CHAPTER 11-10
AQUATIC INSECTS:  HOLOMETABOLA – COLEOPTERA, SUBORDER POLYPHAGA

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Figure 1. *Ilybius erichsoni* adult on *Sphagnum*. Photo by Niels Sloth, with permission.

Suborder Polyphaga

This suborder includes more than 90% of the Coleoptera species. As its name suggests, it eats a tremendous variety of foods.

Helophoridae

This is a family of North America and Europe and has only one genus, *Helophorus* (Helophoridae 2014). They are relatively small (2-9 mm) (Helophoridae 2014) and live primarily in wetlands (Helophoridae 2015). Most adults live in shallow standing water where they are saprophagous (Fikáček 2009) (organism that feeds on decaying organic matter). Larvae, on the other hand, live in terrestrial, but moist, habitats near water and are predators on small invertebrates.

*Helophorus grandis* (Figure 2) occurs among the aquatic mosses in a stream in Yorkshire, UK (Gilbert *et al.* 2005). In Canada, *Helophorus orientalis* (Figure 3) occurs in wet mosses beside small streams (Majka 2008).

*Helophorus strigifrons* (Figure 4) lives in bogs in North Hampshire, UK, among moss and litter (Denton 2013).

Figure 2. *Helophorus grandis*, an inhabitant of stream mosses in the UK. Photo by Tim Faasen, with permission.
Figure 3. *Helophorus orientalis* adult, a species that lives among wet mosses along streams in Ontario, Canada. Photo by Tom Murray, through Creative Commons.

Figure 4. *Helophorus strigifrons* adult, a bog dweller in North Hampshire, UK, among moss and litter. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

**Hydrochidae**

Although this family is worldwide, it has only one genus, and most of the records are from Europe (Hydrochidae 2015a). Adults and larvae live in both quiet and flowing water where they are herbivores – shredders (Hydrochidae 2015b). The adults range 4-60 mm long. Some of these are associated with bryophytes.

*Hydrochus ignicollis* (Figure 5), a very rare species in Ireland, appeared in collections only twice between 1988 and 1996 (Nelson 1996). Both finds were from mossy calcareous fens adjacent to marl lakes. These are alkaline lakes with unconsolidated calcium carbonate or lime-rich mud or mudstone which contains variable amounts of clays and silt (Figure 6-Figure 7).

Figure 5. *Hydrochus ignicollis* adult, a rare inhabitant of mossy calcareous fens in Ireland. Photo by Tim Faasen, with permission.

Figure 6. Marl lake in Jasper National Park, Canada. Photo by Janice Glime.

Figure 7. Marl at margin of marl lake in Jasper National Park, Canada. Photo by Janice Glime.

**Hydrophilidae – Water Scavenger Beetles**

This is a worldwide, mostly aquatic family, typically in open water (Cotinus 2005). The larvae often emerge from the water to pupate, usually hanging from moss at the edge of the water (Water Beetles 2014). The final larval skin is found beneath the pupa. The adults (1-40 mm) are mostly scavengers, but some are predators; larvae are often predators (Cotinus 2005).
Some Hydrophilidae join the Dytiscidae as common beetles swimming in bog waters. *Enochrus* (Figure 8-Figure 9) is a common genus there (Denton 2013). *Enochrus affinis* (Figure 10) is often abundant in Sphagnum-dominated (Figure 51) areas of acidic heathland pools (Figure 11) of North Hampshire, UK. *Enochrus coarctatus* (Figure 12) is a mire dweller, preferring older detritus pools but also living in Sphagnum-filled large bog pools. *Enochrus ochropterus* (Figure 13) does not occur in areas of pure Sphagnum where the *Enochrus* is exclusively *E. affinis*. However, it does occur in richer areas with *E. coarctatus*. The importance of the Sphagnum in its habitats may be due to its role in acidification. *Enochrus fuscipennis* (Figure 14) lives in the Sphagnum-choked shallow pools of undisturbed blanket bogs in Dartmoor, UK (Boyce 2011). *Enochrus hamiltoni* (Figure 15), on the other hand, lives in wet mosses next to small streams on Prince Edward Island, Canada (Majka 2008). In the Appalachian Mountain streams, eastern USA, the genus *Enochrus* can occasionally be found among mosses, as well as the genus *Tropisternus* (Figure 16-Figure 17) (Glime 1968).

Figure 8. *Enochrus* larva, common among bog bryophytes. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 9. *Enochrus* larval head. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Figure 10. *Enochrus affinis* adult, an abundant species in Sphagnum-dominated heathland pools in North Hampshire, UK. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 11. Heathland with a pool. Photo by Jim Champion, through Creative Commons.

Figure 12. *Enochrus coarctatus* adult, an inhabitant of mire pools, often among Sphagnum. Photo by Udo Schmidt, with permission.
Figure 13. *Enochrus ochropterus* adult, a species of rich mires, often associated with *Sphagnum*. Photo by Niels Sloth, with permission.

Figure 14. *Enochrus fuscipennis* adult, a species that lives in *Sphagnum*-filled shallow pools in blanket bogs. Photo by James K. Lindsey, with permission.

Figure 15. *Enochrus hamiltoni* adult, a dweller of wet mosses next to small streams on Prince Edward Island, Canada. Photo by Tom Murray, through Creative Commons.

Figure 16. *Tropisternus* sp. larva, an occasional moss inhabitant in Appalachian Mountain, USA, streams. Photo by Tom Murray, through Creative Commons.

Figure 17. *Tropisternus natator* adult, an occasional moss inhabitant in Appalachian Mountain, USA, streams. Photo by Donald S. Chandler, with permission.

