CHAPTER 11-11
AQUATIC INSECTS: HOLOMETABOLA – TRICHOPTERA, SUBORDER ANNULIPALPIA

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Figure 1. ***Fontinalis antipyretica*** in a small stream. This moss is often home to many kinds of insects, including even larger Trichoptera. Photo by Betsy St. Pierre, with permission.

LEPIDOPTERA – Moths and Butterflies

This predominantly terrestrial order has a number of aquatic members whose larvae live on tracheophytes. These include such families as the **Pyralidae** (Figure 2) and **Noctuidae**. Larvae of some aquatic species possess gills (Bouchard *et al*. 2004). The aquatic **Pyralidae** are the only **Lepidpotera** with aquatic pupae.

I have not been able to find any records of this order on bryophytes. However, on one occasion I found a caterpillar of the **Nymphalidae** in a bed of ***Fontinalis*** in the Red Cedar River, East Lansing, MI. Unfortunately, I was there for a different purpose and don't have any further details.

Figure 2. ***Petrophila*** larva (ventral view), a common aquatic moth that lives among aquatic plants. Photo by Bob Henricks, with permission.

TRICHOPTERA – Caddisflies

The **Trichoptera** are distinguished as adults by the hairs on their wings (Figure 3) and the resting position that looks like a pup tent (Figure 4). Their distribution is worldwide and size varies greatly. Most build cases that serve as retreats for both larvae and **pupae** (immature stages, often immobile) between larvae and adults).

Figure 3. ***Brachycentrus appalachia*** adult wings showing hairs. Photo by Jason Neuswanger, with permission.

Figure 4. ***Limnephilus frijole*** adult showing wings folded like a pup tent. Photo by Bob Newell, with permission.

Caddisflies are common inhabitants among mosses (Oswood 1979; Glime 1994; Ogbogu 2000; Ogbogu & Akinya 2001). Berg and Petersen (in Macan 1963) found a mean of 260 Trichoptera in just 1 sq meter of ***Fontinalis*** (Figure 1) in Lake Gribso. And Frost (1942) found 492,200 individuals per gram of mosses in Ireland. Several families of caddisfly larvae have members that use bryophytes in the construction of their homes (Glime 1978).

In North America, caddisfly larvae are closely associated with mosses such as ***Fontinalis*** (Figure 1) (Ogbogu 2001a). As the density of these mosses increases, so does the density of the caddisfly larvae. Ogbogu suggested that use of the mosses as part of their life cycle strategy permits these larvae to survive in the unstable habitats of streams.

Krno (1990) found that some **Trichoptera** were able to climb out of the water to move about among the wet emergent mosses. However, the fauna there was not as rich as that among submerged mosses. Galdean (1994) found that some caddisflies were common on the mosses lining the walls of the Somequl Cald Gorges. These mosses were clean, lacking **detritus** (organic matter produced by the decomposition of organisms), and formed a felt on the walls.

Some insect assemblages even partition the moss into several habitats. The caddisfly ***Brachycentrus*** (**Brachycentridae**; Figure 5) uses mosses (as well as rocks and sticks) for attachment; ***Tricorythodes*** (**Ephemeroptera**: **Leptohyphidae**) burrows among the stems and rhizoids; and the caddisfly ***Chimarra*** (**Philopotamidae**; Figure 6) lives in the gravel and sand at the base of the mosses, all in the riffles of one Wyoming river (Armitage 1961).

Figure 5. ***Brachycentrus occidentalis*** larvae. Photo by Arlen Thomason, with permission.

Figure 6. ***Chimarra tsudai*** larva, member of a genus that lives in gravel and sand at the bases of mosses in riffles. Photo by Takao Nozaki, with permission.

In the case of ***Helicopsyche sperata*** (**Helicopsychidae**; Figure 7), the aquatic surroundings are achieved by living on mossy rocks out of the stream but in the sun in locations kept wet by constantly dropping water (McLachlan 1880).

Figure 7. ***Helicopsyche*** sp. larva and case, a genus that lives on wet mosses in the splash of streams. Photo by Stephen Moore, Landcare Research, with permission, NZ.

Drift

Unlike most of the drifting aquatic insect species, many species of Trichoptera are day-active and do most of their drifting during the day (Waters 1972). This makes this group more vulnerable to predation by fish (White 1967), and this would particularly apply to the caseless caddisflies that are the most common caddisflies among bryophytes. However, Brusven (1970) found that among the caseless net-spinning caddisflies, ***Arctopsyche*** (Figure 8) drifted mostly at night and ***Hydropsyche*** (Figure 9) was rare in the drift. It is reasonable to assume that the bryophyte habitat may help to keep these caddisflies anchored as they move about, hence offering a safe refuge.

Figure 8. ***Arctopsyche ladogensis*** (**Hydropsychidae**) larva, a night drifter. Photo by Donald S. Chandler, with permission.

Figure 9. ***Hydropsyche pellucidula*** larva (**Hydropsychidae**), a rare drifter that can be found among bryophytes. Photo by Niels Sloth, with permission.

Food

Slack (1936) compared the food of twelve species of caddisflies. Among these, all but three had bryophyte leaf fragments in the gut. Those with more than half the larvae having bryophyte fragments were **Limnephilidae**: ***Glyphotaelius*** sp. (Figure 10), ***Limnephilus rhombicus*** – an opportunist in using a variety of materials to build its case (Figure 11), ***Stenophylax*** sp. (Figure 12), and ***Halesus*** sp. (Figure 13) and **Sericostomatidae**: ***Sericostoma personatum*** (Figure 14). Among common bryophyte dwellers, ***Hydropsyche*** sp. (Figure 9) had none and ***Rhyacophila dorsalis*** (Figure 15) had bryophyte fragments in only one out of nine larvae. An image on Garden World Images by Dave Bevan (Bevan 2014) suggests that some ***Stenophylax*** species eat mosses. (The image looks like either protonemata or a filamentous alga.)

Figure 10. ***Glyphotaelius pellucidus*** larva in its case, a genus known to eat bryophytes. Photo by Niels Sloth, with permission.

