the somewhat rare ***Adicrophleps hitchcockii*** (Figure 1, Figure 73) in several cold, rapid streams (1-10 m wide) from the aquatic leafy liverwort ***Scapania*** (Figure 74) growing in riffle areas (Henricks 2013; D. N. Bennett, pers. comm. September 2014). But the case is not made of liverworts, but rather it displays mosses. Wiggins (1977) described these as "4-sided, tapered, and constructed of pieces of moss arranged transversely; trailing ends frequently left attached to the moss pieces give the case a furry appearance."

Figure 73. ***Adicrophleps hitchcocki***, a species that lives among bryophytes and makes its case from mosses. Photo by D. N. Bennett, with permission.

Figure 74. ***Scapania undulata***, home for ***Adicrophleps hitchcocki*** but not used for case building. Photo by Hermann Schachner, through Creative Commons.

Phryganeidae – Giant Casemakers

This family with relatively large larvae lives mostly in lakes and rivers (Neuswanger 2015a). The pupae crawl from their watery location to shore to emerge. Females run across the water surface to lay their eggs. The larvae are most common among aquatic plants in ponds and marshes, but some occur in streams and others in temporary pools and deep in lakes (Holzenthal *et al*. 2007). Larvae are typically either predators or herbivores.

This family is not common among the bryophytes. But, ***Yphria californica*** (Figure 75), a species restricted to the west coast states of USA, lays its eggs (Figure 76) underwater among mosses that dangle over the stream in the Sierra Nevada, North America (Erman 1984). To do that, the adult must swim underwater.

Figure 75. ***Yphria californica*** adult, a USA west coast species that lays its eggs among mosses. Biodiversity Institute of Ontario, through Creative Commons.

Figure 76. **Trichoptera** eggs, often laid on bryophytes. Photo by Bob Armstrong, with permission.

The larvae of ***Eubasilissa regina*** (Figure 77) in Japan begin their construction days by making cases of liverworts, but as they develop they change to terrestrial leaf litter and move their abode from the liverworts to pools (Ito 1988).

Figure 77. ***Eubasilissa regina*** adult, a large Japanese caddisfly for which the larvae begin their case construction using liverworts. Photo through Creative Commons.

Oligostomis ocelligera (Figure 78) lives in moist places such as under mosses where it is protected (Redell *et al*. 2009). It usually occupies positions with a mean distance of 6.1 cm below the surface.

Figure 78. ***Oligostomis ocelligera*** larva, a species that lives under mosses. Photo by Tom Murray, through Creative Commons.

Hagenella clathrata is a rare caddisfly in Europe, inhabiting the disappearing bog habitat (Buczyńska *et al.* 2012). In particular, the species often occurs in bog pools that occur only in rapidly disappearing floating bogs, hence being dependent on the particular habitat created by ***Sphagnum*** (Figure 10) (Kleef et al. 2012).

Sericostomatoidea

Beraeidae

This family is scattered about the globe, being concentrated in the western **Palaearctic Region** (Eurasia from western Europe to the Bering Sea), but also occurs in Tanzania, Japan, and eastern North America (Hamilton 1985; Holzenthal *et al.* 2007). Adults have forewings that are only 4-6 mm long (Watson & Dallwitz 2003). Larvae live in springs, seeps, and small streams where they utilize a variety of substrates, including bryophytes (Hamilton 1985; Holzenthal *et al.* 2007). They eat plant and fungal material, but there seem to be no records of eating bryophytes.

Beraea maura (Figure 79) represents this family in the River Rajcianka, Slovakia, where it inhabits the submerged bryophytes (Krno 1990). Unlike several members of the **Limnephilidae** and **Rhyacophilidae**, this species is not found above the water level in the wet mosses there. In the Pyrénées, Décamps (1968) found larvae of this family among mosses, but this family had a wide range of habitats in addition to the mosses.

Figure 79. ***Beraea maura*** adult, a species that lives among submerged bryophytes as larvae. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Conoesucidae

Among the unfamiliar **Trichoptera** names (to those of us in the northern hemisphere), the **Conoesucidae** (Figure 80) is another of bryophyte-dwelling families from down under (Winterbourn & Gregson 1981). The family is endemic to Australia, New Zealand, and Tasmania (Johanson *et al.* 2009). Among the bryophyte dwellers is ***Confluens hamiltoni***, an endemic on the North Island, New Zealand, where it is associated with mosses, liverworts, and algae in rapid-flow streams (Winterbourn & Gregson 1981). On the South Island, this species is replaced by ***C. olingoides***, occupying conditions like those of ***C. hamiltoni***.

Figure 80. ***Pycnocentrodes aureolus*** adult, member of a family (**Conoesucidae**) with bryophyte dwellers in the Australian region. Photo by Maurice, through Creative Commons.

Helicophidae

This family of 6-14 mm length (Helicophidae 2015b) is mostly known from Australia, New Zealand, and New Caledonia, but also from southern South America and scattered locations in North America (Helicophidae 2015a). The larvae live in slow streams and are mostly detritivores (Helicophidae 2015b).

Trichoptera are not as common in New Zealand as in other parts of the planet, but the **Helicophidae** are represented there, sometimes associated with mosses (Winterbourn & Gregson 1981). ***Zelolessica cheira*** (Figure 81) occurs among ***Fissidens rigidulus*** (Figure 82) in the torrential waters near the middle of stream channels in the Southern Alps (Cowie & Winterbourn 1979). ***Zelolessica cheira*** is usually associated with mosses and liverworts in rapid streams with a stable, rocky substrate (Winterbourn & Gregson 1981; Eward *et al.* 1994). The cases are curved, comprised variously of sand grains, liverworts, and mosses.

Figure 81. ***Zelolessica*** larvae. Some members make their cases from bryophytes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 82. ***Fissidens rigidulus***, home for ***Zelolessica cheira*** in torrential New Zealand waters. Photo by Bill & Nancy Malcolm, with permission.

