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CHAPTER 11-14
AQUATIC INSECTS: HOLOMETABOLA – DIPTERA, SUBORDER BRACHYCERA

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Figure 1. ***Limnophora*** sp. larva (**lower**) and pupa (**upper**) (**Muscidae**), occasional bryophyte inhabitants. Photo by Stephen Moore, Landcare Research, NZ, with permission.

DIPTERA – FLIES

Suborder Brachycera

This suborder is less aquatic than the **Nematocera**. Furthermore, few of its members use aquatic bryophytes. Nevertheless, it is a convenient way to break up the chapter into shorter segments.

Athericidae/Rhagionidae – Watersnipe Flies

The larvae of these flies occur in pristine streams with the adults nearby (Kits 2005). They include predaceous members that eat other invertebrates, including caddisflies, and saprophagous members on wooden debris (Athericidae 2014). The larvae are distinguished by **crochets** on their abdominal prolegs (Figure 2), permitting them to live in rapid montane streams and torrents without being washed away.

Figure 2. ***Atherix ibis*** larva showing crochets in two rows in each proleg. Photo by Urmas Kruus, with permission.

This family is not well represented among bryophytes. ***Atherix ibis*** (Figure 3) includes bryophytes among its substrates in streams (Neveu 1976). The larvae eat small invertebrates (McLeod 2005), most likely finding the bryophytes to serve as an adequate dinner table. In Carpathian streams, this species is positively correlated with stream order and warmer water temperatures (Bulánková & Duricková 2009). Its eggs are laid on overhanging leaves and hatched larvae slide into the water; the larvae are henceforth very sensitive to desiccation. They are, however, quite tolerant of human activity and pollution.

Figure 3. ***Atherix ibis*** larva, a stream-dweller that can be found among bryophytes. Photo by Niels Sloth, with permission.

In the acid streams in the Appalachian Mountains, USA, ***Atherix variegata*** occurred in all of the common moss habitats [***Fontinalis dalecarlica*** (Figure 4), ***Hygroamblystegium fluviatile*** (Figure 5), ***Platyhypnidium riparioides*** (Figure 6), and ***Scapania undulata*** (Figure 7)] (Glime 1968).

Figure 4. ***Fontinalis dalecarlica*** with capsules, home to ***Atherix variegata*** in Appalachian Mountain, USA, streams. Photo by Janice Glime.

Figure 5. ***Hygroamblystegium fluviatile***, home to ***Atherix variegata*** in Appalachian Mountain streams. Photo by Janice Glime.

Figure 6. ***Platyhypnidium riparioides***, home to ***Atherix variegata*** in Appalachian Mountain streams. Photo by Andrew Spink, with permission.

Figure 7. ***Scapania undulata***, home to ***Atherix variegata*** in Appalachian Mountain streams. Photo by Michael Lüth, with permission.

In the Plitvice Lakes National Park in the Dinaric karst region of Croatia, the **Athericidae** preferred moss on tufa (P <0.05, n = 12) (Čmrlec *et al*. 2013). These flies pupate on mosses, and that substrate is the preferred substrate for emergence of the adults (Thomas 1997; Čmrlec *et al*. 2013).

Spaniidae/Rhagionidae

This family, well known from records in amber, exhibits only scattered records throughout the world today (Arillo *et al*. 2009). The only bryophyte dweller I know in this family is the snipe fly, ***Spania nigra*** (Figure 8), from **ghyll** (deep ravine) woodlands in Sussex, UK (Roper 2001).

Dolichopodidae – Long-legged Flies

These are small (1-9 mm) flies with a worldwide distribution (Dolichopodidae 2015). The larvae are predominantly terrestrial, but there are also many semi-aquatic taxa that live in or near water margins. Some can even walk on the water surface. Larvae are typically predatory, although a few live in the stems of reeds and other monocots near water.

Figure 8. ***Spania nigra*** adult, with a larval bryophyte dweller in Sussex. Photo by Marko Mutanen through Creative Commons.

This family does not seem to be reported as a moss dweller, but it does occasionally live among mosses in the Appalachian Mountain, USA, streams (Glime 1968). I was able to identify ***Hydrophorus*** larvae (Figure 9-Figure 10) in these collections. But it is also possible that they fell in or got swept in by flooding.

Figure 9. ***Hydrophorus oceanus*** larvae, member of a genus that sometimes occurs among stream bryophytes. Photo by Hans Hillewaert, through Creative Commons.

Empididae – Dance Flies

These are small flies with a worldwide distribution and that can be aquatic, but can also live in semiaquatic habitats, in dung, in bird nests, among roots, and associated with fungi (Cresswell 2004). Larvae mostly feed on decaying matter, but also can be predatory.