The genus *Laccobius* (Figure 18-Figure 19) associates with mosses in both stream and mire habitats. *Laccobius reflexipennis* (see Figure 18) live in wet mosses next to small streams on Prince Edward Island, Canada (Majka 2008). *Laccobius atratus* in Ireland and Great Britain occurs in *Sphagnum* (Figure 51) bogs and other peatlands (Friday 1987; Nelson 1996; Denton 2013). *Laccobius ytenensis* adults live among mosses around the tiny pools that occur in the seepage lines of UK bogs (Denton 2013).

Figure 18. *Laccobius* sp. adult, a genus with several species that live in water or bog mosses. Photo by Gerard Visser <www.microcosmos.nl>, with permission.

Figure 19. *Laccobius* adult with open wings showing the membranous wings under the hardened elytra. Photo by Michael Schmidt, through Creative Commons.
Chaetarthria siminulum (Figure 20) can be present in "huge" numbers among mosses at the edges of ponds (Denton 2013). It also lives among mosses in fens and in fen litter.

Figure 20. Chaetarthria siminulum adult with plastron. When the plastron is full of air, the beetle must cling to vegetation in order to descend into the water column. Photo by Gerard Visser, with permission.

Hebauer (1994) found Crenitis punctatostriata (Figure 21) in the high moors, living as a tyrphobiont. Hydrobius fuscipes (Figure 22-Figure 23) on Prince Edward Island (Majka 2008) occurs in Sphagnum (Figure 51) bogs and other peatlands.

Figure 21. Crenitis punctatostriata adult, a beetle that lives in bogs of the high moors. Photo by Udo Schmidt, with permission.

Figure 22. Hydrobius fuscipes adult, a species of Sphagnum bogs. Photo by Tim Faasen, with permission.

Figure 23. Hydrobius larval head showing large mandibles. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.

Friends are wonderful, and I recently received this story and all the images from Andrea Ares. She found an "amazing place" covered with the leafy liverwort Jungermannia vulcanicola (Figure 24-Figure 25) in Chatubomigoke Park, Gunma Prefecture, Japan. Soon she also discovered a small (6-7 mm) black beetle wending its way upon and within the "big, robust carpet" of the liverwort in this acid stream. This beetle was identified by Itouga san as Hydrobius pauper (Figure 26-Figure 28), the only member of the genus in Japan. There was not just one, but the bases of the liverworts were "full" of them.

Figure 24. Cushions of Jungermannia vulcanicola (chartreuse-colored cushions) in Chatubomigoke Park in Japan. Photo courtesy of Angela Ares.
Berosus luridus (Figure 29, Figure 30) is tyrrophilic, living among Sphagnum (Figure 51), but can also be found in other places (Tim Faasen, pers. comm.). I have found no other records of it living among Sphagnum, but it is rare in the Netherlands and may be rare elsewhere. Perhaps the Sphagnum provides a relict habitat, a safe site where conditions are still tolerable.

Figure 28. Hydrobius pauper adult. Photo by Itago san.

Berosus luridus adult on moss, a rare beetle in the Netherlands, but present in bogs among Sphagnum there. Note the air bubbles on the moss; these can be used to replenish the air supply. Photo by Tim Faasen, with permission.

Figure 29. Berosus luridus larva, a moss dweller in bogs of New Zealand. Photo by Stephen Moore, Landcare Research, NZ, with permission.
In tropical Africa, the genus *Anacaena* is probably more common than is recognized. Komarek (2004) described nine new species. Among these, four were from mosses. *Anacaena capensis* occurs among the mosses and leaf litter of mountain rivulets in South Africa. *Anacaena glabriventris* lives among mosses in small streams; *A. reducta* likewise lives among mosses in small streams, but with steep channels. *Anacaena tenella* lives among hygropetric mosses (mosses growing on vertical rock faces where a thin film of water flows) in mountain streams. *Anacaena limbata* (Figure 31) lives in wet mosses next to small streams on Prince Edward Island, Canada (Majka 2008).

*Anacaena limbata* adult, an inhabitant of wet mosses adjacent to streams. Photo by Tim Faasen, with permission.

*Anacaena globulus* (Figure 32) lives among *Sphagnum* (Figure 32) in bogs in Europe and can be collected by squeezing the moss (Buczyński et al. 2014). However, Faasen (personal communication) does not find them typically in *Sphagnum* bogs in the Netherlands, but considers them widespread, occasionally occurring in bogs.

*Helochares punctatus* (Figure 33) is an obligate mire species, living among saturated *Sphagnum*, particularly *S. cuspidatum* (Figure 34), of pools and acid flushes.

*Helochares punctatus* adult on moss. Photo by Niels Sloth, with permission.

*Nelson* (1996) found several additional species of *Hydrophilidae* in Irish mossy fens. These included *Cercyon convexiusculus* (Figure 35-Figure 36) in mossy fens. In North Hampshire, UK, Denton (2013) found this species to be abundant in detritus and rotted leaf litter, but also among mosses that bordered richly vegetated sites. *Cercyon marinus* similarly occupied mosses or decaying organic matter at the water’s edge in Ireland (Nelson 1996). *Cercyon ustulatus* (Figure 37) occurs in mossy areas of ponds and also occurs among mosses growing on sewage filter beds (Denton 2013).

*Cercyon convexiusculus* adult, an inhabitant of mossy fens. Photo by Tim Faasen, with permission.

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Hydraenidae – Minute Moss Beetles

Adults of Hydraenidae (Figure 39), known as minute moss beetles (1-3 mm length), are aquatic, but the larvae drown if completely submersed (Watson & Dallwitz 2012). Even adults are poor swimmers (EOL 2014); most eat plants, but a few are carnivorous or saprophagous (feeding on decaying organic matter) (Hydraenidae 2014). They are sparsely distributed worldwide with a concentration in Europe (EOL 2014).

