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CHAPTER 12-11
TERRESTRIAL INSECTS: HOLOMETABOLA – TRICHOPTERA

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Figure 1. ***Eniocyla pusilla*** larva, the most common terrestrial caddisfly and often a moss dweller. Photo by John Bingham, with permission.

The adults of caddisflies are terrestrial, but most caddisflies have aquatic larvae. Nevertheless, a few have adapted to living in wet places on land. And mosses can provide those wet places. For example, Sleight (1913) described one member of **Limnephilidae** in mosses at tree roots, but not in the water.

Some aquatic larvae are able to feed near the surface of water. The aquatic ***Pycnopsyche guttifera*** (Figure 2) will sometimes eat terrestrial mosses, but this occurs when the mosses are just below the water line (Williams & Williams 1982).

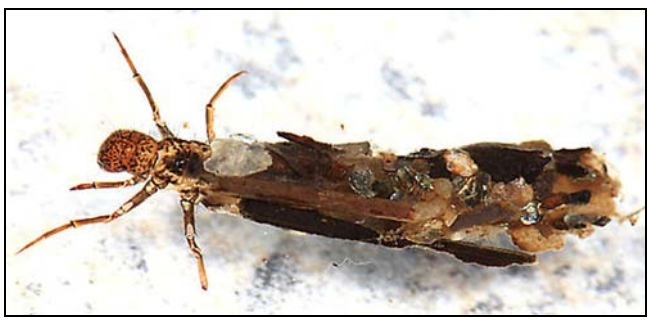

Figure 2. ***Pycnopsyche guttifera*** larva, a larva that eats terrestrial mosses when they become submersed. Photos by Tom Murray, through Creative Commons.

Larvae

We now know that there are three species of terrestrial ***Enoicyla*** (**Limnephilidae**; Figure 1) in Europe, and that larvae of these live in the humid and temperate mosses of deciduous forests and rock crevices (Crampton 1920; Meidl & Molenda 2000), often far from water (Crampton 1920). Perhaps the best known of these terrestrial larvae are those of ***Enoicyla pusilla*** (Figure 3-Figure 5). These larvae build cases from fine grains of sand and vegetable matter among mosses (Butler 1886). In Britain, ***Enoicyla pusilla*** is restricted to woodlands, and Harding (1998) suggested that it may have been accidentally introduced from the European continent. This species has five larval instars, becoming more scarce by late summer. Eggs hatch in October and November, and larval success may depend on rainfall during those months. The larvae of this species typically occur among mosses and leaf litter.

Figure 3. ***Enoicyla pusilla*** larvae, a species that inhabits mosses and leaf litter. Photo by Ernest van Asseldonk, through Creative Commons.

Figure 4. ***Enoicyla pusilla*** larva feeding on a slime mold. Photo by John Bingham, with permission.

Figure 5. ***Enoicyla pusilla*** adult, a species whose larvae live among terrestrial mosses. Photo by James K. Lindsey, with permission.

Green (1997) reported that in the UK the larvae of ***Enoicyla pusilla*** (Figure 3) feed on the soft tissues of dead leaves, mosses, and algae. In one observation, 50 or more individuals were actively climbing up logs and apparently browsing on black slime molds (Green 2012). Their requirement for nearly 100% humidity limits their terrestrial habitats. They have no gills and must rely on cutaneous respiration. If they get too wet, they climb upward and "hang themselves out to dry." When the humidity decreases to 70%, they drop again to the ground. Sometimes many larvae occur together on the surfaces of mosses and liverworts on stream banks after a rain (Green & Westwood 2005; Green 2012).

Flint (1958) considered that *Ironoquia pusilla* in northeastern United States closely resembled ***Enoicyla pusilla*** in its pupal stage. He reported that the larvae of *I. parvula* left the water and climbed to land where they spent their pupal stage among the leaf litter.