Figure 10. ***Hydrophorus praecox*** adult, member of a genus that can be found among Appalachian Mountain stream bryophytes. Photo by James K. Lindsey, with permission.

The **Empididae** (Figure 11) are little flies, so it is not any surprise to find them among mosses as larvae. In fact, larvae and pupae of many species occur among mosses in streams (Ivković *et al.* 2007).

Figure 11. **Empididae**, a frequent larva on bryophytes in streams. Photo by Stephen Moore, Landcare Research, NZ, with permission.

Because of their small size and the tedious process of sorting through moss samples, this family is not well known among the mosses and more species are likely to be found on close observation. Pusch and Wagner (1993) found and described the new species ***Bergenstammia aurinae*** in the eastern Alps where it lived among wet mosses in two small brooks with a steep elevation gradient but no glacial melt water.

In the Plitvice Lakes National Park in the Dinaric karst region of Croatia, the **Empididae** preferred moss on tufa and macrovegetation where they have shelter and food (Watson & Rose 1985; Nolte 1991; Linhart *et al.* 1998, 2002a, b, c; Ivković *et al.* 2007). Emergence was almost equal above substrates of moss on tufa, pebbles, and tufa with detritus (Ivković *et al.* 2012).

Suren (1991) experimented with artificial bryophytes in two New Zealand alpine streams. He found that whereas most insects had densities similar to that on natural bryophytes, the **Empididae** had lower densities on the artificial ones, suggesting that the bryophytes themselves have an important role for these larvae.

Fast-water Refuge

Those larvae that are truly aquatic stream-dwellers usually live among the mosses in fast water. Ivković *et al*. (2012) recorded the highest abundance of dance flies from Plitvice Lakes National Park, Croatia, in stream habitats that had moss, gravel, and particulate tufa with detritus and fast current. In Malaysia, larvae of ***Hemerodromia*** (Figure 12-Figure 13) live at least 10 cm beneath the water surface in the **hyporheic** zone (Grootaert 2004). They are sensitive to light and disappear from streams when the forest is gone. Light plays an important role in their mating – a behavior that earns them the name of dancing flies. Unlike many Diptera that rely on gills or spiracles, the aquatic larvae of ***Hemerodromia*** exchange oxygen directly from the water, whereas many other members of the family use spiracles positioned to be in direct contact with the air. Larvae are predacious and often feed on their cohabitants such as blackflies or **Chironomidae** (Vaillant 1951, 1967; Vaillant & Gagneur 1998; Grootaert 2004). The adults are small (3-5 mm) are mostly yellow or black and prefer boulders covered with moss or a splash zone where moisture loss is not a problem (Grootaert 2004). In Europe, ***H. praecatoria*** (syn. of ***Chelifera precatoria***?) live among mosses in nearly stagnant water (Bischoff 1924b; Johannsen 1969). In Belgium this species occurs in pools of ***Sphagnum*** bogs (Dipterainfo 2014). This same genus occurred among ***Fontinalis dalecarlica*** (Figure 4) in Appalachian Mountain, USA, streams (Glime 1968). The species resembled ***H. rogatoris*** and ***H. seguyi***.

Figure 12. ***Hemerodromia*** larva, a frequent bryophyte inhabitant. Photo courtesy of the State Hygienic Laboratory, University of Iowa, with permission.

Bischoff (1924a) reported that the genus ***Clinocera*** occurred (Figure 14-Figure 15) among mosses in swift streams. In Malaysia, the larvae, like those of ***Hemerodromia***, live at least 10 cm below the water surface in the hyporheic zone and exchange oxygen directly through the cuticle (Grootaert 2004). Sinclair (2000) described a new species, ***Clinocera gressitti*** (Figure 14), from mosses on submerged stones in New Zealand. Adrian Plant (pers. comm. 27 August 2014) observed that members of this genus often pupate (Figure 15) among the mosses.

Figure 13. ***Hemerodromia superstitiosa*** female adult, member of a genus with moss-dwelling larvae. Photo by Seth Burgess, through Creative Commons.

Figure 14. ***Clinocera*** larva, an inhabitant of mosses in swift streams. Photo from <www.dfg.ca.gov>, through public domain.

Figure 15. ***Clinocera nigra*** pupal exuvia. Photo by Adrian Plant, with permission.

In a springbrook in the Southern Alps of New Zealand, Cowie and Winterbourn (1979) found three zones of bryophytes. In the torrential waters near the middle of the channel, **Empididae** (Figure 11) were among the most abundant species living among ***Fissidens rigidulus*** (Figure 16). Not surprisingly, these were accompanied by several abundant species of **Chironomidae** (see Chapter 11-13b).