Sarr et al. (2013) found that Hydraena was correlated with a moss substrate in Northwest Spain. Berthélemy (1966) found this family commonly among mosses in the Pyrénées, including Hydraena gracilis (Figure 40), H. minutissima, and H. pygmaea (Figure 41), with the latter two being considered muscicoles (thriving among mosses). He also considered Hydraena pulchella (Figure 42) and Hadrenya to be muscicoles. Nelson (1996) reported Hydraena gracilis as a common and widespread species in Britain where it lives on mossy rocks in fast-flowing streams and rivers.

Paracymus scutellaris (Figure 38) occurs among peat mosses in Ireland (Nelson 1996).
Hebauer (1994) found similar species representation from this family in middle Europe. Among the stream mosses he found *Hydraena minutissima*, *H. pygmaea* (Figure 41), and *H. pulchella* (Figure 42). Several more used mosses or algae as a substrate: *Ochthebius granulatus* (Figure 44), *O. metallescens* (Figure 45), *O. exsculptus* (Figure 46), *O. melanescens*, *O. colveranus*, and *O. halbherri*. Eggs of *Ochthebius* are either naked or somewhat covered by loosely applied silk provided by the mother; the eggs hatch in 7-10 days. In rivers in Northwest Spain, Sarr *et al.* (2013) found that *Ochthebius heydeni* was likewise correlated with a moss substrate.

**Hydraena nigrita** is a tiny beetle that lives among mosses at the edges of streams, but it will climb out if the moss is placed under water (Anderson 2014). It is considered vulnerable because of siltation and loss of habitat (Foster *et al.* 2009). *Hydraena rufipes* (Figure 43) lives among mosses (Nelson 1996; Knight 2014) and fine shingle (mass of small rounded pebbles) along rivers (Nelson 1996).
Limnus nitidus (Figure 47) is among the smallest of the water beetles and in addition to wet mud, it makes mosses in swamps and at the edges of pools and streams its home (Nelson 1996). Adults are a mere mm long, so these scavengers of dead plants and animals are easily overlooked (Hilsenhoff 1975). Eggs of this genus are either naked or somewhat covered with loosely applied silk and hatch in 7-10 days (Usinger 1956). In my studies in the Appalachian Mountain streams of the eastern US, this genus likewise occurred among submerged mosses (Glime 1968).

Figure 47. Limnus nitidus adult, one of the smallest of all water beetles and a moss dweller in swamps. Photo through United States public domain.

Hygrotus decoratus (Figure 48) lives in shallow, mossy fens in North Hampshire, UK, where mosses may provide safe sites for larvae and adults (Denton 2013). Hygrotus novemlineatus was reared with Chironomidae larvae as a food source (Nilsson 1983). Mosses were provided in the culture chamber. After a few days, the beetles laid eggs, attaching them to branches of mosses. But is this a normal substrate for egg-laying in nature? The habitat seems suitable, providing lots of Chironomidae larvae as food. This genus should be sought among bryophytes in other fens.

Figure 48. Hygrotus decoratus adult, a species of shallow mossy fens, at surface getting air. Photo by Niels Sloth, with permission.

Ptiliidae – Featherwing Beetles

This is a large, worldwide family of minute (0.3-2 mm long) beetles (Ptiliidae 2015). The egg size is half the length of the body and only one is developed at a time, permitting the female to store a large energy supply in the egg. Their wide-ranging habitats include moist leaf litter, under bark of dead trees, along sand and gravel banks of rivers and streams, beneath seaweed on beaches, in mammal nests, on dung, rotting cacti, ant and termite colonies, and other habitats containing rotting or damp organic material. And some seem to live their entire lives in bogs.

The small size of several Ptiliidae beetles – Tychobythinus bythinioides (Staphylinidae or Ptiliidae; Figure 65), Ptiliopycna moerens (Figure 49), Acrotrichis (Figure 50) – and other small beetles in bogs seems to correlate with a high incidence of parthenogenesis (reproduction from an unfertilized egg) in relict (habitat that survived from an earlier period) bogs (Dybas 1978), most likely having poor dispersal as an additional selection factor.

Figure 49. Ptiliopycna moerens adult, a parthenogenetic inhabitant of relict bogs. Photo © Stephen Luk for non-commercial use, with permission.

Figure 50. Acrotrichis sp. adult, a parthenogenetic inhabitant of relict bogs. Photo by Joyce Gross, with permission.
*Ptiliopycna moerens* is minute, less than 1.0 mm long, and lives in the northeastern United States and adjacent Canada (Dybas 1978). It lives in *Sphagnum* in bogs and swamp forests, confined within the limits of Wisconsian glaciation. Males are seemingly restricted to the northern part of the range. More southern locations have parthenogenetic females, a common character of small beetles in relict bogs. (See the chapter on Terrestrial Insects – Coleoptera for further discussion of beetles in bogs.)

**Silphidae – Large Carrion Beetles**

This family is predominantly in the Northern Hemisphere, although scattered records exist in the Southern Hemisphere (Silphidae 2015a). Ranging in size from 7-45 mm, the family is rare in the tropics where ants might out-compete them (Silphidae 2015b). As the common name implies, the family feeds on decaying organic matter. Because of this feeding behavior, forensic scientists use their stage of development to determine how long a body has been dead.

Despite the need to find new carcasses as their carcass home ages, the *Silphidae* use walking as their primary means of locomotion (Silphidae 2015b). Most of their activity occurs at night.

The *Silphidae* have a variety of defenses (Silphidae 2015b). These include color warnings from *aposematism* (use of bright colors to advertise danger or unpalatability) to *Batesian mimicry* (mimicking coloration or behavior of poisonous or unpalatable species), chemical defenses, and parental care. Many of them use camouflage, having dark colors with a mix of gold, black, and brown to blend with their environment.