Figure 11. ***Limnephilus rhombicus*** larva showing two very different cases for the same species. This species eats bryophytes. Photo by Niels Sloth, with permission.

Figure 12. ***Stenophylax permistus*** adult, a genus known to eat bryophytes. Photo by Wouter Bosgra, through Creative Commons.

Figure 13. ***Halesus radiatus*** larva, a genus which has bryophyte consumers. Photo by Malcolm Storey, through Creative Commons.

Figure 14. ***Sericostoma personatum*** larva, a genus known to eat mosses. Photo by J. C. Schou, with permission.

Figure 15. ***Rhyacophila dorsalis*** larva, a common bryophyte dweller that had no moss in the gut of 8 out of 9 individuals. Photo by Walter Pfliegler, with permission.

Trichoptera is a large order, surpassing Ephemeroptera, Odonata, and Plecoptera in the number of genera (Wiggins & Mackay 1978). Most of the filter-feeders are in eastern North America in the deciduous forest biome. In addition to filter feeders, they are represented by grazers, especially upstream in the mountains where waters are cool. Shredders, especially in the **Limnephilidae**, can be found in lakes, ponds, streams, and even terrestrial habitats. Shredder-collectors are more common upstream and grazer-collectors are more common downstream. Some are predators.

Cairns (2005) reported that some caddisfly larvae consumed stream mosses. Kalachova *et al*. (2011) used acetylenic acids as biomarkers of ***Fontinalis antipyretica*** (Figure 1) to demonstrate consumption of this moss by Trichoptera in the Yenisei River.

Case Building

Case building provides most species of Trichoptera with a mobile home that protects them from predation. Some of these case-builders use bryophytes in their construction, including the New Zealand genus ***Zelolessica*** (**Helicophidae**; Figure 16) that sometimes uses bryophytes exclusively (Suren 1988). Frost (1942) found that a rather dominant caddisfly in her acid site on the River Liffey, Ireland, made cases from fragments of ***Fontinalis*** (Figure 1), but the larvae were too small for identification.

Figure 16. ***Zelolessica***, a caddisfly that sometimes uses bryophytes in case construction. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Elliot and Spribille found that in a northwest Montana fen caddisfly larvae use living ***Scorpidium scorpioides*** (Figure 17) to build cases. The larvae harvest small tips of branches (*ca*. 2 cm) of the ***S. scorpioides*** from plants that grow submerged in shallow water and attach them to their cases. Elliot and Spribille suggested that the moss provides a "buoyant platform" from which the caddisfly can emerge, prey on the invertebrate fauna, and then fly off without being trapped by the surface tension.

Figure 17. ***Scorpidium scorpioides***, a moss used for building caddisfly cases. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

SUBORDER ANNULIPALPIA

Hydropsychoidea

Ecnomidae

This is a relatively small family with worldwide distribution (Holzenthal *et al*. 2007). Although records of this family are worldwide, their main distribution is Gondwanan (Ecnomidae 2014). The larvae are of moderate size (5-10 mm) and live in retreats that they construct of silk in slow-water streams or lakes. They are predators, but some eat algae and detritus.

From Ceylon, Schmid (1958) reported ***Ecnomus ceylanicus*** (see Figure 18) and a new species, ***Ecnomus vaharika***, from large, mossy rocks in the torrent.

Figure 18. ***Ecnomus tenellus*** adult, member of a genus in which some species live in mossy torrents in Ceylon. Photo by Dick Belgers, through Creative Commons.

Hydropsychidae – Net-spinning Caddisflies

This worldwide family occupies a wide range of rivers and streams, always requiring flowing water to obtain its food (Hydropsychidae 2014). For example, in Ceylon Schmid (1958) reported ***Pseudoleptonema ceylanicum*** (see Figure 19) from a small, mossy creek in the jungle.

Figure 19. ***Pseudoleptonema supalak*** adult. In Ceylon, larvae of ***P. ceylanicum*** live in a mossy creek. Photo from Biodiversity Institute of Ontario, through Creative Commons.

The larvae can be relatively large, ranging 5-25 mm (Hydropsychidae 2015). The larvae of this family build retreats from plant and mineral fragments. These retreats open into the nets used to catch their food, including algae, detritus, and small animals. When another caddisfly attempts to occupy the retreat, the current occupant uses its hind legs, rubbing them under the head, to produce stridulations that warn the intruder to vacate (Jansson & Vuoristo 1979).

Larvae of ***Hydropsyche angustipennis***, ***H. siltalai***, ***H. nevae***, and ***H. pellucidula*** will enter any suitable retreat when forced to leave their own, and it need not be their own species or unoccupied. When it is already occupied, a vigorous fight will ensue. Larger defenders lost more fights as the size of the intruder increased. Stridulation increased the likelihood of a defender winning the fight.

Several researchers have supported the importance of mosses in the habitats of net-spinning caddisflies (Sprules 1947; Tanaka 1968). Oswood (1979) found that in a lake outlet stream in Montana, USA, larvae of **Hydropsychidae** had greater densities on moss-covered substrata (up to >1400 0.2 m^{-2}) than elsewhere. In a gorge of the Some River, Galdean (1994) considered the mosses on the walls of the gorge to create the conditions needed for the **Hydropsychidae** to develop. The boulders were cleaned by the river velocity on the concave bank, permitting the mosses, hence the **Hydropsychidae**, to develop there.

Parapsyche cardis preferred substrata in the order of mossy rock face > cobble riffle > pebble riffle > sandy reach (Gurtz & Wallace 1986). This relationship held true for all instars (larval stages) in both studied streams. Thus, mossy rock faces accounted for 94.8% of the total production of ***Parapsyche*** (Figure 20) in Hugh White Creek (with 36.5% rocky channel) and 87.3% in Big Hurricane Branch (with 16.8% rocky channel) in the southern Appalachian Mountains, USA. Haefner and Wallace (1981a, b) likewise found that the distribution of ***P. cardis*** was highly correlated with the distribution of moss in Sawmill Branch. In several Maryland, USA, streams, ***Parapsyche apicalis*** occurred among bryophytes, mostly ***Fontinalis dalecarlica***, and at the time were new records for Maryland, but it was not one of the more common **Hydropsychidae** represented among the mid-Appalachian bryophytes (Glime 1968).