Alloecentrella (Figure 83) is known from China, Australia, New Zealand, and the Antarctic. In New Zealand, ***Alloecentrella magnicornis*** and an unnamed species occur among mosses and liverworts in rocky streams where they build their cases using bryophytes (Eward *et al*. 1994).

Figure 83. ***Alloecentrella*** sp. larva, a species that covers its case with mosses and liverworts. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Sericostomatidae – Bushtailed Caddisflies

These caddisflies are of moderate size, with wings 8-15 mm long (Watson & Dallwitz 2011). This family is cosmopolitan except for the Australian region (Sericostomatidae 2015). Nevertheless, many of the genera are endemic to small areas of their continents. At least some larval members of the family move little. For example, more than 120,000 larvae of ***Gumaga nigricula*** (Figure 84-Figure 85) were released in pools of a California mountain stream and 87-93% of them remained within 4 m of the pools (Jackson *et al*. 1999). In this clever experiment, the larvae were provided with bright gold or magenta sand grains to complete their cases so that they could easily be tracked.

Figure 84. ***Gumaga*** sp. larva, a relatively immobile caddisfly. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 85. ***Gumaga nigricula*** adult, a relatively immobile caddisfly in the larval stage. Photo from Biodiversity Institute of Ontario, through Creative Commons.

The **Sericostomatidae** live in both streams and lakes and mostly feed on leaf litter (Family Sericostomatidae 2015). They build slightly to strongly curved tubular cases from sand grains or just silk. Because of their interesting designs and strength, the Tupi-Guarani Indians in Brazil used the cases of ***Grumicha*** as adornment.

Some of the moss dwellers are quite rare. Stern and Stern (1969) found the larvae of ***Sericostoma*** sp. (Figure 86) only among algae and mosses in a Tennessee, USA, springbrook.

Sericostoma pedemontanum (Figure 86), a caddisfly of fast-running streams, refused ***Fontinalis antipyretica*** (Figure 11) when provided a diet of birch, beech, and oak leaves with it (Higler 1975). Birch was the preferred food.

Figure 86. ***Sericostoma pedemontanum*** larva, a species that refused ***Fontinalis*** and chose various species of leaf litter in a feeding experiment. Photo by Massimo Del Guasta, with permission.

SUBORDER SPICIPALPIA

Glossosomatoidea

Glossosomatidae – Tortoise or Saddle-case Makers

This worldwide family makes its larval cases from pebbles in the shape of a turtle shell (Glossosomatidae 2014). It is probably this structure that forces them to build a new case in each new instar, rather than adding to the old one as most caddisfly families do. These small to medium-sized larvae usually occur in cool mountain streams where they scrape algae from the rocks as their food. The female adults lay their eggs in gelatinous masses under rocks at the water surface or on floating objects, probably including mosses. The gelatinous material protects the eggs from desiccation.

From Ceylon, Schmid (1958) reported ***Agapetus rawana*** (see Figure 87-Figure 90) from large, mossy rocks in the torrent. In the Appalachian Mountains, ***Glossosoma*** (Figure 91) larvae and pupae were often present among the bryophytes (Glime 1968).

Figure 87. ***Agapetus fuscipes*** larva and case, a genus known from large, mossy rocks of torrents in Ceylon. Photo by J. C. Schou, with permission.

Figure 88. ***Agapetus fuscipes*** larvae showing the unusual shape of the case. Photo by Dragiša Savić, with permission.

Figure 89. ***Agapetus*** prepupa in larval case. Photo by Mark Melton, with permission.

Figure 90. ***Agapetus*** pupa removed from case. Photo by Mark Melton, with permission.

Figure 91. ***Glossosoma*** sp. larvae, showing its "turtle shell" case. Photo by Jason Neuswanger, with permission.

Hydroptiloidea

Hydroptilidae – Microcaddisflies, Purse-case Caddisflies

This is a worldwide family, less than 5 mm long, that builds flattened cases often resembling an eyeglass case (Hydroptilidae 2015). The members of the family solve the problem of locating food by depositing their eggs near a suitable food source (Leader 1970). They typically feed on algae by sucking out the cell contents or by feeding on diatoms.

In the Appalachian Mountain streams where I worked, this tiny caddisfly is usually not very common, but Percival and Whitehead (1929) found them more commonly among mosses on stones than on other substrates in the UK. Hughes (1966) found them to be more abundant in open areas than in shaded ones, a factor that usually contrasts with bryophyte preferences. Percival and Whitehead (1929) found that the hydroptilids from mosses feed on algae and diatoms. The larvae of this family have mouthparts that are able to pierce and suck, enabling them to suck the contents from filamentous algae or to scoop up diatoms (Nielsen 1948).

It is perhaps telling that at least in Denmark, the genera ***Agraylea*** (Figure 92), ***Hydroptila*** (Figure 93), ***Oxyethira*** (Figure 94-Figure 95), and ***Orthotrichia*** (Figure 96) are very common in eutrophic lakes (Nielsen 1948). This suggests that in streams we should look for the bryophyte dwellers deep within the mat where there is reduced flow. But even in the lakes these genera occupy vegetation near the surface. ***Agraylea*** and ***Orthotrichia*** occur in slowly flowing water, and this is where mosses can add possible niches. ***Orthotrichia*** often becomes coated in detritus and will pass one of its hind legs down the dorsal side of its abdomen to clean the tracheal gills there.

Figure 92. ***Agraylea sexmaculata*** larva, a genus that lives among bryophytes in slowly flowing water. Photo by Massino Del Guasta, with permission.

Figure 93. ***Hydroptila sparsa*** larvae, member of a genus that occurs among bryophytes in lakes and streams. Photo by Massimo Del Guasta, with permission.

Figure 94. ***Oxyethira*** larva, a moss dweller in Danish lakes. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 95. ***Oxyethira*** pupa. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Figure 96. ***Orthotrichia*** sp larva and case, a species that lives among mosses in lakes. Photo by Urmas Kruus, with permission.