Figure 16. ***Fissidens rigidulus***, home for **Empididae** in torrents. Photo by Bill and Nancy Malcolm, with permission.

In a German stream, larvae of ***Wiedemannia bohemani*** (see Figure 17) were abundant in the middle reach, with many occurring in partly submerged mosses on stones, both at and below the water lever (Wagner & Gathmann 1996). Vaillant (1967) likewise found both larvae and pupae of ***Wiedemannia*** in streams and rivers of France, with adults remaining nearby on stones that were partially submersed. The larvae feast on the **Chironomidae** that are so abundant among mosses.

Figure 17. ***Wiedemannia bistigma*** emerging on stones. Photo by Adrian Plant, with permission.

Harper (1980) found that ***Hemerodromia*** (Figure 12-Figure 13), ***Neoplasta*** (Figure 18-Figure 19), and ***Roederiodes*** (Figure 20) in the Laurentian watershed, Quebec, Canada, typically inhabit the mainstream and the larger tributaries. These species usually prefer fast water with a substrate of moss and rubble.

Figure 18. ***Neoplasta*** larva, a bryophyte inhabitant. Photo from <dfg.ca.gov>, through public domain.

Figure 19. ***Neoplasta*** adult, a genus with larval bryophyte inhabitants. Photo by Adrian Plant, with permission.

Figure 20. ***Roederiodes recurvatus*** adult, a genus whose larvae are associated with mosses in fast water in the Laurentian watershed of Canada. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Hemerodromia (Figure 12-Figure 13) larvae occur primarily in lotic habitats and among mosses on stream

cobble (Merritt & Cummins 1996), but also live in mosses at or just above the water level (Brammer *et al*. 2009). Larvae of ***Hemerodromia*** consume blackfly larvae that are living on the mosses (Vaillant 1953). Some of these **Empididae**, especially ***Hemerodromia***, larvae have an interesting habitat choice, living in cases and nets of other insects. Larvae of the ***Hemerodromia empiformis*** complex have been found inside the tubes of the midge ***Rheotanytarsus*** (Figure 21-Figure 22) in southern California, USA. The last instar larvae and pupae of ***H. brevifrons*** have been found inside cocoons of **Simuliidae** (Figure 23) in a stream in Los Angeles County, California, USA. Pupae of a South American ***Neoplasta*** (Figure 18) can occur inside cocoons of caddisflies (Brammer *et al*. 2009). Thus their habitation of mosses may be indirect.

Figure 21. ***Rheotanytarsus exiguus*** larval tubes made by the moss inhabitant larvae, but these tubes also house the larvae of ***Hemerodromia empiformis***. Photo by D. N. Bennett, with permission.

Figure 22. ***Rheotanytarsus*** sp. larva from the above tubes. This genus inhabits mosses and other sites. Photo by Jason Neuswanger, with permission.

Figure 23. ***Simulium aureum*** pupa with cocoon where the empidid ***Hemerodromia brevifrons*** sometimes lives. Photo by Malcolm Storey, Discover Life, through Creative Commons.

Where Shall We Go for Dinner?

Some adult members of the family devour their food from invertebrates trapped by the surface film. ***Wiedemannia bistigma*** (Figure 24) adults climb about on floating algae for just this purpose (Laurence 1953). Like maggots on a road kill, the empidids gather in numbers on the carcass of a dead insect. This adult behavior may not be as effective for most larval bryophyte-dwellers because the bryophyte habitats are often in fast water.

Figure 24. ***Wiedemannia bistigma*** adult, a species whose larvae can live among stream mosses. Photo by Adrian Plant, with permission.

Empididae larvae include both predaceous and non-predaceous larvae (and adults) (Oldroyd 1964). Many species of the subfamily **Hemerodromiinae** live in streams where their predatory larvae live among mosses and on wet rocks (Gerson 1969; Roper 2001). Some members are predators on larval blackflies (Vaillant 1951, 1953; Sommerman 1962; Wirth 1983; Werner & Pont 2003).

Empididae in the Cold

The **Empididae** are particularly adept at surviving cold conditions, whereas most insects lack cold resistance (Irons *et al*. 1993). Nevertheless, they cannot survive temperatures even 1°C below zero. In Alaska many insects survive by moving away from a freezing front or living in one that will not freeze. The **Empididae**, like the **Chironomidae**, will spend the winter in a frozen habitat. The **Empididae** have a high survival rate under freezing and thawing conditions. The ice serves as insulation

against sub-zero temperatures, with flowing water remaining typically at about 0.8°C.

