

# CHAPTER 12-9b

## TERRESTRIAL INSECTS: HOLOMETABOLA – COLEOPTERA FAMILIES

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# CHAPTER 12-9b

## TERRESTRIAL INSECTS:

### HOLOMETABOLA – COLEOPTERA

### FAMILIES



Figure 1. *Elaphrus* sp. on moss, a genus known to live on and among bryophytes. Photo by Bob Armstrong, with permission.

The **Coleoptera** are divided into the **Adephaga** and **Polyphaga**. This chapter has used this division and within the larger group **Polyphaga**, superfamily groupings are used. However, the order if these superfamilies and the families within them is alphabetical.

#### ADEPHAGA

Whereas five families of **Adephaga** are among the aquatic bryophyte-dwelling beetles, I know of only one family (**Carabidae**) with bryophyte dwellers among the terrestrial beetles. Nevertheless, there are a number of species among the terrestrial members of this family that live among bryophytes.

#### Carabidae – Ground Beetles

The **Carabidae** have many genera and species represented among bryophytes and were among the early reported bryophyte dwellers. For example, Westwood (1839) reported *Carabus coriaceus* (Figure 2) larvae living under mosses. Several species of *Carabus* have been

photographed on mosses, perhaps only traversing them or getting a bit of remoistening (Figure 3-Figure 5).



Figure 2. *Carabus coriaceus* adult, a species that seeks refuge among mosses. Photo by Rotatebot, through Creative Commons.



Figure 3. *Carabus cancellatus* adult on moss. Photo by Ladislav Tábi, with permission.



Figure 4. *Carabus glabratus* adult on moss. Photo by Ladislav Tábi, with permission.



Figure 5. *Carabus nemoralis* adult on moss. Photo by Ladislav Tábi, with permission.

Waterhouse (1871) reported *Bradycellus collaris* (Figure 6) from mosses. Later, Lindroth (1974) reported that *Bradycellus sharpi* (Figure 7) lives under leaves and mosses in shady places, usually near water. Luff (1998) noted that *Bradycellus csikii* (Figure 8) occurs on mosses and other substrata in Central Europe.



Figure 6. *Bradycellus collaris* adult on *Sphagnum*. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 7. *Bradycellus sharpi* adult with moss where it dwells near water. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 8. *Bradycellus csikii* adult, a moss dweller in Central Europe. Photo through Creative Commons.

In Japan, Bates (1883) reported *Leistus subaeneus* living under forest mosses at high elevations and *Leistus obtusicollis* occurs in mosses on the trunks of *Cryptomeria*. In Europe, *Leistus rufomarginatus* (Figure 9) and *L. ferrugineus* (Figure 10) occur among mosses (Lindroth 1974).



Figure 9. *Leistus rufomarginatus*, a moss dweller in Europe. Photo by Niels Sloth <www.biopix.com>, with permission.



Figure 10. *Leistus ferrugineus*, a moss dweller in Europe. Photo by František Šaržík, through Public Domain.

This family has 40,000 species worldwide and are among the 10 largest families of animals worldwide (Wikipedia 2015a). Common habitats are under the bark of trees, under logs, or among rocks or sand by the edge of ponds and rivers. Most species are active nocturnal carnivores. Some are able to run swiftly to catch prey, up to  $9 \text{ km h}^{-1}$  (Friedlander 1998). They are larger than most moss-dwelling beetles and most don't seem to have any camouflage adaptations. Rather, these most likely visit the mosses to find food organisms and to replenish moisture.

Many members of the family overwinter under mosses (Anonymous 1879). This habit of overwintering under mosses serves for *Elaphrus fuliginosus* (Figure 11) and *E. clairvillei* (Figure 12) in low woodlands (Kilman 1889).



Figure 11. *Elaphrus fuliginosus*, a species that overwinters under mosses. Photo by Yves Bousquet, through Creative Commons.



Figure 12. *Elaphrus clairvillei* adult, a species that hibernates under mosses in winter. Photo by Gimenez de Cordoba, Beatriz through Creative Commons.

Unlike the many tiny beetles with limited distribution, many of these species are widespread. *Pterostichus diligens* (5-7 mm; Figure 13) is numerous among mosses, widespread (Eurasian Boreo-temperate), and common in wet heath, mire, and grass tussocks (Stenhouse 2007). *Pterostichus strenuus* (Figure 14) stays in shady places, especially damp deciduous forests on clayish soil, where it lives among mosses and leaf litter (Lindroth 1974). *Ocys harpaloides* (4-6 mm; Figure 15) is widespread among mosses in the UK (Stenhouse 2007) and along the European and African Atlantic coast (Anderson *et al.* 2000).



Figure 13. *Pterostichus diligens* adult, a species that is numerous among mosses in mires in the UK. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 14. *Pterostichus strenuus* adult, a species of shady places, especially damp deciduous forests on clayish soil, where it lives among mosses and leaf litter. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 16. *Notiophilus germinyi* adult on *Sphagnum*. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 15. *Ocys harpaloides* adult on moss, a widespread moss-dweller in the UK. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 17. *Blethisa multipunctata* adult, a moss inhabitant. Photo ©Roy Anderson <habitas.org.uk>, with permission.