Hydroptila (Figure 93) can build a case of detrital matter and sand grains in about four hours (Nielsen 1948). To increase the size of the case, the larva splits it open along the ventral edge, adding sand grains to the edge. The completed case, as in most members of the family, looks like a case for eye glasses (Figure 93) – the one with an open end – which is where the head protrudes in the caddisfly version. Some cases are built with algal filaments, especially in ***Agraylea*** (Figure 92), and I have observed cases made almost entirely of diatoms. In both ***Hydroptila*** and ***Agraylea*** the outer coating of sand or algae will wear off as the larva nears maturity, leaving only the smooth inner wall made of silk spun by the larva as it cements the case together. ***Orthotrichia*** (Figure 96) and ***Ithytrichia*** (Figure 97) species use only silk in the construction of their cases. These genera feed by sucking the contents out of algal cells.

Figure 97. ***Ithytrichia lamellaris*** larva & case, a genus that uses only silk in its case. Photo by Urmas Kruus, with permission.

When these four genera (***Agraylea***, ***Hydroptila,*** ***Orthotrichia***, ***Ithytrichia***) emerge, they split the pupal case, then move about until they find a protruding object to climb up and out of the water (Nielsen 1948). Once out they can flit about on the water surface and in the air.

The moss-dwelling genus ***Oxyethira*** (Figure 94-Figure 95), including more than one species, comprised 44.5% of the Trichoptera fauna at the acid site in Frost's (1942) moss fauna study of the River Liffey, Ireland. It was absent at the alkaline site. ***Oxyethira frici*** lives in the angle between the leaf and the stem of the moss and pupates among the mosses, a behavior that is uncommon among caddisflies. By contrast, ***Ithytrichia lamellaris*** (Figure 97), a species almost restricted to mosses, was common at the alkaline site and absent from the acid site. It likewise lives in the angle between the leaf and the stem of the moss and pupates among the mosses. Both of these genera were present, but rarely, among the bryophytes of Appalachian Mountain mostly acid streams, USA (Glime 1968). They were more common on ***Fontinalis***, where larvae of ***Oxyethira*** and ***Hydroptila*** sometimes decorated the branches of ***Fontinalis dalecarlica*** (Figure 98).

From Ceylon, Schmid (1958) reported ***Chrysotrichia hapitigola***, and ***Hydroptila kirilawela*** from large, mossy rocks in the torrent.

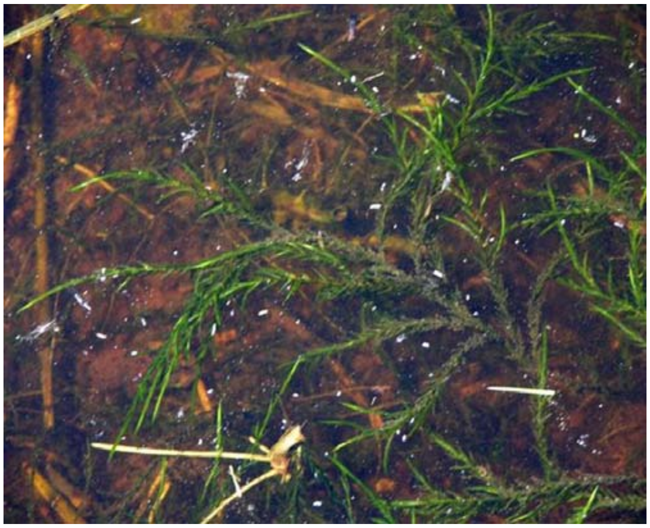

Figure 98. ***Fontinalis dalecarlica***, home to many insects. Photo by J. C. Schou, with permission.

Woodall and Wallace (1972) found ***Ochrotrichia*** sp (Figure 99) on moss-covered granite outcrops in the Appalachian, USA, streams that they studied. They considered the moss-covered rock outcrops to be the central factor influencing the distribution of this species in the area. In my own studies of the mid-Appalachian Mountain streams, this genus was not present, but I did occasionally find ***Mayatrichia***, ***Neotrichia***, and ***Stactobiella*** in addition to the more common ones discussed above under this family (Glime 1968).

Figure 99. ***Ochrotrichia eliaga*** larva and case, a genus found on moss-covered granite outcrops in Appalachian streams. Photo by Trevor Bringloe, Biodiversity Institute of Ontario, through Creative Commons.

In a Tennessee, USA, springbrook, ***Ochrotrichia unio*** (see Figure 100) live among algae and mosses as larvae, then move to bare rocks to pupate (Stern & Stern 1969). In Great Britain, the larvae of this species feed on diatoms and other algae (Percival & Whitehead 1929).

Figure 100. ***Ochrotrichia*** larva, a genus in which some larvae live among mosses, then migrate to bare rocks to pupate Photo from California Department of Wildlife, through public domain.

Ptilocolepus

Ptilocolepus granulatus is **crenophilic**, living in montane to subalpine regions of central Europe (Waringer & Graf 2002). Wesenberg-Lund (1943) reported that ***Ptilocolepus granulatus*** lives in moss cushions and makes its case from moss fragments. Similarly, González *et al*. (2000) reported that ***P. extensus***, an endemic on the Iberian Peninsula and a close relative, uses leaf pieces of several moss and liverwort species to make its final instar case. Unlike most of the **Hydroptilidae**, this case is flattened dorsiventrally, but still has the typical elongate-oval shape.