Oreogetonidae

The **Oreogetonidae** is a small family, a segregate from the **Empididae** (Bayless 2011). The larvae are freshwater carnivores (Cresswell 2004). The family is widespread, with a concentration in South America, but also occurring in North America, Europe (one species), Asia, Australia, and New Zealand (Oreogetonidae 2014).

The genus ***Oreogeton*** (Figure 25) associates with mosses, but they are sprawlers-burrowers that engulf their prey, including blackflies and caddisflies (Aquatic Insects 2008; National Park Service 2014). These prey insects may be the reasons they enter the moss realm.

Figure 25. ***Oreogeton*** sp. adult. Larvae in this genus are sprawler-burrowers among mosses, feeding on blackflies and caddisflies. Photo by Tom Murray, through Creative Commons.

Syrphidae – Hoverflies

These worldwide flies are mostly 10-20 mm long, but can range up to 35 mm (Bartlett 2004). Many of the terrestrial larvae live in ant nests, but some occur in bogs. The larvae are mostly predators, although the family include a wide range of food sources. Some aquatic members have a long breathing tube, earning them the name of rat-tailed maggots. ***Sericomyia borealis*** (Figure 26) larvae occur in pools of peat bogs (Bloomfield 1897).

Figure 26. ***Sericomyia silentis*** adult, member of a genus in which some larvae live in bog pools. This one, like many syrphids, is a bee mimic. Photo by Richard Bartz, through Creative Commons.

Ephydridae – Shore-flies

The name **Ephydridae** literally means "living on the water" (Moisset 2004). The larvae filter microorganisms, including bacteria, one-celled algae, and yeasts, but some are predators on **Chironomidae** larvae. They are small to medium in size (2.5-9 mm) and have a worldwide distribution.

This is not typically a bryophyte family. ***Discocerina*** (Figure 27) burrows into moss mats or lives among algae at the borders of streams, ponds, and lakes (Merritt *et al*. 1996). ***Gymnoclasiopa plumosa*** (see Figure 28) breeds in algae and mosses in the forest (Grünberg 1910).

Figure 27. ***Discocerina obscurella*** adult, a genus that burrows into moss mats at water's edge. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 28. ***Gymnoclasiopa taxoma*** adult. ***Gymnoclasiopa plumosa*** breeds in forest mosses. Photo from USFWS, through public domain.

Sciomyzidae – Marsh Flies

The **Sciomyzidae** family (Figure 29-Figure 30) has worldwide distribution. The adults are 5-10 mm long and

live around marshes, lakes, ponds, and wooded areas, but the larvae are aquatic (Leung 2004). These larvae feed on snails, either as predators or parasites. ***Poecilographa decora*** is the only American species in this genus (Usinger 1974). Its pupae are known from woodland mosses.

Figure 29. **Sciomyzidae** larva indicating spiracular disc. Photo by Stephen Moore, Landcare Research, NZ.

Figure 30. **Sciomyzidae** pupa; some species pupate among mosses. Photo by Stephen Moore, Landcare Research, NZ.

Agromyzidae – Leaf-miner Flies

The **Agromyzidae** are 1-5 mm long and are leaf miners (Murray 2005). Although these are mostly miners on tracheophytes, the **Agromyzidae** are known from liverworts from scattered locations around the world in such distant locales as the West Indies, Mexico, Peru, the Juan Fernandez Islands, New Zealand, and France (Spencer 1990).

The leaf miner ***Phytoliriomyza mesnili*** (see Figure 31) develops successfully on the floating liverwort ***Ricciocarpos natans*** (Figure 32) (d'Aguilar 1945). It also occurs on ***Riccia beyrichiana*** (Figure 33) where the larva feeds within the thallus, then pupates there. This miner is known exclusively from liverwort and hornwort thalli.

Figure 31. ***Phytoliriomyza melampyga*** larva showing leaf mine trail in a tracheophyte leaf. Photo by Malcolm Storey.