Another genus of caddisfly that lives on land as larvae is ***Manophylax*** (**Apataniidae**) (Chuluunbat *et al*. 2010). ***Manophylax futabae*** larvae can be found on the vertical sides of large rocks 10-30 m from mountain streams, as well as on vertical rocky outcrops. Chuluunbat and coworkers found that these larvae were often covered with mosses and lichens, but assumed that their only water usually came from precipitation. ***Manophylax alascensis*** and ***M. annulatus*** both construct their cases (4.0-9.8 mm) from fine rock fragments with attached moss and algal fragments dorso-laterally.

It may be that the movement of Trichoptera to land began with species that moved there to feed. *Desmona bethula* (**Limnephilidae**) is one such species (Erman 1981). When it reaches its fifth instar, it adventures from the water to feed on semiaquatic plants. But for this species, inclusion of bryophytes is not known.

Oviposition

If there are larvae on land, then there must be oviposition on land, at least for species that are not adjacent to water. It is interesting that the information I have found on the terrestrial caddisflies is not well linked. We know about the larvae of ***Enoicyla*** (Figure 3-Figure 5) feeding on bryophytes, but I have found no discussion of their oviposition. On the other hand, I have found information on egg-laying in the **Leptoceridae**.

Leptorussa darlingtoni (**Leptoceridae**) females become active in late afternoon in oviposition (Towns 1983). In Australia, most had congregated in damp mosses near the water surface, with 30 adults along an 80-cm line at 10-20 cm above the water. ***Leptorussa darlingtoni*** deposits its egg masses in communities above the water, whereas ***Lectrides varians*** (Figure 6), also in the **Leptoceridae**, deposits a single egg mass at 65-95 cm above the water. For ***Leptorussa darlingtoni***, the egg masses are placed in small crevices, but they are always near extensive moss cover. Nevertheless, the moss moisture does not seem to be important as the eggs survive in these same locations when the mosses are dry in years with little rainfall. Towns suggested that the terrestrial deposition may be an avoidance of the fluctuating oxygen levels in the water. In fact, when Towns attempted to rear the eggs on damp mosses in the laboratory, fungal infections caused death of the eggs. Towns asserted that ***Leptorussa darlingtoni*** is the only species of caddisfly that has communal oviposition and hatching without water.

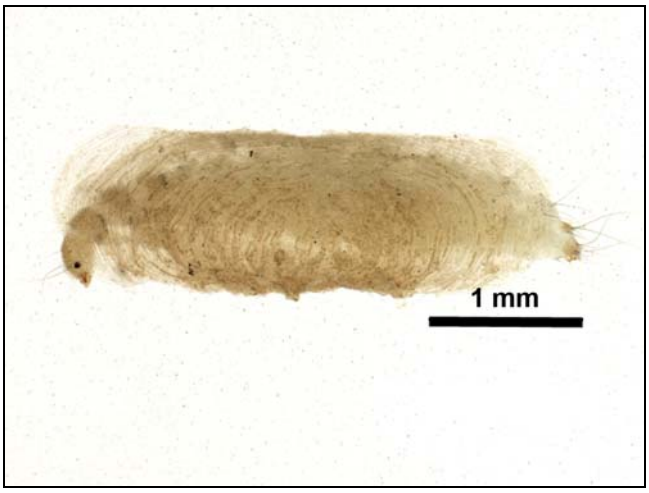

Figure 6. ***Lectrides varians*** larva, a species that deposits its eggs where there are lots of mosses. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Pupation

Most of the aquatic larvae of **Trichoptera** remain in the water to pupate, emerging onto vegetation or rocks to climb out of the water as adults. But if larvae can live on land, we can assume that their pupae, and perhaps pupae of others, may survive terrestrial life. Erman (1984) suggested that terrestrial pupation in this group evolved as an adaptation to living in intermittent streams. Some larval members of **Limnephilidae** leave the water in the final instar to pupate on land. ***Limnephilus peltus*** (see Figure 7) leaves spring streams shortly after the snow melts in the Sagehen Creek basin, California, USA, to burrow into the mosses at the edges of fen streams. If the spring flow ends too early and the mosses dry, some pupae may die without any adult emergence.