Some carrion beetles (*Silphidae*) occur in bogs. Beninger and Peck (1992) described the resource use by *Nicrophorus* species (carrion beetles, *Silphidae*) in a *Sphagnum* (Figure 51) bog near Ottawa, Canada, and found that resource use differed little from resource use in forested habitats. However, *Nicrophorus vespilloides* (Figure 52) used only small carrion (Figure 53) in the bog for reproduction, whereas the closely related *N. defodiens* (Figure 54) went to the nearby forest for reproduction. Likewise, *N. sayi* (Figure 55), *N. orbicollis* (Figure 56), and *N. tomentosus* (Figure 57), also bog inhabitants, were rarely associated with the small carrion of the bog, but rather reproduced mostly in the forest.
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Figure 55. *Nicrophorus sayi* adult, a bog dweller that goes to the forest to reproduce. Photo by Tom Murray, through Creative Commons.

Figure 56. *Nicrophorus orbicollis* adult, a bog dweller that goes to the forest to reproduce. Photo by Tom Murray, through Creative Commons.

Figure 57. *Nicrophorus tomentosus* adult, a bog dweller that goes to the forest to reproduce. Photo by Tom Murray, through Creative Commons.

**Staphylinidae – Rove Beetles**

These beetles are distinctive in having short wings that cover less than half the abdomen (Bartlett 2004). This large family has about 58,000 species, ranging in size from 1 to 35 mm, but mostly 2-8 mm (Rove Beetle 2014). Distribution is worldwide, but records are lacking in vast areas of Asia and Africa. They live in every imaginable type of habitat and likewise eat everything – except living plants! There is now one exception to that – a recent discovery of a herbivore.

Like the *Carabidae*, the *Staphylinidae* are not aquatic, but likewise inhabit bogs (Boyce 2011). In Dartmoor, UK, *Gymnusa brevicollis* (Figure 58) is *stenotopic* (able to tolerate only a restricted range of habitats or ecological conditions). Its preferred habitat is saturated *Sphagnum* (Figure 51) in extremely wet acid mires where they can be found at the edge of bog pools.

Figure 58. *Gymnusa brevicollis* adult, a beetle that lives among saturated *Sphagnum* at the edge of bog pools of wet acid mires. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

*Myllaena kraatzi* (Figure 59), a nationally (UK) rare species, is restricted to very high quality acid mires with abundant bog mosses (Boyce 2011). It is collected by shaking the *Sphagnum* (Figure 51) and litter, suggesting close ties with these two substrates. *Oxypoda procerula* (Figure 60) is likewise sampled by shaking the litter and *Sphagnum*, indicating that it is directly a moss dweller.

Figure 59. *Myllaena vulpina* adult. *Myllaena kraatzi* is a rare species of high quality acid mires in the UK. Photo by Reginald Webster, Jan Klimaszewski, Georges Pelletier, and Karine Savard through Creative Commons.
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Figure 60. *Oxypoda procerula* adult, a *Sphagnum* and litter dweller. Photo by Udo Schmidt, through Creative Commons.

*Philonothus nigrita* (Figure 61) is a characteristic species in *Sphagnum*-dominated (Figure 51) acid mires (Boyce 2011). It can be found by treading on the moss cushions, causing it to float out of the saturated *Sphagnum*. *Stenus brevipennis* (see Figure 62) lives among *Sphagnum* in blanket bogs. *Stenus kiesenwetteri* (Figure 63) is rare in the UK, occurring in very wet *Sphagnum* (Butler 1886).

Unlike the other *Staphylinidae* discussed here, *Dianous coerulescens* (Figure 64) lives where water trickles over mosses and liverworts (Butler 1886).

Figure 61. *Philonothus nigrita* adult, a species that characterizes *Sphagnum*-dominated acid mires. Photo by Marko Mutanen, through Creative Commons.

Figure 62. *Stenus biguttatus* adult. *Stenus brevipennis* lives among *Sphagnum* of blanket bogs. Photo through Creative Commons.

Figure 63. *Stenus kiesenwetteri* adult, a rare beetle inhabiting very wet *Sphagnum*. Photo by Udo Schmidt, through Creative Commons.

Figure 64. *Dianous coerulescens* adult on leafy liverwort. Photo by Malcolm Storey, through Creative Commons.

The *Pselaphinae* beetles are represented along the postglacial fringe in the central and eastern United States where they inhabit *Sphagnum* (Figure 51) bogs (Reichle 1966). More than 20 species of psealphids characterize these bogs. They are relict species with specific habitat requirements and poor dispersal ability. Some have very specific temperature range requirements: *Tychobythinus bythinioides* (=*Bythinopsis tychoidea*; Figure 65), 21.5±0.81, 25.9-15.3°C; *Decarthron defectum*, 28.5±0.55, 31.4-24.0; *Pselaphus ulkei*, 19.5±0.86, 24.7-13.0; *Reichenbachia borealis* (a short-winged mold beetle; Figure 66), 21.±0.99, 26.2-14.4; *Rybaxis clavata* (Figure 67), 28.3±0.41, 29.9-25.1 (Reichle 1967). The moss microhabitats provide them with both the required near-saturation humidities and the multiple temperature ranges they require. Changes in temperature stratification regimes result in different species occurring at different seral stages in the bogs.
Scirtidae (=Helodidae) – Marsh Beetles

This is a worldwide family, but is most diverse in the temperate region (Murray 2005). The larvae live in both stagnant and flowing water where abundant decomposing plant material is present. Adults live on vegetation and on rotting vegetation. The Scirtidae are soft-bodied relative to other beetles and are slightly flattened to nearly subglobular (almost globe-shaped) (TOL 2011). Their sizes range 1-15 mm long. Some females secrete substances that may be pheromones used to stimulate males into courtship (Ruta 2008).

This is typically a beetle of open water, but in a subalpine springbrook in the southern Alps of New Zealand, Scirtidae (Figure 68) are most abundant in the moss Acrophyllum quadrifarium (=Pterygophyllum quadrifarium; Figure 69) at the edge of the inner spray zone where the mosses are saturated (Cowie & Winterbourn 1979).