In the Pyrénées, Thienemann (1950) and Décamps (1968) found ***Ptilocolepus granulatus*** among mosses and liverworts. These bryophytes also formed a significant portion of their food as well as construction material for their cases. Ito (1998) reported that this genus lives among, eats, and builds its cases from the leafy liverworts ***Chiloscyphus polyanthos*** (Figure 67) and ***Scapania undulata*** (Figure 74). Depisch (1999) and Ito and Higler (1993) all found that the species commonly lives among and feeds on the liverwort ***Scapania undulata***. In Belgium ***Ptilocolepus granulatus*** uses ***Jungermannia riparia*** for food, but surprisingly, it also sometimes builds its case from the moss ***Fontinalis*** (Figure 11) (Ito & Higler 1993). Thus it is not surprising that Dittmar (1955) found it associated with ***Fontinalis***. Ito and Higler found that it does not seem to feed on the moss, but later Ito (1998) states that it is the only species in the subfamily **Ptilocolepinae** that is able to feed on ***Fontinalis*** (and other mosses), attributing this ability to its large mandibles.

Palaeagapetus

Microcaddisflies such as ***Hydroptila*** (Figure 93) often attach their tiny homes to the moss leaves and stems, but ***Palaeagapetus*** in the same family constructs its home strictly out of leafy liverworts (Flint 1962; Glime 1978; Ito & Hattori 1986; Ito 1991), even when these are growing side by side with mosses such as ***Fontinalis*** (Figure 11). The species of liverwort depends on availability, with cases of ***Paleagapetus celsus*** from the eastern USA known from ***Scapania nemorea*** (Flint 1962; Glime 1978) (Figure 101), ***S. undulata*** (Glime 1978) (Figure 74), ***Plagiochila porelloides*** (Glime 1978) (Figure 102), ***Frullania*** sp. (Glime 1978) (Figure 103). In those I observed, the pieces of liverwort were cut into nearly circular pieces and cemented together along their margins, forming a case typical of many hydroptilids – the shape of an eyeglass case. Ito and Vshivkova (1999) described the pieces of liverworts comprising the cases of ***Palaeagapetus finisorientis*** from the Russian Far East similarly as being roughly rounded fragments.

Figure 101. ***Scapania nemorea***, one of the species used for making cases of ***Palaeapetus celsus***. Photo by Bernd Haynold, through Creative Commons.

Figure 102. ***Plagiochila porelloides***, a species used by ***Palaeagapetus celsus*** for making its case. Photo by Hermann Schachner, through Creative Commons.

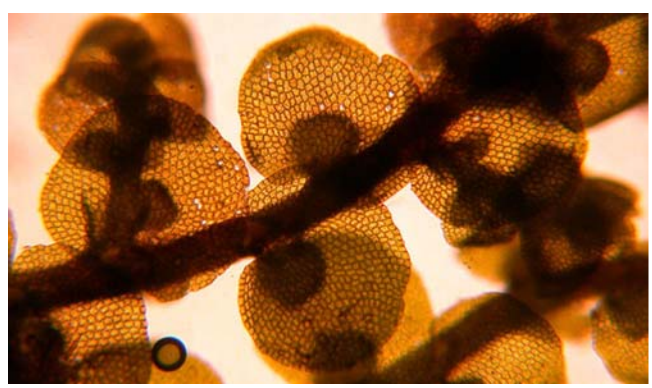

Figure 103. ***Frullania eboracensis***, a terrestrial epiphytic species that may fall into the water and be used in the case of ***Palaeagapetus celsus***. Photo by Bob Klips, with permission.

Not only do members of this genus use liverworts in the construction of their cases, but the liverworts are also a primary food source (Botosaneanu & Levanidova 1987). In his review of four species of ***Palaeagapetus***, Ito (1998) found that all of them used the liverworts ***Chiloscyphus polyanthos*** (Figure 67) and ***Scapania undulata*** (Figure 74) for food, housing, and case construction. It appears that all known members of the genus have this same strong dependence on leafy liverworts, including those in the eastern part of the former Soviet Union (Botosaneanu & Levanidova 1987), Japan (Ito & Hattori 1986; Ito 1988, 1991), and North America (Flint 1962; Glime 1978). In the western USA, ***Palaeagapetus nearcticus*** uses ***Scapania uliginosa*** for its case and food (Ito *et al*. 2014). The larvae pierce the cells and consume the liverwort one cell at a time. Ito and Vshivkova 1999) found that in the ***Palaeagapetus*** species they observed, the early instars fed on the contents of the liverwort cells, whereas the final instar cut off the leaves and apparently ingested them, reminiscent of human babies who also shift from sucking to chewing. Ito (1991) found that ***Palaeagapetus rotundatus*** feeds on the leaves of leafy liverworts ***Chiloscyphus polyanthos*** and ***Scapania undulata*** (Figure 74), but will not feed on the moss ***Platyhypnidium riparioides*** (Figure 13).

Ito (1988) followed the life history of ***Palaeagapetus ovatus*** in a spring stream in Japan. He found that the density changed with season, reaching the highest in winter and being low in summer. Living with it was a predatory **Trichoptera**, ***Eubasilissa regina*** (**Phryganeidae**; Figure 77), that preyed upon it among the liverworts.

We know more about this genus and its liverwort relationship through the description of a new species, ***Palaeagapetus ovatus***, in Japan (Ito & Hattori 1986). This liverwort dweller fed exclusively on the leaves of the leafy liverwort ***Chiloscyphus polyanthos*** (Figure 67). Its fifth and final instar made the typical oval case from the leaves of this liverwort. And the females, within two days of emergence, laid 50-85 eggs on the leaves of this liverwort. The eggs do not form a mass and at 10.5-12°C they hatch in 21-23 days. ***Palaeagapetus nearcticus*** also deposits its orange eggs on liverwort leaves (Ito *et al*. 2014).

More recently, Woods (2002) was surprised to find the thallose liverwort ***Riccardia chamedryfolia*** (Figure 104) moving in a slow, jerky motion on the sandy bottom of a pool in Wales. Investigation revealed that two matching pieces of the thallus had been cemented together by a caddisfly larva that was using it for a home (case). The larva was not identified but could have been a member of **Hydroptilidae**.