One of the more comprehensive treatments of the **Carabidae** is that of Lindroth (1974). He cited many species that live among mosses in the British Isles. These include *Notiophilus germinyi* (Figure 16) among mosses in the open; *Blethisa multipunctata* (Figure 17) with mosses and *Carex*; *Elaphrus lapponicus* (Figure 18) on wet mosses near wells and streams and in bogs; *Asaphidion pallipes* (Figure 19) on fine, slightly moist sand with patches of "tiny moss;" *Miscodera arctica* (Figure 20) on fine, dry sand with fine mosses; *Platyderus depressus* (Figure 21) in open country among leaves and mosses; *Amara communis* (Figure 22) under mosses and dry leaves in a wide range of open habitats and forests with light shade; *Amara lunicollis* (Figure 23) in similar shade situations on peaty soil and under moss carpets of rocks; *Harpalus pimalicus* (see Figure 24) among mosses and leaves under bushes and trees on gravel moraines; *Badister unipustulatus* (Figure 25) among leaves and mosses on moist, shaded places, typically near pools; and *Syntomus obscuroguttatus* (Figure 26) in moist habitats on heavy soil among mosses.



Figure 18. *Elaphrus lapponicus*, a species of bogs and wet mosses. Photo by Gimenez de Cordoba, Beatriz through Creative Commons.



Figure 19. *Asaphidion pallipes* adult on mosses; this species occurs on sand with patches of tiny mosses, as shown here. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 22. *Amara communis* adult, a species that lives under mosses and dry leaves. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 20. *Miscodera arctica* adult on leafy liverwort. This species lives on fine, dry sand with fine mosses. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 23. *Amara lunicollis* adult, a species of peaty soil or under moss carpets of rocks. Photo by Tom Murray, through Creative Commons.



Figure 21. *Platyderus depressus*, a litter and moss inhabitant. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 24. *Harpalus rufipes* adult. *Harpalus pimalicus* lives among mosses and leaves under bushes and trees on gravel moraines. Photo by Rasbak, through Creative Commons.



Figure 25. *Badister unipustulatus* adult, a species that lives among leaves and mosses near pools. Photo by Gábor Keresztes (xespok.net), with permission.



Figure 26. *Syntomus obscuroguttatus* adult, a species that lives among mosses in moist habitats. Photo by Brian Eversham, with permission.

Such widespread species as *Notiophilus biguttatus* (Figure 27) will traverse mosses in some of their habitats as they travel across the terrain. They may find cover there from the sun, search for food, gain moisture, or even take a drink, but they do not necessarily live there.



Figure 27. *Notiophilus biguttatus* adult on moss. Photo by Ladislav Tábi, with permission.

*Trechus rivularis* (Figure 28) occurs among mosses in lowland fens and upland mires of northern and eastern Europe (Luff 1998). *Patrobus septentrionis* (Figure 29) lives near water as well, living among mosses in the UK, but at lower elevations in other parts of its circumpolar distribution. Its widespread distribution is most likely facilitated by its ability to fly.



Figure 28. *Trechus rivularis* adult, an inhabitant of lowland fen mosses and upland mires. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 29. *Patrobus septentrionis*, a species that lives among mosses near water. Photo ©Roy Anderson <habitas.org.uk>, with permission.

The genus *Agonum* has a number of bryophyte-dwelling species (Lindroth 1974), occurring in the Holarctic and Mediterranean regions to a southern limit in Central Asia (Wikipedia 2015b). These beetles are small to mid-sized and often have a metallic sheen. *Agonum obscurum* (Figure 30) lives among leaves and mosses in

damp deciduous forests and densely vegetated marshes (Lindroth 1974). The very **hygrophilous** (water-loving) *A. livens* (Figure 31) lives in marshy deciduous forests among leaves and *Sphagnum*. *Agonum versutum* (Figure 32) lives at the margin of fresh water where it keeps sufficiently moist among mounds of the sedge *Carex* and mosses. *Agonum fuliginosum* (Figure 51) lives among mosses and leaves in moist, shady places under bushes and forest trees. *Agonum gracile* (Figure 33) likewise lives in very damp, shady places such as quagmires with *Sphagnum* (Figure 35-Figure 36) and mossy lake shores. *Agonum sexpunctatum* (Figure 34) lives in wet peatlands in Europe (Wikipedia 2015c). It also occurs on moist, mossy ground near water where low, mossy vegetation occurs, including damp patches in otherwise sandy heathland in Europe (Luff 1998).



Figure 30. *Agonum obscurum* adult, a species typical of leaves and mosses in damp deciduous forests and densely vegetated marshes. Photo by Brian Eversham, with permission.



Figure 31. *Agonum livens* adult, a species of marshy deciduous forests among leaves and *Sphagnum*. Photo by Brian Eversham, with permission.



Figure 32. *Agonum versutum* adult, a species at the margin of fresh water among the sedge *Carex* and mosses. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 33. *Agonum gracile* adult, a species of quagmires with *Sphagnum* and mossy lake shores. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 34. *Agonum sexpunctatum* adult on mosses, a species that seems to be tied to bryophytes in its habitat. Photo by Christoph Benisch <www.kerbtier.de>, with permission.



In comparing *Sphagnum* bog habitats (Figure 35) on several continents, Främbs (1994) considers the open *Sphagnum* mat to be an extreme habitat with only a few carabid species. Furthermore, the behavior of *Agonum ericeti* (Figure 36) and *Pterostichus rhaeticus* (Figure 37) indicates that the carabids may only use the damp *Sphagnum* lawn habitats in the summer, moving to drier hummocks (Figure 38) to overwinter. In fact, these two species of ground beetles are scarce in bog areas in which there is no clear pattern of hummocks and hollows to allow them to escape the water.