Figure 65. *Tychobythinus bythinioides* adult, a minute beetle that takes advantage of the temperature and moisture stratification in a *Sphagnum* bed to meet its needs. Photo from Biodiversity Institute of Ontario, through Creative Commons.

Figure 66. *Reichenbachia borealis* adult, a minute beetle that takes advantage of the temperature stratification in a *Sphagnum* bed to meet its temperature needs. Photo by Tom Murray, through Creative Commons.

Figure 67. *Rybaxis clavata* adult, a minute beetle that takes advantage of the temperature stratification in a *Sphagnum* bed to meet its temperature needs. Photo by Tom Murray, through Creative Commons.

Figure 68. *Helodidae* adult, a beetle that is abundant among *Acrophyllum quadrifarium* in the subalpine springbrooks of the southern Alps of New Zealand. Photo from Pybio at <www.pybio.org.>, with permission.

Figure 69. *Achrophyllum quadrifarium*, a bryophyte habitat for *Helodidae* in streams in the Southern Alps of Australia. Photo by Jan-Peter Frahm, with permission.
Cyphon (Scirtidae; Figure 70-Figure 72) has been collected from wet mosses at the edge of a cold spring (Usinger 1974). Cyphon hilaris (Figure 71) in Dartmoor, UK, prefers bog pools that have Sphagnum (Figure 51) (Boyce 2011). In North Hampshire, UK, C. hilaris occurs infrequently in wetlands with peaty soils, acidic bogs, and fens (Denton 2013). Cyphon padi (Figure 72), also in North Hampshire, prefers peaty areas in wooded sites where the Sphagnum is flooded.

Elmidae – Riffle Beetles

These are small beetles (1-8 mm) (Gordon & Post 1965). The Elmidae have a distribution similar to that of the Silphidae, but there are more known locations, including southern Africa (Harrison 2009). As the common name describes, these beetles usually live in the riffles of cool, rapid streams (Arnett et al. 2002; Harpootlian 2005). They feed mostly on decaying plants and algae (Epler 2010).

Only three species of Elmidae are considered to be frequent aquatic bryophyte dwellers: Promoresia tardella (Figure 73), Atractelmis wawona (Figure 74), and Cleptelmis addenda (Figure 75) (Brown 1972; Shepard & Barr 1991; Bowles et al. 2003; Elliott 2008a), all from North America where the family has many more species (80 species) than in Europe (46 species) (Elliott 2008a). But if one looks among the liverworts in the Pacific states of USA, a fourth genus, Bryelmis (Figure 108-Figure 110) is lurking (Bowles et al. 2003 – see below); further searching among submerged leafy liverworts may expand this Bryelmis distribution. Nevertheless, a number of species use bryophytes at some stage in their lives. Both larvae and adults of some Elmidae are able to feed on mosses (Usinger 1974). When disturbed, Elmidae may play dead for a number of hours before attempting to relocate (Usinger 1956). Cleptelmis (Figure 75) may wait for 12-15 hours before moving. Such patience!
Elmidae colonize mosses when insect-free mosses are introduced, but some of the elmids may be slow to colonize. This is no surprise since they creep and don't swim. For example, Maurer and Brusven (1983) found that the elmid *Cleptelmis ornata* (Figure 76) was the only insect that was slow to colonize insect-free test clumps of *Fontinalis neomexicana* (Figure 77) during a field experiment in Idaho, USA.

Elliott (2008a) summed up some of the characters that define the bryophyte dwellers. Their larvae have a triangular cross section. Among this group he included *Elmis* (Figure 87-Figure 86), *Esolus* (Figure 84-Figure 85), and *Oulinnius* (Figure 88-Figure 89), none of which were considered by earlier researchers mentioned above to be the frequent bryophyte dwellers. All members of the family have aquatic larvae and most have aquatic adults. The pupae are terrestrial. This means that the newly emerged adults must re-enter the water – no small feat for such a small insect. They must break through the surface tension – easy for us, but nearly impossible for them unless they have something to cling to and provide leverage for them to break through (see Figure 78). Bryophytes, plants, and rocks can help here.

The aquatic adults use the plastron for oxygen availability (Thorpe & Crisp 1949) – they are air breathers. The plastron apparatus is seen as a silvery layer (Figure 79) on the ventral side of the beetle. Some members include the antennae as part of the apparatus that holds the air bubble. They groom the plastron with brushes on the femur of the leg and also use these brushes to add air bubbles to the plastron apparatus by smearing bubbles over the plastron. Most do not need to return to the surface, using the mouthparts to capture oxygen bubbles emitted by plants. If the plastron air layer is thick, it has a silvery sheen and is called a macroplastron (Figure 116). When air diminishes from the macroplastron to the normal, smaller plastron, air exchange with the water is generally adequate to maintain the duller-looking air bubble and meet their needs. This low need for fresh air is likely possible because these beetles do not swim, requiring less oxygen for their clambering movements.

In a tributary of the Danube, *Elmis maugtii* and *Riolus subviolaceus* (Figure 80) were abundant in high flow areas among coarse mosses, whereas *Esolus parallelepipedus* (Figure 81) and *Limnius volckmari* (Figure 82-Figure 83) were among algae in moderately flowing water (Dietrich & Waringer 1999). *Esolus*...
angustatus (Figure 84-Figure 85) and Oulimnius tuberculatus (Figure 88-Figure 89) were more common in moderate flow with abundant moss-covered pebbles.

Figure 82. Limnium volckmari larva, an elmid that seems to prefer algae to mosses as a substrate. Photo by Urmas Kraus, with permission.

Figure 79. Riolus subviolaceus adult with thin plastron showing as a silver line where the elytra meets the ventral plastron. Photo by Tim Faasen, with permission.