Scelotrichia

My email makes Christmas come all year-round. One of these nice surprises came when Andi Cairns sent me pictures of a caddisfly that was a bryological surprise. This new species, actually in a genus new to Australia, was ***Scelotrichia willcairnsi*** (Figure 105) living among the mosses in a waterfall (Figure 106). It was feeding on ***Rhynchostegium brevinerve*** (Figure 107), a new species previously thought to be ***Platyhypnidium muelleri*** and renamed by Huttunen and Ignatov (2010), in north-eastern Queensland, Australia. This microcosm was full of surprises!

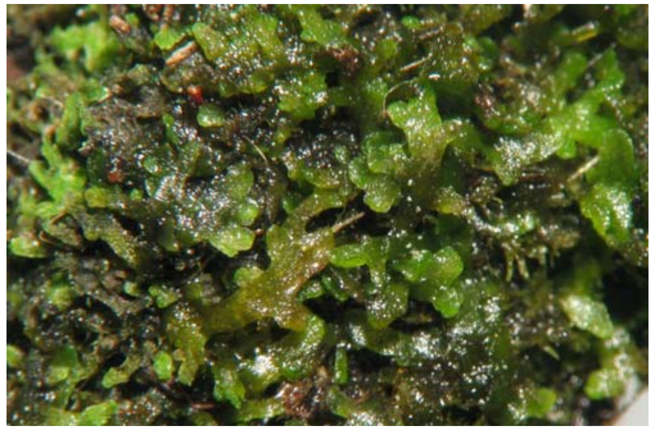

Figure 104. ***Riccardia chamedryfolia***, a liverwort that some caddisflies use to make a case. Photo by Kristian Peters, with permission.

Figure 105. The caddisfly ***Scelotrichia willcairnsi*** (**Hydroptilidae**) with a case made of pieces of the moss ***Rhynchostegium brevinerve***. Note the way pieces fit together as parallel rings. Photo courtesy of Andi Cairns.

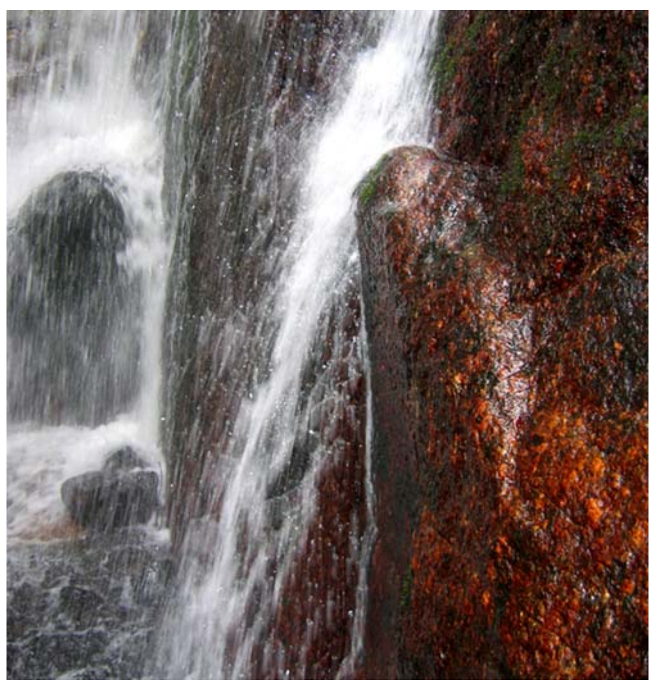

Figure 106. ***Rhynchostegium brevinerve*** in Fishery Falls, Australia, home to ***Scelotrichia willcairnsi***. Photo courtesy of Andi Cairns.

Figure 107. ***Rhynchostegium brevinerve***, home to the caddisfly ***Scelotrichia willcairnsi***. Photo courtesy of Andi Cairns.

The ***Scelotrichia willcairnsi*** larva had a case (Figure 105) it had built by cementing moss leaf fragments together (Figure 108) – the same species of moss it was eating (Cairns & Wells 2008). It remained in this case to pupate, cementing it to the moss stems (Figure 109). When making a case, the larvae cut the leaves longitudinally, in parallel with the long axis of the leaf and its cells, giving them long pieces (Figure 108). Cairns and Wells described these: "neatly, the fragments fitted together, almost in rings." Ohkawa and Ito (2002) had already distinguished the types of cuts for leaves and for food in ***Scelotrichia ishiharai***. This microcaddis uses the moss ***Rhynchostegium*** sp. (Figure 107-Figure 109) for food (Figure 110-Figure 111) and case building (Figure 105-Figure 109), likewise using different orientations for the two kinds of cuts

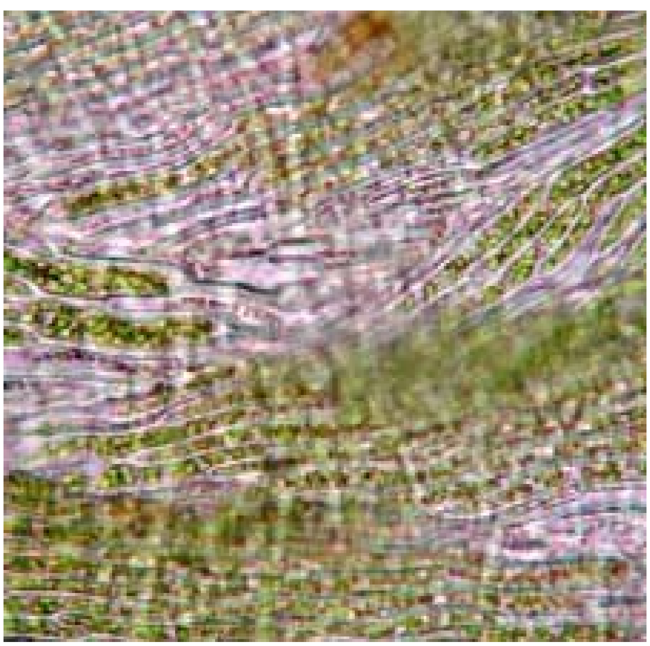

Figure 108. Pieces of the moss ***Rhynchostegium brevinerve*** from the case of the caddisfly ***Scelotrichia willcairnsi*** (**Hydroptilidae**). Photo courtesy of Andi Cairns.