Figure 35. *Sphagnum* in Turbal in Valle de Andorra in the east Pyrenees. Photo through Creative Commons.



Figure 36. *Agonum ericeti* adult on *Sphagnum*, its summer habitat. Photo by Niels Sloth <www.biopix.dk>, with permission.



Figure 37. *Pterostichus rhaeticus* on wet mosses. Photo by Christoph Benisch <www.kerbtier.de>, with permission.



Figure 38. *Sphagnum papillosum* and *Sphagnum capillifolium* forming a hummock where Carabidae can spend the winter. Photo by Janice Glime.

The carabid species *Carabus menetriesi* (Carabidae) is associated with *Sphagnum* (Figure 35) in northern Europe and northern Russia (Barbara Knoflach-Thaler, pers. comm. 9 June 2011). It is an **FFH-species** (endangered all over Europe) and needs *Sphagnum* for overwintering; otherwise it would disappear. *Carabus arvensis* (Figure 39) hibernates under mosses as well as tree stumps (Lindroth 1985). *Carabus glabratus* (Figure 40), a widespread species of central and northern Europe, is day active and prefers damp areas such as peat hummocks (Figure 38) and other mosses (Weiss-Roessler 2015).



Figure 39. *Carabus arvensis*, a species that hibernates under mosses. Photo by Christoph Benisch <www.kerbtier.de>, with permission.



Figure 40. *Carabus glabratus* adult on moss, a species that prefers damp areas such as peat hummocks and other mosses. Photo by Stanislav Krejčík, through Creative Commons.

*Carabus clathratus* (23-24 mm; Figure 41), a widespread Palearctic species, is day active and lives an amphibious life style, including under mosses (Obydov 2006), diving under water to search for food. Its larvae develop in the summer and it overwinters as an adult to breed in early to late summer (Wallin *et al.* 1999). This overwintering can be far from water where it hibernates on drier land.



Figure 41. *Carabus clathratus* adult on *Sphagnum*. Photo ©Roy Anderson <habitas.org.uk>, with permission.

In Finland, several species of **Carabidae** live in *Sphagnum* habitats (Figure 41) (Ljungberg 1999; Wallin *et al.* 1999). Among these is *Chlaenius costulatus* (striped velvet runner, hairy ground beetle; Figure 42; Figure 43). This species is a 13-14 mm predator. In other European mires, with mosses like *Drepanocladus* (Figure 44), one can find *Chlaenius sulcicollis* (swamp velvet runner; Figure 45). In Sweden, *Chlaenius sulcicollis*, a species of Europe and Asia north to the Arctic Circle, is a critically endangered species that lives among *Sphagnum* in bogs (Wallin *et al.* 2000). *Chlaenius nigricornis* (Figure 46) lives in sheets of mosses in damp places (Bates 1843). *Chlaenius nitidulus* (Figure 47) lives among grasses and mosses in silty and damp places along the coast (Lindroth 1974).



Figure 42. *Chlaenius* sp. larva, frequently a moss dweller. Photo by Tom Murray, through Creative Commons.



Figure 43. *Chlaenius costulatus* adult, a *Sphagnum* inhabitant. Photo by Tim Faasen, with permission.



Figure 44. *Drepanocladus aduncus*, home for several beetle species in the Czech Republic. Photo by Heike Hofmann ©swissbryophytes <swissbryophytes.ch>, with permission.



Figure 45. *Chlaenius sulcicollis* adult, a species found in *Drepanocladus* in mires. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.



Figure 46. *Chlaenius nigricornis* adult on moss like the sheet mosses where it lives. Photo by Niels Sloth <www.biopix.dk>, with permission.



Figure 47. *Chlaenius nitidulus* adult, a coastal species that lives among grasses and mosses in silty and damp places. Photo by Gernot Kunz, with permission.

In other European mires with mosses like *Drepanocladus* (Figure 44), one can find *Panagaeus cruxmajor* (great cross runner; 8-10 mm; Figure 48). The Wikipedia author for this family recounted this from Charles Darwin (1846), regarding his attempted capture of *Panagaeus cruxmajor*:

"I must tell you what happened to me on the banks of the Cam in my early entomological days; under a piece of bark I found two carabi (I forget which) and caught one in each hand, when lo and behold I saw a sacred *Panagaeus crux major*; I could not bear to give up either of my carabi, and to lose *Panagaeus* was out of the question, so that in despair I gently seized one of the carabi between my teeth, when to my unspeakable disgust and pain the little inconsiderate beast squirted his acid down my throat and I lost both carabi and *Panagaeus*!"

In European mires with mosses like *Drepanocladus* (Figure 44), one can find *Agonum hypocrita* (lacquer runner; Figure 49). In Finnish boreal forests, *Sphagnum* (Figure 41) is a refuge for some carabids following cutting of the forests (Figure 50) (Koivula 2001). *Agonum fuliginosum* (Figure 51), *Amara brunnea* (Figure 52), *Carabus glabratus* (Figure 53), *Carabus hortensis* (Figure 54), *Cychrus caraboides* (Figure 55), and *Pterostichus niger* (Figure 56) were almost exclusively in the *Sphagnum* mires after cutting. On the other hand, *Calathus micropterus* (Figure 57) did not inhabit the mires and diminished in numbers after cutting, presumably due to

increased exposure. *Platynus mannerheimii* (Figure 58) likewise disappeared after clearcutting, but distribution of *Agonum fuliginosum* is not affected by canopy cover, permitting it to survive in the more open *Sphagnum* mires. Hence, the *Sphagnum* provides a refugium that can permit at least some of the **Carabidae** to re-inhabit the forest when it regrows.