Figure 80. Riolus subviolaceus adult, inhabitants of high flow areas among coarse mosses. Photo by Tim Faasen, with permission.

Figure 81. Esolus parallelepipedus adult, a species with a high drift rate. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 83. Limnium volckmari adult, an elmid that seems to prefer algae to mosses as a substrate. Photo by Urmas Kraus, with permission.

Figure 84. Esolus angustatus larva, member of a genus that has the triangular cross section that characterizes many bryophyte dwellers. Photo by Tim Faasen, with permission.

Figure 85. Esolus angustatus adult, member of a genus that is common among bryophytes. Photo by Tim Faasen, with permission.
In British streams and rivers, *Elmis aenea* (Figure 86-Figure 87), a moss dweller in rapid streams and rivers (both above and below water), occurred among bryophytes as both adults and larvae, but larvae were more abundant among small stones or under larger ones (Elliott 2008a). In these rivers and streams, *Oulimnius tuberculatus* (Figure 88-Figure 89) preferred tracheophytes.

In a 39-month study, Elliott (2008b) examined the effect of density on drift rate. Most of the larvae and adults of *Elmidae* drift at night with very few drifting in daytime. Elliott found that the *Elmidae* in the study, including the bryophyte dwellers, did not drift on the basis of density. Drift losses accounted for only about 0.07% of total losses in the benthos. The exception to this was the high drift, during a heavy rainfall, of early stages of immature adults of *Elmis aenea* (Figure 87), *Oulimnius tuberculatus* (Figure 88-Figure 89), and *Esolus parallelepipedus* (Figure 81), all species known from bryophytes. For *Elmis aenea*, the highest drift density was in the earliest life stage soon after egg hatching; for *O. tuberculatus* it was the start of the larval overwintering period. Frost (1942) found that *Oulimnius tuberculatus* lives among mosses (and other habitats); moving to land for pupation most likely subjects this insect to the drift.

Nelson (1996) described *Elmis aenea* (Figure 86-Figure 87) as a species from moss-covered rocks in rapid rivers and streams. Berthélemy (1966) found larvae (Figure 86) and adults (Figure 87) of *E. aenea* and *E. maugetii* were often abundant among mosses and liverworts in the Pyrénées. The moss-dwelling species were generally smaller than those among stones. Nelson found that the proportion of *E. aenea* vs *E. rioloides* (Figure 90) among mosses was related to elevation.

Gurtz and Wallace (1984) found larvae of the elmid *Promoresia* in only one sample in Big Hurricane Branch.
They had learned from J. Haefner (personal communication) that these larvae in Sawmill Branch occurred almost exclusively among aquatic mosses (Haefner & Wallace 1981). I found *Promoresia elegans* (Figure 91-Figure 92) frequently among the bryophytes [*Fontinalis dalecarlica* (Figure 93-Figure 94), *Hygroamblystegium fluviatile* (Figure 95), *Scapania undulata* (Figure 112)] of Appalachian Mountain, USA, streams. This is a genus that exhibits the triangular cross section that Elliott (2008a) suggested to be characteristic of bryophyte dwellers.

Figure 91. *Promoresia elegans* adult, a common stream moss inhabitant. Photo through Creative Commons.

Figure 92. *Promoresia elegans*, a larva that is common among bryophytes. Photo by Erin Hayes-Pontius, through Wikimedia Commons.

Figure 93. Riffles with *Fontinalis dalecarlica*, home for *Promoresia elegans*. Photo by Janice Glime.

In addition to *Elmis*, Berthélemy (1966) found *Riolus cupreus* (Figure 96-Figure 97), *Esolus parallelepipedus* (Figure 81), and *Oulimnius tuberculatus* (Figure 88-Figure 89) among mosses in streams in the Pyrénées. *Elmis* and *Oulimnius* were strong *muscicoles* (living among or in association with mosses). Hebauer (1994) found *Elmis obscura*, *E. rioloides* (Figure 90), and *Oulimnius tuberculatus* among mosses in streams in Central Europe.

Figure 94. *Fontinalis dalecarlica* showing the dangling streamers. Photo by Jan-Peter Frahm, with permission.

Figure 95. *Hygroamblystegium fluviatile*, home to several species of *Elmidae*. Photo by Janice Glime.

Figure 96. *Riolus cupreus* larva, an inhabitant of Pyrénées stream mosses. Photo by Urmas Kruus, with permission.
Figure 97. *Riolus cupreus* adult, an inhabitant of Pyrénées stream mosses. Photo by Urmas Kruus, with permission.

The Elmidae spend their larval life in the water, pupate on land, then after their initial dispersal flight they return to the water. The interesting note here is that once they return to the water, they lose their ability to fly (Ward 1992). This locks them into their habitat no matter what the water conditions. For those inhabiting stream mosses, this means that if the water level drops, they must remain in the habitat of the mosses, unable to disperse for any significant distance. But for them it seems to be no problem because they have a high drought tolerance (Larimore et al. 1959; Iverson et al. 1978).

Steffan (1961) suggested that the mosses such as *Fontinalis* (Figure 94) were necessary for some Elmidae and Dryopidae to make the transition from water to land (and back to the water) during their amphibious life. Bryophytes would permit them to gain a firm hold while breaking through the surface tension in either direction.