Figure 20. ***Parapsyche apicalis*** larva, a species I collected among bryophytes in several Maryland streams. ***Parapsyche carda*** distribution is correlated with moss cover. Photo by Donald S. Chandler, with permission.

Wulfhorst (1994) examined the relative abundance of the caddisfly larva ***Diplectrona*** (Figure 29) in mosses and in **interstitial spaces** (spaces between individual sand grains in soil or aquatic sediments) in the **hyporheic** zone (region beneath and alongside a stream bed, where mixing of shallow groundwater and surface water occurs) of two streams in the Harz Mountains of West Germany. She found that ***Diplectrona*** was 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 30 cm depths (Figure 21).

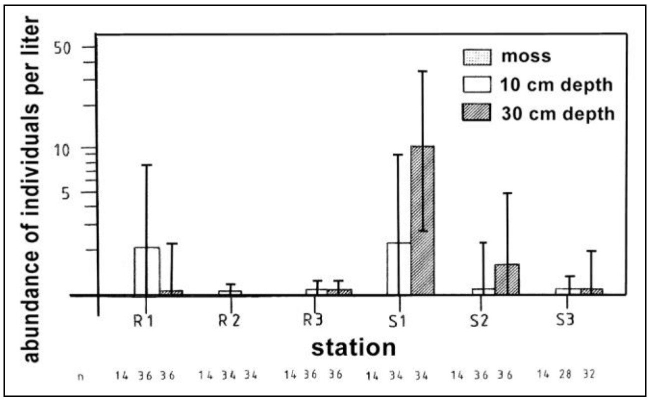

Figure 21. Mean abundance ± 95% CI of ***Diplectrona*** spp. in moss clumps in two streams in the Harz Mountains, West Germany. Numbers of samples are shown at the bottom. Redrawn from Wulfhorst 1994.

The high density of **Hydropsychidae** among stream mosses is supported by their ability to colonize that habitat rapidly. Smith-Cuffney (1987) found that artificial mosses reached their capacity of these net-spinning colonizers in only 7 days; Georgian and Thorp (1992) found that 6-9 days provided enough time for them to reach their constant colonization density among the artificial mosses. Mosses provide a particularly easy place to colonize relative to other stream habitats because their rough surface makes it easy to gain a hold that rescues them from the speeding water.

The **Hydropsychidae** can be considered ecosystem engineers (Nakano *et al*. 2005). In Japan, ***Hydropsyche orientalis*** (Figure 22, Figure 23) make their larval retreats on the upper surfaces of stones. These retreats provide a safe site for naiads of the mayfly ***Serratella setigera***, providing them with the slower flow that they prefer. It is likely that in the absence of these caddisflies and their nets that mosses could play a similar role in creating a suitable refuge. And in some cases it appears that the hydropsychids use the mosses in place of some, but not all, nets (Figure 24).

Ogbogu (2000) found **Hydropsychidae** associated with ***Fontinalis*** (Figure 1) in Nigeria and reported that the density of larvae increased when the moss grew. Both ***Cheumatopsyche*** (Figure 45) and ***Amphipsyche*** formed close associations and Ogbogu (2001a, b) suggested that the moss served as a **refugium** (area in which population of organisms can survive through period of unfavorable conditions, even glaciation) during vulnerable life cycle stages.

Figure 22. ***Hydropsyche orientalis***, a species that provides shelter used by the mayfly ***Serratella setigera***. Photo by Takao Nozaki, with permission.

Figure 23. ***Hydropsyche orientalis*** net where ***Ephemerella setigera*** takes refuge. Photo by Takao Nozaki, with permission.

Figure 24. **Hydropsychidae** nets among mosses. Photo by Janice Glime.

Pupal Sites

Frost, in her 1942 study of the River Liffey, Ireland, found that few Trichoptera pupae were present among the mosses. She considered this an expected absence because the caddisfly larvae usually seek another type of environment instead of mosses for **pupation** (period of development of pupa). For example, ***Ceratopsyche morosa*** (Figure 25) lives among moss and algae in young larval stages (Stern & Stern 1969), but just prior to pupation it moves to stones.

Temperature can signal that it is time to pupate. At least some ***Hydropsyche*** species cannot live below 8°C (Kaiser 1965). Instead, they build loose cases and go into the pupa state in autumn. Sleight (1913) found ***Hydropsyche*** pupae (Figure 26-Figure 28) among mosses in strong currents in the eastern USA. At maturity, these pupae moved to the surface where the pupal case would split and adults would emerge. The larval hooks made it possible for these caddis larvae to climb over the vegetation to find a suitable place for the pupa.

Figure 25. ***Ceratopsyche morosa*** larva, a moss dweller that leaves the mosses to pupate among stones. Photo by Bob Henricks, with permission.

Figure 26. ***Hydropsyche*** pupae, a genus that pupates among the protective mosses in strong currents. Photo by Mark Melton, with permission.

Crowding and Niche Separation

It appears that mosses might separate the niches of co-habiting net spinners. Late instar ***Diplectrona modesta*** (Figure 29) has a somewhat uniform occupancy among substrata in Big Hurricane Branch (Gurtz & Wallace 1986). The first three instars are most abundant on the (mossy) rock face and the fourth and fifth are more evenly distributed. But in Hugh White Creek, the rocks have a lower density of moss, and ***D. modesta*** is less common than in Big Hurricane Branch, where the moss is thicker. In fact, in Hugh White Creek, ***D. modesta*** is most abundant in the cobble riffle and least abundant in the rock face samples, while first instars are most common on sand. Gurtz and Wallace suggested that the lower density of moss in the Hugh White Creek may not provide enough microhabitats and that differences in available substrata could account for the differences in productivity. Mosses provide a suitable substrate for attaching the nets (Figure 30) and retreats of these caddisflies while providing a range of current velocities. The nets themselves do not, however, appear to contribute directly to their food; none were found in the gut analysis (Haefner & Wallace 1981a). The larvae are also relatively common among ***Hygroamblystegium fluviatile*** (Figure 31), ***Platyhypnidium riparioides*** (Figure 32), and ***Fontinalis dalecarlica*** (Figure 33) in Appalachian Mountain streams (Glime 1968).