Figure 48. *Panagaeus cruxmajor* adult, a species found in *Drepanocladus* in mires. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 49. *Agonum hypocrita* adult, a bog dweller. Photo by Marko Mutanen, through Creative Commons.

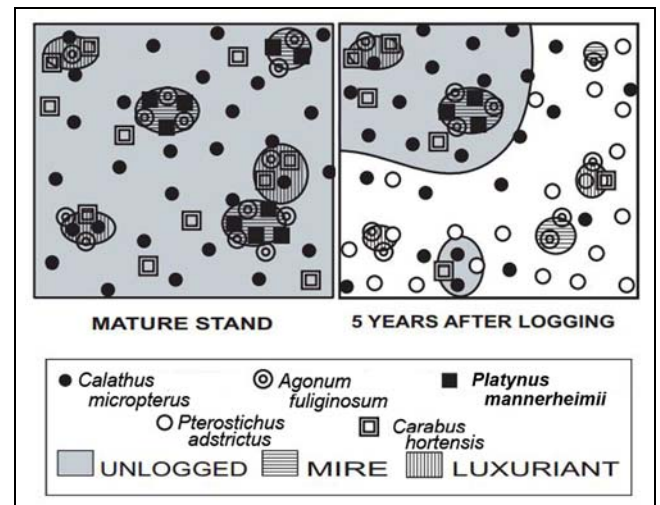


Figure 50. Response in abundance of major **Carabidae** species following clearcut logging in a mature spruce forest with three mires and three "luxuriant" sites. Modified from Koivula 2001.



Figure 51. *Agonum fuliginosum* adult, a species that associates with *Sphagnum* in boreal forests. Photo by Niels Sloth <www.biopix.dk>, with permission.



Figure 52. *Amara brunnea* adult, a species that associates with *Sphagnum* in boreal forests. Photo by Niels Sloth <www.biopix.dk>, with permission.



Figure 53. *Carabus glabratus* adult on moss. Photo by Dodoni, through Creative Commons.



Figure 54. *Carabus hortensis* adult, a moss dweller shown here on moss. Photo from <brouci.fotobarvinek.cz>, for non-commercial use.



Figure 55. *Cychrus caraboides* adult on moss, a species that uses *Sphagnum* as a refuge following forest disturbance. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 56. *Pterostichus niger* adult, a moss dweller shown here on moss. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 57. *Calathus micropterus* adult on moss in forest. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 58. *Platynus mannerheimii* adult, a species that is unable to live in mires and thus disappears after clearcutting. Photo by Derek Sikes, through Public Domain.

It is unusual for any invertebrate to show host specificity among the bryophytes, although some bryophytes are certainly avoided by many bryophagous species. However, the carabid beetle *Acupalpus dubius* (Figure 59) seems to be restricted to the wetland moss *Drepanocladus aduncus* (Figure 44), at least in one study in the Czech Republic (Kopecký 2001). On the other hand, *A. brunripes* (Figure 60) and *A. flavicollis* (Figure 61) seem to lack such specificity (Luff 1998). *Acupalpus brunripes* occurs in both mosses and litter on mud near water in northern and western Europe, Greece, and North Africa. *Acupalpus flavicollis* sometimes occurs in bogs, but it is more common on river banks and in gravel pits in fine silt-covered sand where there is sparse vegetation and some mosses.

Cold temperatures seem to preclude most *Carabidae*. In the geothermal areas of Iceland, some of the geothermal areas are covered by the mosses *Archidium alternifolium* (Figure 62) and *Campylopus introflexus* (Figure 94) and the leafy liverwort *Gymnocolea inflata* (Figure 63) (Elmarsdottir *et al.* 2003). In some of these hotter areas, the carabids *Bembidion bipunctatum* (Figure 64) and *Nebria rufescens* (Figure 65) could survive, whereas they were not present in the colder, non-geothermal areas. Lindroth (1974) reported *Nebria brevicollis* (Figure 66)

among mosses in UK forests and Barry (2014) found it under moss in a flower bed.



Figure 59. *Acupalpus dubius* adult on liverwort, a beetle that lives among *Drepanocladus aduncus* in the Czech Republic. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 60. *Acupalpus brunripes* adult, a species that lives among mosses and litter on mud near water. Photo by Wim Rubers, through Creative Commons.



Figure 61. *Acupalpus flavicollis* adult, a species that sometimes occurs in bogs as well as river banks and in gravel pits where there are some mosses. Photo by Tim Faasen, with permission.



Figure 62. *Archidium alternifolium*, a geothermal moss that supports several species of *Carabidae*. Photo by Michael Lüth, with permission.



Figure 63. *Gymnocola inflata* with perianths, a geothermal leafy liverwort that supports several species of *Carabidae*. Photo by Malcolm Storey, through Creative Commons.



Figure 64. *Bembidion bipunctatum*, moss inhabitants in geothermal areas of Iceland. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 65. *Nebria rufescens* adult, a species that takes advantage of geothermal mosses in cold regions. Photo ©Roy Anderson <habitas.org.uk>, with permission.



Figure 66. *Nebria brevicollis* adult with moss, a species known to occur under mosses. Photo by Fritz Geller-Grimm, through Creative Commons.