Figure 109. Pieces of the moss ***Rhynchostegium brevinerve*** with numerous cases of the caddisfly ***Scelotrichia willcairnsi*** (Trichoptera: Hydroptilidae). Photo courtesy of Andi Cairns.

When Cairns and Wells (2008) examined the gut contents, they discovered that these tiny caddisfly engineers cut the pieces of moss very differently for food than they did for cases. For food, they cut the leaves perpendicular to the long axis and across the cells (Figure 110-Figure 111). Such a cut would give the gut enzymes more access to the contents of the cells.

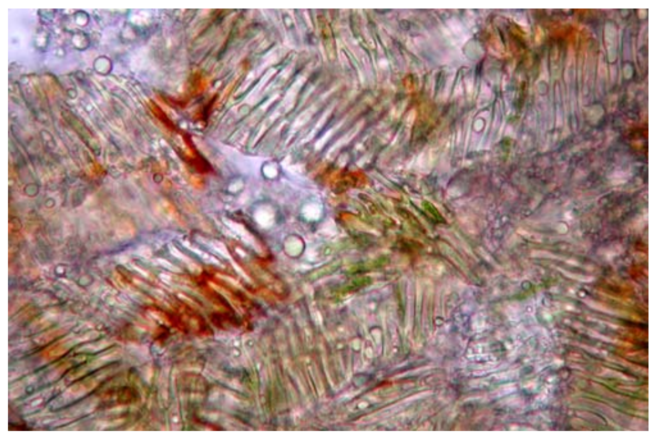

Figure 110. Pieces of the moss ***Rhynchostegium brevinerve*** from the gut of the caddisfly ***Scelotrichia willcairnsi*** (**Hydroptilidae**). Photo courtesy of Andi Cairns.

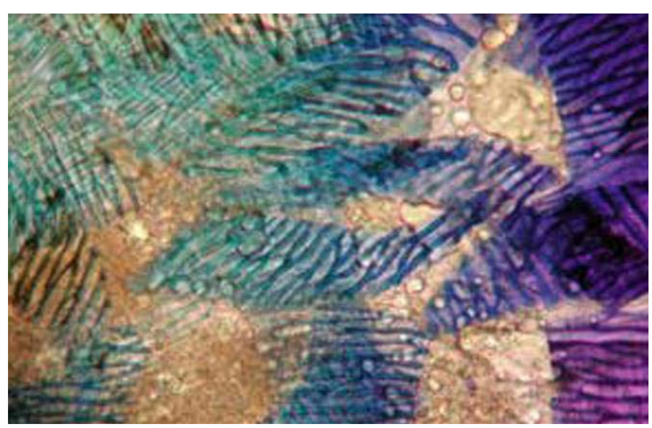

Figure 111. Pieces of the moss ***Rhynchostegium brevinerve*** from the gut of ***Scelotrichia willcairnsi***. The moss fragments are stained with Toluidine blue to make cell walls more evident. Note that cell contents appear to be gone in nearly all fragments, suggesting digestion. Photo courtesy of Andi Cairns.

One of these larvae had included moss leaves, liverwort leaves, and even hornwort thallus all in one case (Chris Cargill, pers. comm. 30 March 2016). And all these pieces were still alive! Chris Cargill told me she later found discarded cases made of thalli from liverworts or hornworts and new thalli had started to grow from the case (Figure 112). I think we have just added a new means of bryophyte dispersal!

Figure 112. ***Scelotrichia willcairnsi*** caddis fly case old with living liverworts. Photo courtesy of Chris Cargill.

Elsewhere, in Papua New Guinea, ***Scelotrichia*** was similarly collected from mosses in the strong currents at the crest of a short waterfall (Wells 1990). They likewise made their cases of the moss leaves and later attached their pupal cases to the stems of the same species of moss. Wells found adults of two other species of ***Scelotrichia*** near waterfalls or soaked mosses. As in ***S. willcairnsi*** (Figure 105), the caddisfly larvae from Papua New Guinea had cut slivers of the moss down the long axis of the leaf, making the cells parallel to the length of the fragment. These differed from the pieces cut by ***Paleagapetus*** and ***Ptilocolepus***, which were cut from leafy liverworts and glued together to resemble a patchwork quilt (Ito 1998; Ito & Higler 1993). It appears that cutting behavior can determine the type of bryophyte that is suitable for making the case.

Rhyacophiloidea

Rhyacophilidae – Free-living Caddisflies

This is a Northern Hemisphere family from the temperate parts of North America, Europe, and Asia, extending into India and the tropical areas of southeastern Asia (Kjer 2010). The larvae are 9-16 mm long and are green or brown, blending easily with the bryophytes (Bumble.org 2013). Don't be misled by the pink color they assume in preservative.

Larvae of this family do not build cases (Figure 113), so they do not attach themselves to the substrate by gluing their cases like some caddisflies do. Their life cycle is one year, with two generations overlapping. The larvae prefer rapid, cold streams where they are able to stay themselves in the current by clinging to mosses or debris (Hilsenhoff 1975). Most are carnivorous, but a few are herbivorous. And some can live above the water level among wet emergent mosses: ***Rhyacophila nubila*** (Figure 114), ***R. polonica***, and ***R. tristis***, whereas in the same River Rajcianka, Slavakia, these three species plus ***R. obliterata*** (Figure 115), ***R. philopotamoides***, and ***R. vulgaris*** occur among the mosses under water (Krno 1990).