Figure 27. ***Hydropsyche*** pupae removed from their pebble cases. Photo by Mark Melton, with permission.

Figure 28. ***Hydropsyche*** pupa, common among mosses in strong currents. Photo by Jason Neuswanger, with permission.

Figure 29. ***Diplectrona modesta*** larva, a species that is more common among mosses in early instars but is more evenly distributed between mosses and other substrata in later instars. Photo by Bob Henricks, with permission.

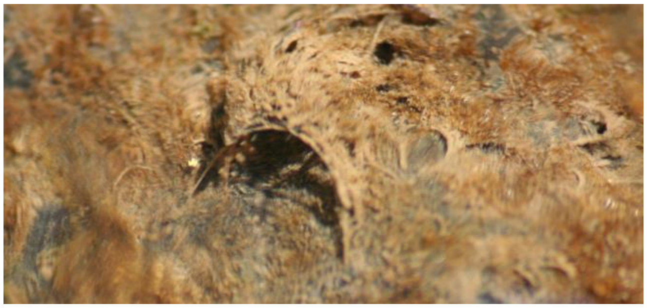

Figure 30. ***Cheumatopsyche*** larval net. These are often attached to bryophytes and are able to trap detritus and algae. Photo by Justin Montem, through Creative Commons.

Figure 31. ***Hygroamblystegium fluviatile***, a home for smaller insects. Photo by Michael Lüth, with permission.

Figure 32. ***Platyhypnidium riparioides***, a home for smaller insects, sometimes serving as food and case-building materials. Photo by David Holyoak, with permission.

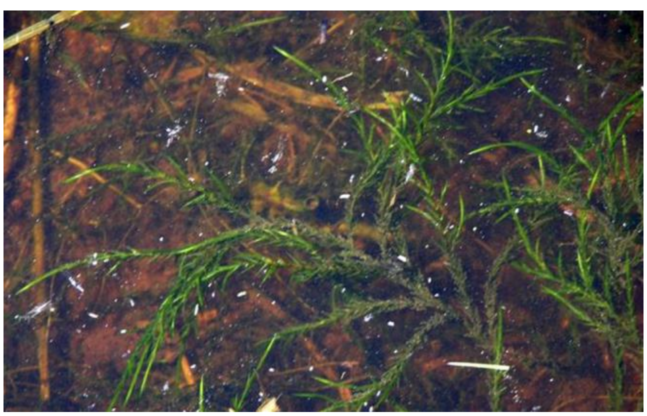

Figure 33. ***Fontinalis dalecarlica***, home to some larvae of ***Cheumatopsyche***. Photo by J. C. Schou, with permission.

When ***Cheumatopsyche*** sp. (Figure 34) reaches high densities it becomes more aggressive (Glass & Bovbjerg 1969). This aggressiveness dictates a pattern of **dispersion** (pattern of distribution of individuals within a habitat) that is a function of density. Hildrew and Edington (1979) found that larvae are able to make ultrasonic sounds to discourage intruders when they approach. Fortunately, for overlapping generations of the same species larval sizes differ at a given point in time, permitting them to use different net sizes (Figure 35-Figure 36) and avoid competition for food.

Figure 34. ***Cheumatopsyche*** larva, a caddisfly that becomes less aggressive when it has shelter. Photo by Bob Henricks, with permission.

Figure 35. ***Hydropsyche*** net showing mesh size that can differ in size with species. Photo by Michael Wiesner <www.waldzeit.ch>, with permission.