Another caddisfly, in the **Goeridae**, ***Archithremma ulachensis***, spends its larval days in a layer of ***Sphagnum*** (Figure 8) on a springbank (Levanidova & Vshivkova 1984). Its pupa seems to be adapted to this dense terrain. It lacks long setae and projections used by other pupae in the family to clean the silk disks that close the case. The first abdominal segment lacks posterior rugosity, and there are no swimming legs. The larvae, however, live in water courses that have cold summer temperatures (3-5°C). The authors consider these cold brooks to have less food competition, thus favoring the larvae of this species.

Figure 7. ***Limnephilus*** sp. larva; ***L. peltus*** burrows into mosses to pupate. Photo by Jason Neuswanger, with permission.

Figure 8. ***Sphagnum capillifolium***; ***Sphagnum*** is home for the larvae of ***Archithremma ulachensis***. Photo by Bernd Haynold, through Creative Commons.

Hayashi *et al*. (2008) cite the terrestrial habits of the limnephilid ***Nothopsyche***. This genus has species in which both pre-pupae and pupae are entirely terrestrial. Their mitochondrial data indicate that this genus was originally aquatic and that just one lineage became terrestrial in the pre-pupal and pupal stages. In this terrestrial lineage, ***Nothopsyche montivaga*** became completely terrestrial. The terrestrial line also exhibit a switch in case materials from plant matter to sand.

Bogs

For an order of insects evolving from water to land, bogs would seem to be the ideal place to begin. The mosses wick water upward, remaining moist most of the year. Furthermore, water can often be reached by moving downward.

Buczyńska *et al*. (2012) searched for the rare ***Hagenella clathrata*** (**Phryganeidae**; Figure 9-Figure 10) in Poland. This species is associated with bogs, making it even more threatened due to habitat destruction. This research team was able to collect larvae in the mountain area using Barber pitfall traps, indicating their mobility in terrestrial habitats.

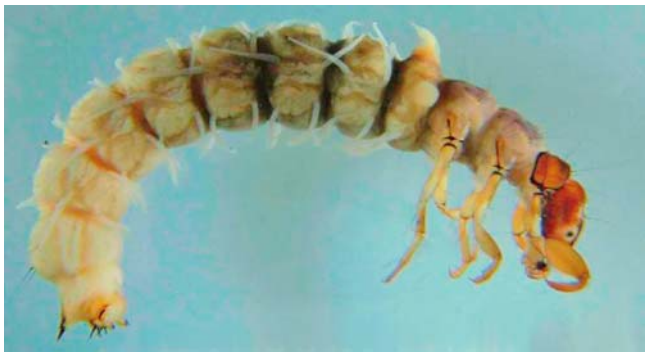

Figure 9. ***Hagenella clathrata*** larva, a species that lives in bogs. Photo by Marko Mutanen, through Creative Commons.

Figure 10. ***Hagenella clathrata*** adult, a bog dweller. Photo by Rob Felix, through Creative Commons.

Summary

Few of the caddisfly larvae have adapted to terrestrial living, and even fewer use bryophytes for their terrestrial adventures. Several of the bryophyte associates are in the **Limnephilidae.** ***Pycnopsyche guttifera*** sometimes eats terrestrial mosses that extend below water. ***Limnephilus peltus*** burrows into mosses to pupate. But the best known example is that of ***Enoicyla pusilla***, larvae that live terrestrially and include mosses in their varied diet.

Larvae of ***Manophylax*** (**Apataniidae**) may include mosses in their cases. ***Leptorussa darlingtoni*** (**Leptoceridae**) lays eggs near water in damp mosses, but the eggs can dry safely and thus may not require mosses. Larvae and pupae of ***Archithremma ulachensis*** (**Goeridae**) live among ***Sphagnum***. ***Hagenella clathrata*** (**Phryganeidae**) likewise live in bogs.

Acknowledgments

Thank you to those photographers who gave me permission or placed their images in Creative Commons. For this chapter, I would welcome additional images!

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