Elsewhere, in the UK, *Bembidion gilvipes*, *B. biguttatum*, and *B. mannerheimii* live among mosses (Lindroth 1974). The first two of these live in forests. *Bembidion mannerheimii* lives in forests and fens. All three species also live among leaf litter and other substrata as well. Darwin even reported the genus from a nest of mosses (Smith & Freeman 1987).

The *Carabidae* are generalist feeders, suggesting they should be able to find food among any of the bryophytes, including fungi, bacteria, detritus, and various invertebrates (König *et al.* 2011). Thus far there seems to be no evidence that they eat the bryophytes.

## POLYPHAGA

### Artemotopoidea

#### Artematopidae – Soft-bodied Plant Beetles

Larvae and adults of beetles often live in different places. And if they are both in the same aquatic habitat, the pupae are typically on land. Even among the terrestrial bryophytes, the physiology and morphology differ sufficiently that many prefer different habitats. On the other hand, many are flightless, restricting their ability to move around.

Such habitat difference seems to be the case for members of *Macropogon*. Adults of *Macropogon testaceipennis* (Figure 67) and *M. piceus* (Figure 68) in western Washington and Oregon, USA, usually live on trees and shrubs near moss-covered boulders or rock outcrops (Loren Russell, pers. comm.). *Macropogon* larvae, on the other hand, can be found under mosses such as *Ceratodon purpureus* (Figure 69) and others growing on sandy loam of a stream bank in Viento State Park, Oregon.



Figure 67. *Macropogon testaceipennis* adult, a species that seems to prefer trees and shrubs with moss-covered rocks nearby. Photo by Joyce Gross, with permission.



Figure 68. *Macropogon piceus*, a species whose adults seem to prefer trees and shrubs with moss-covered rocks nearby. Photo by Jim McClarin, with permission.

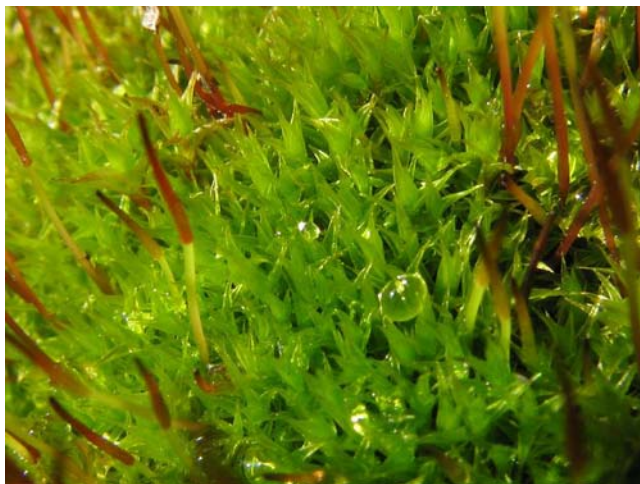


Figure 69. *Ceratodon purpureus*, home for larvae of *Macropogon* species. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Larvae of another member of this family, *Eurypogon* cf. *californicus* (Figure 70), occur under mosses growing on exposed rocks of road cuts at Mary's Peak, Oregon, and near the Alsea River (Loren Russell, pers. comm.).



Figure 70. *Eurypogon californicus*, species that lives under mosses on exposed rocks. Photo from Museum of Comparative Zoology, Harvard, through Creative Commons.

## Byrrhoidea

### Byrrhidae – Pill Beetles

The **Byrrhidae** are known for their habit of living among mosses. Not only do they live there, but the mosses serve as their food source in most cases (pers. comm. Loren Russell & Paul Johnson, 21 March 2012). A few actually feed on liverworts, and some on **tracheophytes** (lignified vascular plants, including flowering plants). In the Pacific Northwest, USA, the genus *Amphicyrta* (Figure 71) is the only member of the family known to feed on tracheophytes and no bryophytes, becoming a pest in lily fields. But generally, members of this family are adapted to living in transitional **ruderal** (wasteland) microhabitats where mosses dominate (Majka & Langor 2011), including such open habitat mosses as *Ceratodon purpureus* (Figure 69), *Polytrichum juniperinum* (Figure 72), and *P. piliferum* (Figure 73) growing on moist, thin or scarified soil (Johnson 2002).



Figure 71. *Amphicyrta* sp. adult, an unusual member of **Byrrhidae** not known to eat bryophytes. Photo by Joyce Gross, with permission.



Figure 72. *Polytrichum juniperinum* with males, common home for **Byrrhidae**. Photo by Dale Vitt, with permission.



Figure 73. *Polytrichum piliferum*, common home for **Byrrhidae**. Photo by Thomas Brown, through Creative Commons.

Several of the byrrhid characteristics suit them for the moss habitat. Their small size (1-10 mm) (Johnson 2002) and convex, compact shape, and retractile appendages (Johnson 2013) permit ease of movement among the moss maze and make them inconspicuous to most predators. When detected, they have the ability to play dead by retracting their legs and antennae into grooves on the lower surface (Figure 74-Figure 75), remaining motionless (Lindquist & Ingram 1968). This motionless behavior along with their shape has earned them the common name of pill beetles. Their ability to subsist on mosses suggests that they may have special digestive adaptations as well.