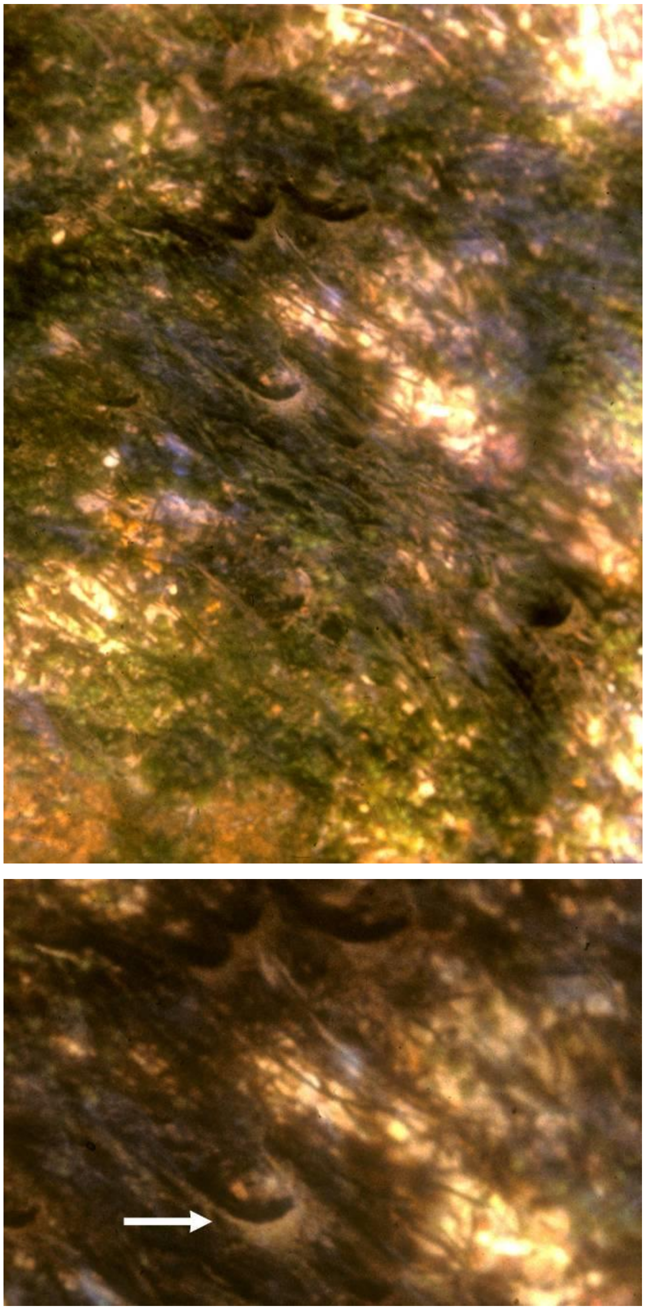

Figure 36. Nets of the net-spinning caddisfly, ***Cheumatopsyche***, on ***Fontinalis***. The number of larvae usually greatly exceeds the number of nets on the ***Fontinalis***, suggesting that they may be using the mosses as nets to gather detritus and diatoms. Photos by Janice Glime.

Williams and Hynes (1973) suggested that mossy habitats provide the greatest number of protected sites. Furthermore, the rapid flow typical of locations where mosses grow will bring more food per unit of time. ***Cheumatopsyche*** (Figure 37) larvae are common among the mosses ***Hygroamblystegium fluviatile*** (Figure 31), ***Platyhypnidium riparioides*** (Figure 32), and ***Fontinalis dalecarlica*** (Figure 33) in the mid-Appalachian Mountain streams (Glime 1968). And ***Cheumatopsyche*** (Figure 34) larvae seem to be less aggressive when shelter is readily available (Glass & Bovbjerg 1969). Williams and Hynes (1973) found that the hydropsychids ***Cheumatopsyche oxa*** (Figure 37) and ***Ceratopsyche sparna*** (Figure 38) occupied the mossy areas of boulders, whereas the philopotamid ***Chimarra aterrima*** (Figure 39), a potential competitor, occupied the spaces under large stones. The two hydropsychid species share the same sites, eat the same foods, and have similar life cycles. In contrast to ***Chimarra aterrima***, these net-spinning caddisflies have mechanisms in their gut for crushing diatoms, important constituents of the diet and one that separates their niche from that of ***C. aterrima***.

Figure 37. ***Cheumatopsyche oxa*** larva, an occupant of mossy areas on boulders. Photo by Trevor Bringloe, Biodiversity Institute of Ontario, through Creative Commons.

Figure 38. ***Ceratopsyche sparna*** larva, a species that prefers mossy areas to those under stones. Photo by Bob Henricks, with permission.

Figure 39. ***Chimarra aterrima*** larva, a species that occupies spaces under rocks in preference to that of mosses. Photo by Stroud Water Research Center, Stroud Water Research Center, through Creative Commons.

Hydropsyche pellucidula (Figure 40-Figure 41) occurs among submerged mosses in the River Rajcianka (Krno 1990). Elsewhere, when ***Hydropsyche pellucidula*** and ***H. siltalai*** (Figure 42) occur together, the moss cover is important in permitting these two caddisflies to partition the rocks into two functional feeding (net-spinning) niches and co-exist throughout their larval lives (Hildrew & Edington 1979). In late winter and early spring, there is rapid growth of moss (particularly ***Fontinalis antipyretica***, Figure 43) on boulders and bedrock in rapids. ***Hydropsyche siltalai*** (but not ***H. pellucidula***) migrates onto the moss in spring. Although large numbers of ***H. siltalai*** occupied the moss, not a single ***H. pellucidula*** could be found there. Plastic artificial grass, similar to moss mats, proved to be a suitable surface for net-spinning.

Figure 40. ***Hydropsyche pellucidula*** larva, a species that occurs among mosses in the River Rajcianka of Slovakia. Photo by Niels Sloth, with permission.

Figure 41. ***Hydropsyche pellucidula*** larva showing the large jaws. Photo by Niels Sloth, with permission.

Figure 42. ***Hydropsyche siltalai*** larva, a species that migrates to mosses to avoid competition from ***H. pellucidula.*** Photo by Urmas Kruus, with permission.

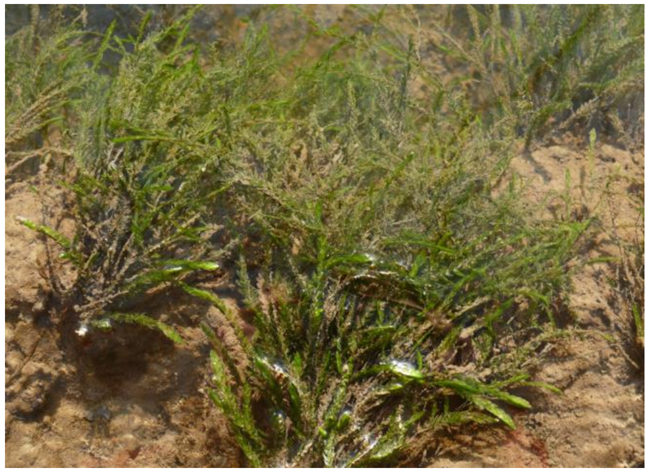

Figure 43. ***Fontinalis antipyretica***. Photo by Bernd Haynold, through Wikimedia Commons.

Hydropsyche siltalai (Figure 42) filters its food with a fine-meshed net (mean 100x70 µm) while ***H. pellucidula*** (Figure 40-Figure 41) is larger and uses nets with a mean mesh of 370x240 µm (Hildrew & Edington 1979). Migration of ***H. siltalai*** onto mosses (***Fontinalis antipyretica***; Figure 43) in spring further separates their niches. Englund (1993) observed that whereas small IV instar larvae were able to construct nets on the mosses, the physical structure seemed unsuitable for the larger V instar larvae to do so.