In Louisiana, USA, the endangered riffle beetle *Heterelmis comalensis* (Figure 98-Figure 99) lives on submerged roots and aquatic mosses (Barr & Chapin 1988). In this same habitat, *Microcylloepus pusillus* (Figure 100-Figure 101) likewise uses these substrata. In the Appalachian Mountain streams, USA, I found a species of *Microcylloepus* among the submerged mosses (Glime 1968).
My experience with *Elmidae* among the stream bryophytes in the Appalachian Mountains, USA, differs from that in many of the reports cited here (Glime 1968). I found six species, and among these only *Microcylloepus* (Figure 100-Figure 101) and *Promoresia elegans* (Figure 91-Figure 92) (both larvae and adults) have been reported in the other studies cited herein. The numbers of *Promoresia elegans* actually exceeded the numbers of *Chironomidae* among bryophytes in one stream in March; in winter I found only two adults. In addition I found two species of *Optioservus* (Figure 102-Figure 103) on *Hygroamblystegium fluviatile* (Figure 95); on *Fontinalis dalecarlica* (Figure 93-Figure 94), I found *Stenelmis crenata* (Figure 105-Figure 104) and one species of *Dubiraphia* (Figure 106-Figure 107).

It is no surprise that new species remain to be discovered among the bryophytes. But one such recent discovery in the western states of the USA was not just a new species, but a new genus, widespread, and with multiple species! And these were among aquatic bryophytes, particularly leafy liverworts (Barr 2011). These three species were *Bryelmis idahoensis* (Figure 108), *B. rivularis* (Figure 109), and *B. siskiyou* (Figure 110) from streams and springs in the states of Washington,
Oregon, California, and Idaho. Once Barr alerted her colleagues in neighboring states of her find, they began searching this new habitat, the leafy liverwort *Chiloscyphus polyanthos rivularis* (Figure 111). After searching through 652 adult and over 200 larval specimens from museum and new collections, she distinguished three species, all previously unknown. And now all these people know the difference between a moss and a liverwort – the latter houses *Bryelmis*.

**Figure 108.** *Bryelmis idahoensis* adult male, a species that seems to be restricted to leafy liverworts. Photo by Traci Grzymala, with permission.

**Figure 109.** *Bryelmis rivularis* adult male, a species that seems to be restricted to leafy liverworts. Photo by Traci Grzymala, with permission.

**Figure 110.** *Bryelmis siskiyou* adult male, a species that seems to be restricted to leafy liverworts. Photo by Traci Grzymala, with permission.

**Figure 111.** *Chiloscyphus polyanthos*, primary home to the recently discovered genus *Bryelmis*. Photo by Jan-Peter Frahm, with permission.

Barr had found *Bryelmis idahoensis* in association with aquatic bryophytes on rocks, but some also occurred on water-soaked wood. *Bryelmis rivularis* preferred *Chiloscyphus polyanthos rivularis* (Figure 111) and *Scapania undulata* (Figure 112) and tended to avoid both of the mosses *Fontinalis neomexicana* (Figure 77) and *Platyhypnidium riparioides* (Figure 113). By targeting aquatic liverworts she discovered another new species, *B. siskiyou*.

**Figure 112.** *Scapania undulata*, home for some members of *Bryelmis*. Photo by Hermann Schachner, through Creative Commons.

**Figure 113.** *Platyhypnidium riparioides*, a habitat rejected by *Bryelmis*, a leafy liverwort inhabitant. Photo by Hermann Schachner, through Creative Commons.
In Mexico, Central America, and the West Indies, *Lara avara* (Figure 114-Figure 115) spends 4-6 years as larvae, going through seven instars (Spangler & Santiago-Fragoso 1992). The larvae leave the stream water in spring and move to mosses at the stream bank in their last instar. In their last instar they burrow into small "cells" under mosses at water's edge (Spangler & Santiago-Fragoso 1992) or under mosses on the upper surface of emergent logs (Elliott 2008a). When the moss dries in early summer the larvae begin pupation (Spangler & Santiago-Fragoso 1992). This pupation lasts only two or more weeks.

![Figure 114. *Lara avara* adult, a species that pupates among mosses. Photo through Creative Commons.](image)

![Figure 115. *Lara avara* larva, a species that crawls out of the water to pupate among mosses at the water's edge. Photo by Arlo Pelegrin, with permission.](image)

**Dryopidae – Long-toed Water Beetles**

The Dryopidae are mostly Northern Hemisphere (Dryopidae 2015), but the scant records in the Southern Hemisphere may reflect limited collecting rather than absence of beetles. This is an interesting family in that the larvae are mostly terrestrial, living in decaying plant material, rotting wood, and soil, whereas the adults (3.5-5.5 mm long) return to running water to lay eggs (Watson & Dallwitz 2003). They are unable to swim and clamber about by clinging to plants. They eat plants as adults, but larvae may also prey on small animals. The Dryopidae occur on every continent except Antarctica and Australia, but they are most common in the tropics (Dryopidae 2015). They use hairs to create a plastron apparatus (see introductory information), enabling them to breathe under water.

The Dryopidae (Figure 116) seem seldom to be reported among the bryophytes of aquatic habitats. Nevertheless, Percival and Whitehead (1930) found that the Helminae (Dryopidae) reached 1244 per dm² in the mossy area of streams in the UK, whereas among stones with no mosses they reached only 10-15 per dm². Buczyński *et al.* (2014) reported that in Poland Dryops anglicanus (Figure 117) lives in canals created by beavers in floating *

![Figure 116. *Dryops luridus* adult with plastron surrounding entire body, a macroplastron. Photo by Tim Faasen, with permission.](image)

![Figure 117. *Dryops anglicanus* adult, an inhabitant of beaver-made canals in floating *Sphagnum* mats. Photo by Stefan Schmidt, through Creative Commons.](image)

![Figure 118. *Helichus lithophilus* adult, member of a genus with bryophyte dwellers in Appalachian Mountain, USA, streams. Photo by Mike Quinn, through Creative Commons.](image)

*Sphagnum* (Figure 51) mats. In rivers of Northwest Spain, *Dryops luridus* preferred moss substrata (Sarr *et al.* 2013). In the Appalachian Mountain, USA, streams, I found a species of *Helichus* (Figure 118) (Glime 1968).
Chelonariidae – Turtle Beetles

These are relatively small beetles (adults 2.5-10 mm long) and somewhat resemble turtles in that their heads are hidden and their legs can be tucked into depressions in the abdomen made for them (Harpootlian 2006). They are best known from eastern North America, western South America, and Central America, but there are some records from eastern Asia (Chelonariidae 2015). They reach their greatest diversity in the Neotropics.