The **Byrrhidae** are common farther north and at higher altitudes than most of the insects. Majka and Langor (2011) suggest that this may be possible due to their ability to eat bryophytes. The bryophyte species diversity changes little with latitude (Shaw *et al.* 2005), whereas tracheophyte diversity diminishes. Furthermore, most bryophytes have longer growing seasons than most tracheophytes and are available immediately upon snow melt as a source of food. We know that bryophytes produce **arachidonic acid** (a fatty acid) (Shinmen *et al.* 1991; Kajikawa *et al.* 2008) and it would be interesting to explore whether the arachidonic acid in bryophytes may help to keep membranes of bryophyte consumers more fluid at cold temperatures. Furthermore, it may be helpful in promoting larval growth (Fraenkel & Blewett 1947), permitting these beetles to

complete their life cycles in the short growing season of cold ecosystems.



Figure 74. *Byrrhus* sp playing dead in Scotland. Photo by Roger S. Key, with permission.



Figure 75. **Byrrhidae** feigning death. Note how the legs fit into grooves on the underside. Photo by Barbara Thaler-Knoflach, with permission.

### **Amphicyrta**

This genus (Figure 71), restricted to California and Oregon, USA, is the exception among the **Byrrhidae**. Larvae and adults of this genus are not bryophyte feeders (Johnson 2013). Rather, they feed on succulent leaves and stems of forest and meadow herbs and on deciduous shrubs.

### **Byrrhus**

*Byrrhus* (Figure 76) ranges from tiny to small (1-10 mm) (Johnson 2013). All the adults in this genus that feed on bryophytes are surface grazers. In addition to bryophytes they may occasionally feed on conifer seedlings, grasses, and clover in the moist areas that have abundant mosses. The larvae, on the other hand, burrow through the bryophyte layers and feed at the tunnel entrance by extending part of the body out to graze on bryophyte leaves and shoots.





Figure 76. *Byrrhus fasciatus* on moss in UK, showing underside with legs tucked into grooves while it plays dead. Photo by Roger S. Key, with permission.

*Byrrhus luniger* eats its own home. In Štramberk, a small town in the Moravian-Silesian Region of the Czech Republic, these beetles spend at least part of their lives among **Polytrichaceae**. Gut analysis reveals cells of these mosses in the gut (Hradílek & Boukal 2003). Papillae on the terminal lamina cells suggest that the mosses were either *Pogonatum urnigerum* (Figure 77) or *Polytrichastrum alpinum* (Figure 78).



Figure 77. *Pogonatum urnigerum*, a likely food of *Byrrhus luniger*. Photo by James K. Lindsey, with permission.



Figure 78. *Polytrichastrum alpinum*, likely food for *Byrrhus luniger*. Photo by David T. Holyoak, with permission.

Some records of this genus among mosses are old. Ferguson (1901) reported *Byrrhus pilula* (Figure 79) from mosses in the Clyde Area of the British Isles.



Figure 79. *Byrrhus pilula*, a moss dweller in the British Isles. Photo by Petr Kočárek and Pavel Drozd, with permission.

In northwestern United States, Loren Russell and Paul Johnson (pers. comm. 21 March 2012) found different species of *Byrrhus* as moss dwellers: *Byrrhus americanus* (Figure 80), *B. concolor* (Figure 81), and *Byrrhus kirbyi* (~6.5 mm; Figure 82). Gut analysis of museum specimens of all three species revealed that mosses had served as food items. Not surprisingly, these beetles have seldom been collected, perhaps because the tiny creatures seldom venture out of their cozy cushions to fall into pitfall traps.



Figure 80. *Byrrhus americanus* adult, a moss dweller and consumer in northwestern United States. Photo by Tom Murray, through Creative Commons.



Figure 81. *Byrrhus concolor*, moss feeder in northwestern USA. Photo by Tom Murray, through Creative Commons.



Figure 82. *Byrrhus kirbyi* adult, a moss dweller in northwestern USA. Photo by Tim Loh, with permission.

### **Chaetophora**

Yes, *Chaetophora* is also a genus of green algae. Neither group of nomenclatural taxonomists has created a rule to prevent using the same name in another kingdom. The byrrhid *Chaetophora* is a native of Eurasia, but it is adventive in northeastern USA (McLeod 2006). It lives in areas with sparse vegetation, but with mosses.

*Chaetophora spinosa* (Figure 83) appears to be invasive in North America as a European immigrant (Johnson 1990). On Prince Edward Island, Canada, *Chaetophora spinosa* occurs on the moss *Mnium hornum* (Figure 84) and the nearby bare mud. In Idaho, USA, adults can be found in large numbers with the mosses *Pohlia atropurpurea*, *Dicranella varia* (Figure 85), and *Aloina brevisrostris* (Figure 86), but *A. brevisrostris* has not been confirmed as a host for food (Johnson 1990). The beetles also consume the Cyanobacterium *Nostoc* (Figure 87) and it would be interesting to know if the occurrence of *Nostoc* on mosses might serve as an attractant and food source there.



Figure 83. *Chaetophora spinosa* adult, an invasive moss dweller in North America. Photo by Tom Murray, through Creative Commons.



Figure 84. *Mnium hornum*, home for *Chaetophora spinosa*. Photo by Malcolm Storey <[www.discoverlife.org](http://www.discoverlife.org)>, through Creative Commons.



Figure 85. *Dicranella varia* with capsules, home for *Chaetophora spinosa*. Photo by Hermann Schachner, through Creative Commons.



Figure 86. *Aloina brevisrostris*, home for *Chaetophora spinosa*. Photo by Michael Lüth, with permission.