Food

Although Frost (1942) reported several studies in which ***Hydropsyche instabilis*** ate primarily **Chironomidae**, and Slack (1936) found that it ate diatoms, it also ingests mosses. In Great Britain (Percival & Whitehead 1929) and in calcareous streams in South Wales, ***Hydropsyche instabilis*** (Figure 44) ingested ***Fontinalis antipyretica*** (Figure 43) (Percival & Whitehead 1929; Jones 1949). Frost (1942) found that ***Hydropsyche instabilis*** (Figure 44) lived primarily among mosses in an acid stream, but in the alkaline stream it was ***Cheumatopsyche lepida*** (Figure 45) that was dominant among the mosses, in this case where there was more silt. Jones (1950) did extensive gut analysis of insects from the River Rheidol; among the **Trichoptera**, only ***Hydropsyche instabilis*** of the six species examined had fragments of ***Fontinalis antipyretica*** (Figure 43) in the gut (7 out of 27). Fragments of this moss were present in nine of the 23 analyses with identifiable gut contents (Jones 1949). Algae and detritus were the most common foods.

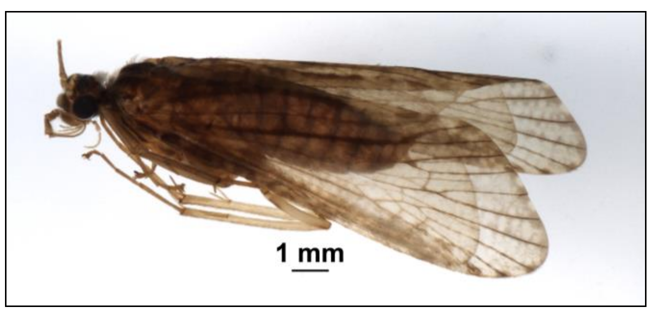

Figure 44. ***Hydropsyche instabilis*** adult, a species whose larvae sometimes eat mosses. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 45. ***Cheumatopsyche lepida*** larva, a dominant caddisfly among mosses with lots of silt in an alkaline stream. Photo through Creative Commons.

On the other hand, occurrence of net-spinning caddisflies among mosses may offer the advantage of a greater number of prey organisms. Although these insects trap their food on finely constructed nets, they are also carnivores. Haefner (1980) found a significantly higher (2x) density of prey organisms (***Baetis*** spp., ***Ephemerella*** spp., ***Nemoura*** spp., ***Hydroptila*** sp., and **Chironomidae**) in rock face samples, where mosses were typically dense. These organisms are common among stream mosses – ***Hydroptila*** less so (Glime 1994), thus the abundance of prey invertebrates may account for the greater productivity of ***Parapsyche cardis*** (see Figure 20) there.

Although ***Diplectrona modesta*** (Figure 29) had little correlation with mossy rocks in one of two Appalachian Mountain streams, and few such rocks existed in the other (Haefner & Wallace 1981a,b), this and other studies (Gurtz & Wallace 1986) suggest that the mosses provide a variety of niches that benefit both the potential prey organisms and the net-spinning caddisflies.

In a study to determine the source of foods for aquatic invertebrates, Torres-Ruiz *et al*. (2007) used the distinctive fatty acids for green algae, diatoms, and bryophytes, each of which also differed from fatty acids of terrestrial food sources. They determined that ***Hydropsyche*** spp. (Figure 40-Figure 42) consumed primarily **autochthonous** (originating from within the stream system) food sources, not the terrestrial **allochthonous** (originating from elsewhere) food such as leaf litter. In Appalachian Mountain streams the **Hydropsychidae**, including species of ***Hydropsyche***, seemed to use the mosses instead of constructing nets to capture their food (Glime 1968). There always seemed to be many more larvae than nets.

Gut *p*H is often important in determining the digestible food sources. ***Hydropsyche betteni*** (Figure 46-Figure 47) had a gut *p*H close to neutral but somewhat alkaline (Barlocher & Porter 1986). Hence, this species was unable to **hydrolyze** (break down a compound by chemical reaction with water) proteins of maple leaves that were not yet conditioned by decomposer organisms. They could, however, digest starch and laminarin (storage product in many seaweeds). Unlike those in the cranefly ***Tipula***, the fungal **carbohydrases** (enzymes that break down carbohydrates) ingested with decomposing leaves remained active in the guts of this species.

Figure 46. ***Hydropsyche betteni*** larva, with a gut *p*H that is alkaline. Photo by Bob Henricks, with permission.

Figure 47. ***Hydropsyche betteni*** larva showing ventral gills. Photo by Donald S. Chandler, with permission.

Role of Water Velocity

The larvae of the **Hydropsychidae** are able to partition the niches of the most immature from those of the nearly mature (Osborne & Herricks 1987; Muotka 1990). Osborne and Herricks (1987) found that ***Hydropsyche*** (Figure 40-Figure 42) species in their study separated the larger larvae into communities at higher velocities, whereas the smaller, less mature larvae sought areas of diminished flow. The same size distribution occurs between species. These larvae seek out depressions where they can gather passing detritus but where sedimentation is minimal. Turbulence seems to play a role in determining distribution, perhaps contributing to food availability and preventing

sedimentation. Larger larvae are apparently able to occupy greater velocities; this is coupled with the construction of a larger mesh size, hence dividing the feeding niche from that of smaller larvae.

The net-spinning caddisflies prefer a habitat with a stable substrate and high water velocity. Georgian and Thorp (1992) showed that 96% of the **Hydropsychidae** larvae selected artificial moss substrates that had high velocity water flowing over them. They estimated that a prey item would be consumed within 5.5 m of travel in the drift. It appears that one advantage afforded these moss dwellers is that they can take advantage of high-flow rates while themselves finding a flow-rate suitable for their own safety.

Current speed also influences net-spinning activity, with a greater percentage of larvae spinning nets at 20 cm sec^{-1} (73%) than at 10 cm sec^{-1} (10%) (Edington 1965). Edington found that hydropsychid larvae formed tunnels into the moss mats with nets at the moss surface. When the nets were removed (and when they were not) and the flow was artificially reduced, the larvae moved to a different area. When something restricts the flow, the larvae move to a new location and construct new nets (Edington 1965, 1968).