Sometimes it is hard to determine if the insects are aquatic or terrestrial. Perhaps it is just a wide niche with a wide water tolerance. In other cases, entrance into the aquatic world may be accidental. Such seems to be the case with *Chelonarium* (Figure 119), a genus that inhabits damp moss (Spangler 1980). From these damp mosses, they may occasionally get washed into the nearby stream by rain or high water (Brown 1972). The larvae, once considered aquatic, lack gills (Spangler 1980). Members of the genus are often associated with the roots of terrestrial epiphytes (plants that grow on other plants but are not parasitic) and often feed on ants and termites.

![Chelonarium lecontei](image1.png)

Figure 119. *Chelonarium lecontei* adult, a species once thought to have aquatic larvae. Note how the legs fit into the exoskeleton. Photo through Creative Commons.

Lampyridae – Lightning Bugs

"When night closes in, fireflies flicker with an ethereal and haunting light" (WWF 2011). This is the family of fireflies (Figure 120) that delighted us as children. And one of them, *Luciola ficta* (see Figure 121), lives in the water as a larva and uses mosses (Ho *et al.* 2010)! The adults court, mate, and females oviposit on mosses (or under leaf litter, in root gaps, or in soil clefts), but on land. The young hatchlings must make their way to the water. This unique Asian beetle is in danger of extinction because its habitat is disappearing. However, the Chinese are attempting to save it by learning its development (Ho *et al.* 2006) and creating small pools for it (WWF 2011).

![Lampyridae adult](image2.png)

Figure 120. *Lampyridae* adult showing the portion that lights up. Photo by Andy Deans, through Creative Commons.

![Luciola lusitanica](image3.png)

Figure 121. *Luciola lusitanica* adult. *Luciola ficta* is a species with aquatic larvae and adults that oviposit on terrestrial mosses. Photo by Tim Faasen, with permission.

Latridiidae – Minute Brown Scavenger Beetles

Minute it is, with sizes up to 3 mm (McClarin 2005). The family mostly eats fungi and slime molds, frequenting decaying vegetation (Latridiidae 2015). Records of this family are concentrated in Europe, with scattered records in North America, South America, Africa, and Australia. But this family is even present in the Antarctic region.

In South Georgia (southern Atlantic Ocean) bryophytes often play an important role as habitats for insects. One such inhabitant is *Aridius malouinensis* (Figure 122) (Arnold & Convey 1998).

![Aridius malouinensis](image4.png)

Figure 122. *Aridius malouinensis* adult, a moss dweller on the island of South Georgia. Photo by Roger S. Key, with permission.

Curculionidae – Weevils

Despite the fact that *Curculionidae* (Figure 123) is the third largest animal family (Curculionidae 2014), its presence is missing among aquatic mosses. Its distribution is worldwide, although records are lacking in vast areas of Asia and Africa (Curculionidae 2015). Adults range 1-40 mm long and are plant feeders.

![Cionus hortulanus](image5.png)

Figure 123. *Cionus hortulanus* adult, showing one of many thousands of bizarre forms present in this family. Photo by Lukas Jonaitis, through Creative Commons.
This terrestrial family has limited associations with the water. The marine weevil *Palirhoeus eatoni*, on the Prince Edward Islands south of Africa, lives among tufts of algae as larvae (Doyen 1976). When it pupates it goes above the high water level among clumps of the shoreline moss *Grimmia amblyophylla* (Jeannel 1940, 1953).

**Lagriidae**

Our records of bryophyte dwellers from Africa seem to be rare, so it is pleasing to see a study on bryophagy in South Africa (Chown 1993). Chown found that members of the *Lagriidae* in the Afromontane forest fed on both green and brown parts of the moss *Braunia secunda*. This is a family with poorly known feeding habits, and the species discovered here was unnamed.

Figure 124. *Lagria hirta* adult, a beetle that eats the moss *Braunia secunda*. Photo by Udo Schmidt, with permission.

Figure 125. *Braunia secunda*, home for some members of the *Lagriidae*. Photo by Efrain De Luna, with permission.

**Summary**

The suborder *polyphaga* includes a number of families of beetles that live among bryophytes, especially the small members.

These include *Helophoridae* that live in both bogs and streams among bryophytes. *Hydrochidae* live among bog mosaes. *Hydrophilidae* are common in bog pools, where diversity is high, but some also occur among stream bryophytes. The *Hydraenidae* are tiny beetles that live primarily among bryophytes in streams and fast rivers. Some small members of the *Ptiliidae* are *parthenogenetic* and live in *relict* bogs. The *Silphidae* are carrion feeders and those in bogs breed on small carrion such as frogs. The *Staphylinidae* are not typical bryophyte dwellers, and are not aquatic, but they live in bogs. The *Scirtidae* find suitable habitat in the saturated moses of the spray zone of the springbrooks in the Alps of New Zealand.

The best adapted family of the beetle bryophyte dwellers is the *Elmidae*. They use a *plastron* to breathe and are small enough to clamber about among the bryophyte stems and leaves. The *Dryopidae* are similarly adapted and both families can be found among stream bryophytes.

Some species of the *Chelonariidae* live among wet mosses of stream banks and seem to occasionally fall in. The species *Luciola ficta* is a firefly in the family *Lampyridae*. Its larvae live in the water and the adults deposit their eggs on mosses and other substrata near water. The *Latridiidae* are among the insects in South Georgia where one species lives among the bryophytes. The *Curculionidae* are weevils and few are associated with aquatic habitats. Some live on floating plants and one species leaves its water home to pupate among shoreline moses.

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