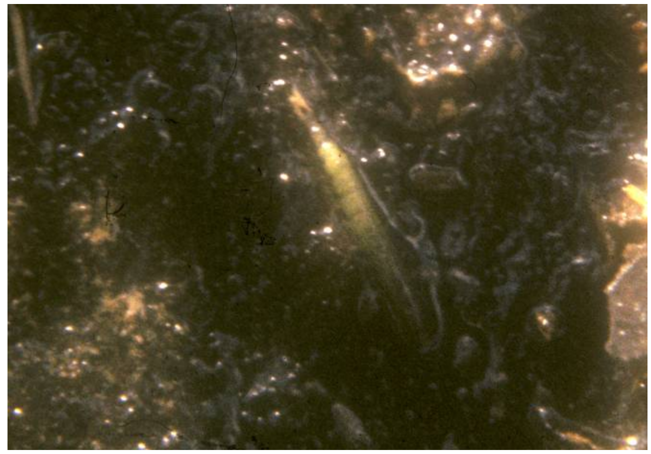

Figure 113. The free-living caddisfly, ***Rhyacophila***, is a common member of the stream moss community. Its color is typically green, and it has large hooks that permit it to cling to mosses and other substrata to avoid being washed away by the fast-flowing water it inhabits. Its lack of a case permits it to traverse the internal chambers of the moss without getting caught by the branches. Photo by Janice Glime.

Figure 114. ***Rhyacophila nubila*** larva, a species that can live among mosses above or below the water surface. Photo by Niels Sloth, with permission.

In my studies of Appalachian Mountain stream mosses in Maryland and Pennsylvania, USA, the genus ***Rhyacophila*** was among the most common and constant of the caddisfly larvae among the bryophytes. Décamps (1967, 1968) found ***Rhyacophila laevis*** to be abundant among mosses in the Pyrénées. In a cool mountain stream of central Japan, Tada and Satake (1994) found that ***R. towadensis*** was significantly more abundant among the moss ***Platyhypnidium riparioides*** (Figure 13) than in bare rock areas.

Many members of **Rhyacophilidae** most likely benefit both from the protection afforded by the bryophytes, but also from the resident fauna that serves as food, especially the numerous **Chironomidae.** In their study of four small Appalachian, USA, streams, Woodall and Wallace (1972) found larvae of ***Rhyacophila torva*** (Figure 125) (see also Roback 1975), ***R. nigrita*** (Figure 116), ***R. carolina*** (Figure

122), ***R. minora*** (Figure 117) (see also Glime 1968), ***R. glaberrima*** (Figure 118), and ***R. fuscula*** (Figure 123-Figure 124) among mats of mosses on rock outcrops. They fed on the **Chironomidae** larvae (Ross 1944) that shared the bryophyte habitat. In one of my collections from the mid-Appalachian Mountains I caught ***R. carolina*** in the act – it was preserved with a chironomid larva in its mouth. Although ***R. minora*** in a wooded Ontario, Canada, stream is typically carnivorous, early instars feed on plant material (Singh *et al*. 1984). This strategy works well until they gain the size and skill to be predators.

Figure 115. ***Rhyacophila obliterata*** adult, a species whose larvae are common among bryophytes. Photo by James K Lindsey, with permission.

Figure 116. ***Rhyacophila nigrita*** larva, a moss dweller in Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Figure 117. ***Rhyacophila minora*** larva, an Appalachian Mountain stream bryophyte dweller. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 118. ***Rhyacophila glaberrima*** larva, a common species among mosses in the Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Food

Most ***Rhyacophila*** species are carnivores that do not make cases, but the ***Verrula*** group eat photosynthetic organisms with their **hypognathous** heads (oriented downwards), feeding on algae, diatoms, and particularly bryophytes (Smith 1968; Thut 1969). Cummins (1973) likewise reported that ***R. verrula*** in western North America is a herbivore and especially eats aquatic mosses (Slack 1936; Gerson 1982; Smith 1968). In his study of diets of the ***Rhyacophila*** species in constructed streams in western USA, Thut (1969) found that ***R. verrula*** feeds predominantly on aquatic mosses. This effect is intensified in winter when several mosses are dominant and diatoms are abundant. Interestingly, diatoms become more important in the fourth and fifth instars than they are in earlier instars.

In a Tennessee cold springbrook, ***Rhyacophila lobifera*** larvae fed among the moss and algae, eating smaller caddisfly larvae, midge larvae, naiads of mayflies and stoneflies, detritus, and diatoms (Stern & Stern 1969). Slack (1936) also reported that one out of nine ***Rhyacophila dorsalis*** (Figure 119) had leaves of ***Fontinalis antipyretica*** (Figure 11) in the gut, but that it is primarily carnivorous. Nevertheless, one specimen contained only diatoms in the gut and the one with ***Fontinalis*** had only plant material. In a study in the English Lake District, Elliott (2005) found that early instars ate primarily diatoms (mostly ***Achnanthes*** spp., Figure 120), with bryophyte fragments also present in nearly all gut samples, but the bryophytes appeared to be undigested, displaying their chlorophyll. These bryophytes may have been eaten to obtain adhering diatoms. Both second and third instars would disappear into the bryophyte clumps to search for prey, but they returned to the surface of those clumps to consume their finds. Fourth and fifth instars fed only at night and used an ambush strategy to capture prey, which includes ***Baetis*** and ***Gammarus***.

Figure 119. ***Rhyacophila dorsalis*** larva, a carnivorous species that sometimes has leaves of ***Fontinalis antipyretica*** in its gut. Photo by Walter Pfliegler, with permission.

Larvae of most of the predominantly carnivorous ***Rhyacophila dorsalis*** (Figure 119) occur among bryophytes [leafy liverwort ***Scapania*** sp. (Figure 74) and mosses ***Platyhypnidium riparioides*** (Figure 13) and ***Fontinalis antipyretica*** (Figure 11)] (Slack 1936). For less active prey they use a searching strategy (**Chironomidae**, **Simuliidae**). The percentage of larvae with bryophytes in the gut was much smaller than that of prey. It appears that this species changes its diet as it grows, but it may also be an opportunist regarding its diet. But if one considers that both the diatoms and bryophytes still had chlorophyll in their cells, it appears that even the first and second instar larvae may have been carnivores, eating these photosynthetic organisms by chance while attempting to capture prey. Instead, the first and second instar larvae eat copepods, rotifers, and tardigrades, common bryophyte inhabitants, but these require special preservation techniques in order to recognize them in gut samples. Instead of a shift from apparent herbivore to carnivore, Elliott (2005) demonstrated a shift in size of prey.