Muotka (1990) considered that it was the flow pattern, rather than the flow velocity itself, that determined the pattern of occupancy by filter-feeding caddisfly larvae. He based this on the ability of multiple sizes of caddisflies, including ***Hydropsyche*** (Figure 40-Figure 42) to coexist at the same flow rates. Nevertheless, he concluded that species were often ecologically closer to other species than to other instars of their own species. In their study, many of the sites were covered with bryophytes [mosses ***Fontinalis antipyretica*** (Figure 43), ***Cratoneuron commutatum*** (Figure 48), leafy liverwort ***Jungermannia exsertifolia*** (Figure 49)] and the uneven surface of this substrate would create multiple flow patterns. It is noteworthy that in the stream that lacked bryophytes only one filter-feeding caddisfly was present – ***Hydropsyche saxonica*** (Figure 50) – whereas seven species occurred in the two streams with heavy bryophyte cover.

Figure 48. ***Cratoneuron commutatum***, a moss that alters flow patterns, as it is doing here. Photo through Creative Commons.

Figure 49. ***Jungermannia exsertifolia*** ssp ***cordifolia***, contributor to flow patterns that allow niche partitioning for **Hydropsychidae**. Photo by Michael Lüth, with permission.

Figure 50. ***Hydropsyche saxonica*** larva, the only filter-feeding caddisfly in a stream with no mosses. Photo by Niels Sloth, with permission.

Food capture is important in the location of nets, and water velocity helps to determine the food available. Mosses on the rocks actually prevent some insects from living there. The caddisfly ***Leucotrichia*** (**Hydroptilidae**; Figure 51) is unable to live on a substrate dominated by heavy moss growth and instead the net spinner ***Hydropsyche*** (Figure 40-Figure 42) occupies those locations (McAuliffe 1983). The larvae arrange their nets very evenly downstream but are often crowded across the substrate, preventing the water from being filtered by a net above them.

Figure 51. ***Leucotrichia pictipes*** larva, a genus that cannot live on a substrate with heavy moss cover. Photo by Stroud Water Research Center, through Creative Commons.

As I already noted in the Appalachian Mountain streams, some caddisflies actually use the mosses to help them gather food. Hildrew and Edington (1979) found that favorable situations for net-spinning caddis larvae (**Hydropsychidae**), such as moss covered rocks, often seem to be occupied to capacity. I have observed the same relationship, but it appeared that the caddisflies in some cases took advantage of the collecting ability of the moss and did not make nets. This would be useful for those species that eat primarily small invertebrates living among the bryophytes (Ross & Wallace 1983), but it could also take advantage of the bryophytes as filter traps.

Role Below Impoundments

Mosses are important habitats at impoundments. In Valley Creek in Minnesota, USA, **Hydropsychidae** caddisflies use mosses and filamentous algae as sites for attachment and building materials for retreats, with the mosses providing an environment that protects the larvae from the abrasive sand deposited by the impoundment (Mackay & Waters 1986).

Ogbogu (2000; Ogbogu & Akinya 2001) likewise found that ***Fontinalis*** (Figure 1) was important to the **Hydropsychidae** in an impoundment at Ile-Ife, Nigeria. They occupied the spillway, among the ***Fontinalis***, in large numbers when sampled in August (1233 m^{-2}), September (900 m^{-2}), and November (1178 m^{-2}). The moss provided refuge from the rapid water of the spillway, protection from predators, and food (epiphytic diatoms and other algae) trapped among the mosses.

Polycentropodidae – Tube Maker Caddisflies

Members of this worldwide family are relatively small to moderate in size, with the forewing reaching 6-13 mm (Hickin 1967). Larvae live in both quiet and flowing waters and trap their food in a tube (Murray 2006).

Polycentropus (Figure 52) is not a caddisfly one thinks of as a moss dweller because of its long, tubular net. But in both Ballysmuttan and Straffan, UK, it does occur among mosses, as well as other locations (Frost 1942). Percival and Whitehead (1929) found that ***Polycentropus flavomaculatus*** (Figure 52) was most abundant in thick mosses compared to other types of substrate. In mid-Appalachian Mountain streams, larvae of this genus are occasional inhabitants of bryophytes (Glime 1968).

Figure 52. ***Polycentropus flavomaculatus*** larva, a species that is more abundant in thick mosses than elsewhere. Photo by Dragiša Savić, with permission.

In one location in the Pyrénées Décamps (1967) found that ***Plectrocnemia scruposa*** (see Figure 53) comprised 4.5% of the **Trichoptera** fauna among mosses. Edington (1965) found that ***Plectrocnemia** conspersa* (see Figure 53) spun more nets at a flow rate of 10 cm sec^{-1} (80% of the larvae) than at 20 cm sec^{-1} (4%), a relationship just the opposite of that of ***Hydropsyche instabilis***. Furthermore, in both species, those few making nets at the less favorable flow rate had a tendency to construct abberrant nets.

Figure 53. ***Plectrocnemia geniculata*** larva, member of a genus in which some larvae live among mosses Photo from Biodiversity Institute of Ontario, through Creative Commons.

From Ceylon, Schmid (1958) reported ***Nyctiophylax devanampriya*** (Figure 54), ***Pseudoneureclipsis watagoda*** (Figure 55), and ***P. thuparama*** from large, mossy rocks in the torrent.

Figure 54. ***Nyctiophylax*** sp larva; ***N. devanampriya*** occurs among mosses in torrents in Ceylon. Photo by Dana R. Denson Florida Association of Benthologists, with permission.

Figure 55. ***Pseudoneureclipsis*** adult, a genus whose naiads can live on mossy rocks in torrents. Photo by Biodiversity Institute of Ontario, through Creative Commons.

But this family relies primarily on food trapped in its funnel-shaped net. Ross and Wallace (1983) demonstrated that 80% of the food for this family in a southern Appalachian Mountain, USA, stream was fine detritus. Another 15% was diatoms. So why do we find them among bryophytes at all?