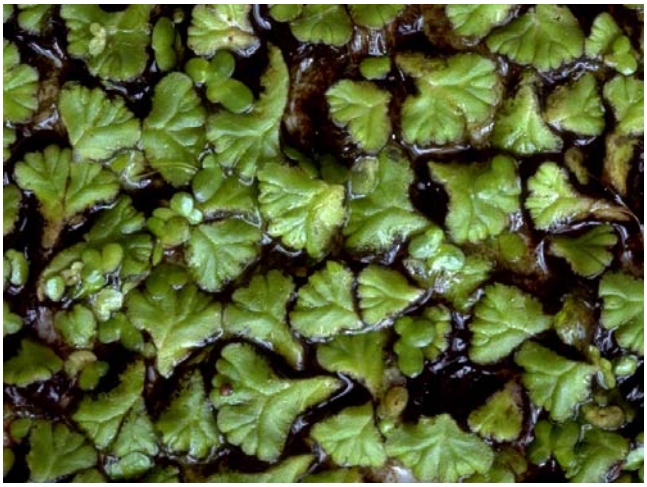

Figure 32. ***Ricciocarpos natans***, a suitable thallus for development of ***Phytoliriomyza mesnili***. Photo by Jan-Peter Frahm.

Figure 33. ***Riccia beyrichiana*** with eggs deposited in a cavity made on the left thallus. This liverwort species serves as home for larvae of the agromyzid fly ***Phytoliriomyza mesnili***. Photo by Malcolm Storey, DiscoverLife, Creative Commons.

Muscidae – House Flies and Kin

This is a worldwide family whose larvae live in dung, carrion, soil, nests, decaying vegetation, and less commonly among bryophytes in running water (Balaban & Balaban 2004). Adults range 2-14 mm in length (Muscidae 2015).

Many species of ***Limnophora*** (Figure 1, Figure 34-Figure 35) carry out their larval development among mosses and liverworts in running water where they are able to prey on **oligochaetes** (segmented worms such as earthworms) and small insect larvae (Glime 1968; Skidmore 1985; Roper 2001). In the Appalachian Mountain, USA, streams these occur most abundantly among clumps of ***Hygrohypnum luridum*** (Figure 36), especially in small waterfalls (Glime 1968). Axelrod and Vorderwinkler (1983) found that the European muscid fly ***Limnophora riparia*** (Figure 35) prefers mosses as a substrate; it is a good place to eat chironomid, blackfly, and other larvae (Wotton & Merritt 1988). This species typically lives among bryophytes in waterfalls, splash zones, and lake outlets. When the larvae were placed under water in enamel trays, all of them drowned within 24 hours. They burrow into any possible substrate to avoid light.

Figure 34. ***Limnophora*** adult, a genus where some members use mosses for egg-laying, larvae, and pupae. Photo by Luis Miguel Bugallo Sánchez, through Wikipedia Commons.

Figure 35. ***Limnophora riparia*** larva, a species that lays its eggs, develops, and pupates in mosses as a preferred site. Photo by Niels Sloth, through Creative Commons.

Figure 36. ***Hygrohypnum luridum***, home to ***Limnophora*** larvae in mid-Appalachian waterfalls. Photo by Hermann Schachner, through Creative Commons.

The larvae of ***Limnophora riparia*** (Figure 35) hatch from the egg as a third instar larva and are immediately ready to prey upon living invertebrates (Merritt & Wotton 1988). One of their peculiar adaptations is to attach the anterior of their prey and to remove and digest the contents of the head and body, leaving the cuticle and guts behind. The life cycle is synchronized with the main prey item, larvae of the blackfly ***Simulium noelleri***, and other invertebrate prey items so that there is always plenty of food for the developing larva. When the larva matures, it continues to select mosses for its site to pupate.

Badcock (1949) found that the muscid ***Calliophrys*** only occurs in mosses on the vertical face of a waterfall in the Welsh Dee.

Summary

The **Brachycera** are mostly terrestrial, but a few have associations with the aquatic bryophytes. Among these, the **Empididae** are probably the most common. Bryophytes seem to be important to them as they colonize bryophytes more readily than they colonize artificial bryophytes. Both larvae and pupae live among the bryophytes. And like the bryophytes, they are often in stream openings that don't freeze.

The most interesting family to a bryologist includes those few members of the leaf miners (**Agromyzidae**) that live exclusively in the tissues of thallose bryophytes – liverworts and hornworts. As such, the thalli provide both protection and food.

Some members of the **Ephydridae** burrow into the mosses at the borders of streams and ponds. **Sciomyzidae** larvae live in the water, but the pupae occur among woodland mosses. Even some **Muscidae** complete their larval development among aquatic bryophytes. Other families with a few members living in association with aquatic or predominantly wet bryophytes are **Athericidae**, **Spaniidae**, **Dolichopodidae**, **Oreogetonidae**, **Syrphidae**, and **Sciomyzidae**.

Acknowledgments

Julian P. Donahue verified some of the Diptera from my mid-Appalachian Mountain study. D. N. Bennett informed me about her findings of larvae and provided me with images. My sister, Eileen Dumire, has provided invaluable help in proofreading and clarifying this chapter.

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