Figure 87. *Nostoc* cf. *commune* on bryophytes. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

### ***Chalciosphaerium***

This moss-dwelling genus (Figure 88-Figure 90) was not known from South Georgia until 2009 when Roger S. Key (2009) found it with larvae (Figure 88) and pupae (Figure 89) that might be the same species. The species was later determined to be *Chalciosphaerium solox* (Figure 90), a species known from the Falklands (Roger S. Key, pers. comm. 4 December 2015). DNA confirmation is pending. If it is indeed that species, it is likely that it arrived with human traffic. Its apparent absence in other relatively nearby locations (indicated by searches for it) further support this interpretation. The location was a few hundred meters from the dis-embarkation site for many tourists and other visitors. Its small size would make it easy to be a hitchhiker on boots or other clothing or backpacks.

This species occurred with *Polytrichum* that was mixed with grasses (Roger S. Key, pers. comm. 4 December 2015). The researchers were unable to find it among nearby grasses that had no moss associates. More were, however, among other patches of the nearby mosses.



Figure 88. Larva, probably *Chalciosphaerium* sp., among mosses and liverworts at Grytviken, South Georgia. Photo by Roger S. Key, with permission.



Figure 89. Pupa, probably *Chalciosphaerium* sp., among mosses and leafy liverworts at Grytviken, South Georgia. Photo by Roger S. Key, with permission.



Figure 90. *Chalciosphaerium* sp. adult on leafy liverworts from Grytviken, South Georgia. Photo by Roger S. Key, with permission.

### ***Curimopsis***

Some of our photographers make great observations! Both my sister and I have been surprised on occasion to find an insect in our pictures when we enlarge them on the computer screen, but we never saw it when we were taking the picture. So I admire and envy these astute photographers who note the interesting behavior of these tiny inhabitants.

One such photographer is Brian Eversham. He shared with me his observations on *Curimopsis* (Figure 95-Figure 98) in Great Britain (Brian Eversham, pers. comm. 21 March 2012). He studied this genus for several years and found that it seems to prefer *Dicranella* [*D. heteromalla* (Figure 91) and *D. cerviculata* (Figure 92)] for shelter and food among the mosses in its habitat. It also eats *Pohlia nutans* (which is common there too; Figure 93) and even the invasive *Campylopus introflexus* (Figure 94).



Figure 91. *Dicranella heteromalla*, home and food for *Curimopsis*. Photo by Janice Glime.



Figure 92. *Dicranella cerviculata* with capsules, home and food for *Curimopsis*. Photo by David T. Holyoak, with permission.



Figure 93. *Pohlia nutans* with capsules, home and food for *Curimopsis*. Photo by J. C. Schou <www.biopix.com>, with permission.



Figure 94. *Campylopus introflexus*, home and food for *Curimopsis*. Photo by Michael Lüth, with permission.

In peat areas, the peat dries out in the summer in Thorne and Hatfield Moors, UK, due to the low rainfall (Brian Eversham, pers. comm. 21 March 2012). When this occurs, the females construct burrows down to 4 cm deep in the peat. These are usually close to the *Dicranella* (Figure 91-Figure 92) species. To build their burrows they collect moss leaves, one at a time, and like ants they carry them in their jaws. These are carried underground to line the burrows in a spiral arrangement around the walls. This "wallpaper" serves to feed the young larvae.

Johnson (1986) found *Curimopsis moosilauke* (Figure 95) to be a characteristic species above the **krummholz ecotone** (transition to stunted windblown trees growing near the tree line on mountains). These beetles often occurred between rocks and boulders where fine, moist, matted mosses grew on the sandy soils.



Figure 95. *Curimopsis moosilauke* adult, a moss associate above the krummholz. Photo by Kirill V. Makarov <www.zin.ru>, through public domain.

*Curimopsis nigrita* (mire pill beetle, bog-hog; Figure 96-Figure 97) is a tiny beetle only about 1.2 mm long. It burrows in peat and under mosses, lining these burrows with moss leaves (Roger S. Key, pers. comm. 31 October 2014). Perhaps this is the species seen by Brian Eversham, both in the UK.



Figure 96. *Curimopsis nigrita*, on Hatfield Moors, South Yorkshire. Photo by Brian Eversham, with permission.



Figure 97. *Curimopsis nigrita* (mire pill beetle), uncovered from its burrow under mosses. Note how well it blends with its surroundings. Photo by Roger S. Key, with permission.

On Mt. Hood, Oregon, USA, *Curimopsis albonotata* (Figure 98) lives at higher elevations (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). Similarly, *C. brevicollis* lives at high elevations on Mt. Rainier, Washington, USA. The latter, collected in northern Idaho, had mosses in its gut. Both of these species seem to be limited to higher elevations.

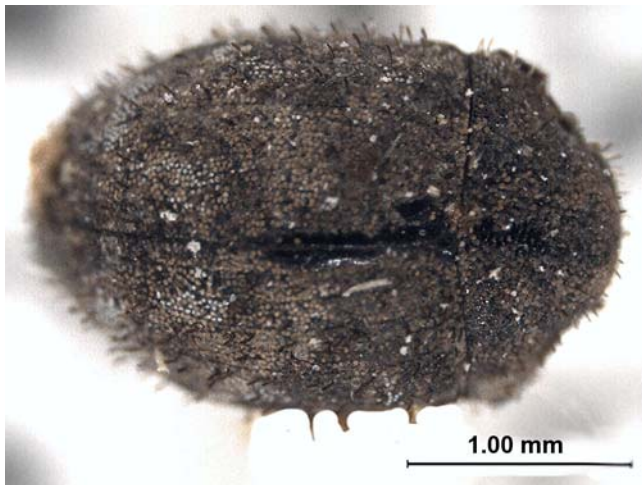


Figure 98. *Curimopsis albonotata* adult, a moss-dwelling, high-elevation species on Mt. Rainier, Washington, USA. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