Psychomyiidae – Net Tube Caddisflies

The **Psychomyiidae** are widespread, but are concentrated in the Oriental Region and absent in the Neotropical Region (Kjer 2010a). The adults are of moderate size (5-8 mm long forewings) (Watson & Dallwitz 2003). This family traps its food in a silken tube (Figure 56), with the diet consisting of algae, leaves, and animal matter (Neuswanger 2015). Grazing may occur both on the tubes and nearby, therefore consisting mostly of diatoms and other algae (Holzenthal *et al*. 2007; Kjer 2010a). Females dive to the bottom of the stream to lay their eggs (Neuswanger 2015).

Figure 56. **Psychomyiidae** net. Photo by Janice Glime.

Mosses occurred in the guts of ***Psychomyia pusilla*** (see Figure 57) and ***Tinodes waeneri*** (Figure 58-Figure 59) in UK streams (Percival & Whitehead 1929), attesting to their residence among bryophytes.

Figure 57. ***Psychomyia flavida*** larva. ***Psychomyia pusilla*** eats mosses. Photo from Stroud Water Research Center through Creative Commons, with permission.

Figure 58. ***Tinodes waeneri*** larva, a species that consumes mosses. Photo by Niels Sloth, with permission.

Figure 59. ***Tinodes waeneri*** larval tube. Photo by Niels Sloth, with permission.

Philopotamoidea

Philopotamidae – Finger-net Caddisflies

The larvae of this worldwide family build nets that can require more than 1 km of silk (Wallace & Malas 1976); these are used to trap small particles for food (McLeod 2005). To use them, the larvae are restricted to fast-flowing water of rivers and streams. The adult body is 5-9 mm long.

The net-building behavior would seem to preclude mosses as a substrate, but exceptions occur. ***Philopotamus montanus*** is not typically a bryophyte inhabitant and captures its food with a tube net. But this net can trap bits of mosses travelling downstream, and of the 15 guts with identifiable contents, two had ***Fontinalis antipyretica*** (Figure 43) (Jones 1949).

Chimarra (Figure 39; Figure 60-Figure 65) lives among mosses but prefers the gravel and sand at their bases (Armitage 1961). Williams and Hynes (1973) suggested that the affinity of ***C. aterrima*** (Figure 39) for moss-covered rocks may have been more related to the large size of those rocks rather than the presence of the moss. For example, in a wooded Ontario, Canada, stream, ***Wormaldia moesta*** (Figure 66) preferred bare stones, whereas ***Rhyacophila minor*** (**Rhyacophilidae**) preferred moss-covered stones in the same area (Singh *et al*. 1984). ***Wormaldia moesta*** grazed on diatoms when its primary food supply, detritus/**seston** (living organisms and non-living matter swimming or floating in a water body), became scarce. In my own studies of the fauna of bryophytes in the Appalachian Mountain streams, ***C. aterrima*** was occasionally present, but in small numbers, among ***Fontinalis dalecarlica*** (Figure 33) in larger streams (Glime 1968). It was absent in the other bryophytes.

Figure 60. ***Chimarra tsudai*** tubes with thallose liverworts at the funnel opening. Photo by Takao Nozaki, with permission.

Figure 61. ***Chimarra*** pupal case. Photo by Mark Melton, with permission.

Figure 62. ***Chimarra*** pupa showing on underside of sand case. Photo by Mark Melton, with permission.

Figure 63 ***Chimarra*** pupa removed from sand case, showing shed sclerotized parts from larva inside the pupal covering. Photo by Mark Melton, with permission.

Figure 64. ***Chimarra*** pupa removed from case. Photo by Mark Melton, with permission.

Figure 65. ***Chimarra tsudai*** adult. Takao Nozaki, with permission.

Figure 66. ***Wormaldia moesta*** larva, a species that prefers bare stones even when mosses are present. Photo by Donald S. Chandler, with permission.

Another occasional visitor to bryophytes in Appalachian Mountain, USA, streams was ***Dolophilodes distinctus*** (Figure 67) (Glime 1968**)**. In this case, it occurred among all four of the primary bryophytes in the study: ***Hygroamblystegium fluviatile*** (Figure 31), ***Platyhypnidium riparioides*** (Figure 32), ***Fontinalis dalecarlica*** (Figure 33), and ***Scapania undulata*** (Figure 68), preferring the mats and turfs over ***Fontinalis*** streamers.

Figure 67. ***Dolophilodes distinctus*** larva, an occasional visitor to Appalachian Mountain stream bryophytes. Photo by Donald S. Chandler, with permission.

Figure 68. ***Scapania undulata***, a leafy liverwort that can modify flow patterns and house insects. Photo by Michael Lüth, with permission.

Summary

Lepidoptera apparently do not use aquatic bryophytes.

Trichoptera, on the other hand, are among the common inhabitants. Those that enter the drift may use bryophytes as a means to get out of the drift. Some larvae use the bryophytes for food and many use them as a safe site for capturing food, using both filtering strategies and predation of smaller inhabitants. The mosses themselves may serve as filter traps for caddisfly food, including drifting algae, bacteria, decomposing organic matter, and detritus. For some caddisflies the bryophytes themselves serve as food and may be a seasonal staple when other foods are unavailable. Some build their cases from bryophytes and liver among the bryophytes to capture food.

Larvae of most **Trichoptera** are aquatic, and many may also use the bryophytes as a site for pupation and emergence. The most common families among bryophytes are The **Hydropsychidae** and **Rhyacophilidae**. These are both caseless caddisflies, and the bryophytes may provide some of the protection otherwise afforded by cases.

Hydropsychidae take advantage of the bryophytes to partition their niches and avoid competition for food. In some cases this is the result of changing diets at later instar stages. Others use differences in flow within the bryophyte mat. They seem to be able to use the bryophytes to trap food, and the bryophytes create locations with a variety of flow regimes. Still other caddisflies are selective about which species of bryophytes they use, with a few selecting leafy liverworts only and others avoiding them.

The importance of the bryophytes as food remains a mystery. It is possible they are ingested along with adhering periphyton and detritus without being digested.

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