Figure 120. ***Achnanthes longipes***. Photo by Victor Chepurnov, through non-commercial license.

The caddis larvae of ***Rhyacophila dorsalis*** (Figure 119) begin their early instars by feeding equally day and night, but by the 4th to 5th instar they shift to feeding almost totally at night (Elliott 2005). They can feed on other insects inhabiting their moss habitat, such as **Ephemeroptera** (mayflies), **Simuliidae** (blackflies), and **Chironomidae** (midges). As they grow older, instars 4 and 5, they adopt an ambush strategy at dusk and dawn, catching such active prey as the mayfly ***Baetis*** and the scud ***Gammarus***. During the night they used a searching strategy to capture the more sedentary prey, for example **Chironomidae** (midges) and **Simuliidae** (blackflies).

Thut (1969) suggested that the high proportion of moss fragments in the diets of the herbivorous ***Rhyacophila*** was at least in part the result of seasonal changes in the available primary producers in streams. Bryophytes are available in winter when most of the algae are dormant in a resting stage.

Substrate Preference

Rhyacophila species typically make their larval homes under rocks or among mosses (Bouchard 2004). They are able to use their claws (Figure 121) to anchor themselves or cling to the mosses, but also use them as they creep along in the stony stream bed (Badcock 1949). Percival and Whitehead (1929) found that ***Rhyacophila dorsalis*** (Figure 119) preferred thick mosses and *Potamogeton* on stones. Elliott (2005) found some larvae found under large stones, but most were among bryophytes growing on the upper surfaces of large stones [***Scapania*** (Figure 74), ***Platyhypnidium riparioides*** (Figure 13), ***Fontinalis antipyretica*** (Figure 11)].

Figure 121. ***Rhyacophila fuscula*** larva showing anal hooks that cling to its substrate. Photo by Jason Neuswanger, with permission.

In the Great Smoky Mountains National Park, ***R. montana*** lives in the films of water that flow over vertical rock faces, crevices, or among wet mosses (Parker *et al.* 2007). ***Rhyacophila evoluta*** and ***R. intermedia*** are characteristic of mosses in torrents in the Pyrénées (Décamps 1967). ***Rhyacophila evoluta*** has the ability to go into a cold-induced diapause at any stage in its development. This permits it to complete its development in one, two, or three years, depending on the temperatures.

Some species seem to prefer liverworts and some to prefer mosses for their homes (locations, not cases). In the mid-Appalachian Mountain streams I found ***Rhyacophila*** cf. ***carolina*** (Figure 122) primarily among liverworts (***Scapania undulata***; Figure 74), whereas ***R. fuscula*** (Figure 121, Figure 123-Figure 124) predominated in ***Fontinalis dalecarlica*** (Figure 98) and ***R. torva*** (Figure 125) in ***Hygroamblystegium fluviatile*** (Figure 4-Figure 5) and ***Platyhypnidium riparioides*** (Figure 13). ***Rhyacophila invaria*** (Figure 126) occurred frequently among clumps of the moss ***Platyhypnidium riparioides*** (36% frequency) but was absent among ***Hygroamblystegium fluviatile*** clumps despite the frequent intermingling of these two mosses. It reached its greatest numbers in ***Scapania undulata***.

Figure 122. ***Rhyacophila carolina*** larva, species that is common among clumps of the leafy liverwort ***Scapania undulata*** in Appalachian Mountain, USA, streams. Photo by Bob Henricks, with permission.

Figure 123. ***Rhyacophila fuscula*** larva, a moss dweller on boulders in the Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Figure 124. ***Rhyacophila fuscula*** pupa. Photo by Bob Henricks, with permission.

Figure 125. ***Rhyacophila torva*** larva, a moss dweller in Appalachian Mountain streams. Photo by Trevor Bringloe, Biodiversity Institute of Ontario, through Creative Commons.

Figure 126. ***Rhyacophila invaria*** larva, a species that occupies both mosses and liverworts in Appalachian Mountain streams. Photo by Donald S. Chandler, with permission.

Summary

The **Limnephilidae** are mostly large and therefore are usually absent from the smaller mosses. However, sometimes several may occur within a clump of ***Fontinalis***.

The **Brachycentridae** are common among bryophytes. Some (***Micrasema***, ***Adicrophleps hitchcockii***) use mosses in their cases and some also eat them.

The genera ***Palaeagapetus*** and ***Scelotrichia***, both in the **Hydroptilidae**, use bryophytes (exclusively?) for food and case construction, the former using leafy liverworts and the latter using mosses. In the same family, ***Ptilocolepus*** uses both mosses and liverworts for food and in case construction.

The family **Rhyacophilidae** is a free-living caddisfly and is mostly carnivorous. However, some of the bryophyte dwellers eat bryophytes, whereas others use them as a place to capture prey.

Other families that can be found among bryophytes less commonly include **Odontoceridae**, **Goeridae**, **Limnephilidae**, **Lepidostomatidae**, **Oeconesidae** (especially in New Zealand), **Uenoidae**, **Phryganeidae**, **Beraeidae**, **Conoesucidae**, **Helicophidae**, **Sericostomatidae**, and **Glossosomatidae**. Among these, the **Limnephilidae** and **Phryganeidae** have mostly large larvae that are unable to move about in most of the bryophytes but that can live among the large branches of ***Fontinalis*** species. Unlike the **Coleoptera**, this order is poorly represented in bogs and fens, but they are common in streams and less so in lakes.

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