## *Cytilus*

In the Atlantic region of Canada, larvae of the boreal *Cytilus alternatus* (Figure 99-Figure 100) live in thick layers of *Sphagnum* (Figure 35) (LeSage 1983; Majka & Langor 2011). *Cytilus* species, unlike those of most **Byrrhidae**, do not burrow and instead feed at the surface as larvae (Johnson 2013). And unlike most of the **Byrrhidae**, members of *Cytilus* are active in open mossy areas in sunlight (Figure 103) (Johnson 2002). The guts of these larvae contain dead leaves, dead wood of Ericaceae (heaths), mosses, liverworts, and other vegetable matter, suggesting that this species is a detritivore. Both adults and larvae include mosses in their diet.



Figure 99. *Cytilus alternatus* larva, a stage that eats mosses, among other things. Photo by Tom Murray, through Creative Commons.



Figure 100. *Cytilus alternatus* eating moss. Note that the tip of the larger *Plagiomnium* at the right has been eaten. Photo by Alex Wild, free for educational use.

In the northwestern United States, *Cytilus alternatus* (Figure 99-Figure 100) is a widely distributed boreal insect of open rocky sites, often near seepages or waterfalls (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). *Cytilus sericeus* (Figure 101-Figure 102) lives among the **Polytrichaceae** (Figure 103), where it feeds on mosses. These are in the typical open habitats known for this genus (Figure 50).



Figure 101. *Cytilus sericeus*, a bryophagid in peatland. Photo by James K. Lindsey, with permission.



Figure 102. *Cytilus* larva, a peatland inhabitant. Photo by Don Loarie, through Creative Commons.



Figure 103. *Cytilus sericeus* habitat with clumps of Polytrichaceae. Photo by James K. Lindsey, with permission.

### **Epichorius**

*Epichorius* hails from the other end of the Earth from Auckland Island, New Zealand (Wahedi *et al.* 1974). Here one can find larvae of *E. longulus* and *E. aucklandiae* among bryophytes in the coastal rata forest (Figure 104-Figure 105). *Epichorius longulus* larvae can be found

among bryophytes on the ground, abundantly occupying species of the thallose liverwort *Riccardia* (Figure 106) and rarely in mats of the leafy liverwort *Bazzania adnexa* (Figure 107). This difference may be one of nutrition. Larvae that fed on *Riccardia* thalli gained more weight than those fed on the leafy liverwort *Bazzania adnexa*. The larvae were absent on bare ground and among tree roots. But the larvae were not immobile. They sought shelter under leaf litter during the day and appeared on the liverworts at night to feed.



Figure 104. Rata forest, Auckland Island, where *Epichorius* lives among liverworts. Photo by James Russell <[islandconservation.auckland.ac.nz](http://islandconservation.auckland.ac.nz)>, with permission.



Figure 105. Rata forest (*Metrosideros umbellata*), Enderby Island in sub-Antarctic New Zealand. This forest is home for *Epichorius* among the liverworts. Photo courtesy of John Barkla.



Figure 106. *Riccardia latifrons*, a genus that is home for *Epichorius longulus* larvae. Photo by David T. Holyoak, with permission.



Figure 107. *Bazzania adnexa*, home for *Epichorius longulus* larvae. Photo by Niels Klazenga, with permission.

### *Exomella*

This genus is restricted to mesic coniferous forests in the Pacific Northwest, USA. *Exomella pleuralis* (Figure 108) inhabits *Racomitrium heterostichum* (Figure 109) (Johnson & Russell 1978). In the lab they both ate and oviposited on *Eurhynchium oregonum* (Figure 110).



Figure 108. *Exomella pleuralis* adult, an inhabitant of *Racomitrium heterostichum* in the Pacific Northwest, USA. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 109. *Racomitrium heterostichum*, home for *Exomella pleuralis*. Photo by Michael Lüth, with permission.



Figure 110. *Eurhynchium oregonum*, suitable food for *Exomella pleuralis*. Photo by Matt Goff <[www.sitkanature.org/](http://www.sitkanature.org/)>, with permission.

### *Lioligus*

Both *Lioligus nitidus* (Figure 111) and *L. striolatus* occur in mossy sites of the coastal mesic coniferous forests in the Pacific Northwest, USA (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). *Lioligus striolatus* is more northern, living in northwest Washington, whereas *L. nitidus* is more common in western Oregon. Russell and Johnson suggest that they may be two forms of the same species. Laboratory experiments indicate that both have broad food choices in both larval and adult stages. In the lab, their foods included the mosses *Eurhynchium oregonum* (Figure 110), *Hylocomium splendens* (Figure 112), *Hypnum circinale* (Figure 113), *Plagiothecium undulatum* (Figure 114), *Racomitrium heterostichum* (Figure 109), *Rhytidiadelphus loreus* (Figure 115), and *R. triquetris* (Figure 116). The moss *Metaneckera menziesii* (Figure 117) was refused. In the lab, Russell and Johnson found that one specimen of *L. striolatus* survived from egg to adult with only leafy liverworts [*Diplophyllum plicatum* (Figure 118) and *Scapania bolanderi* (Figure 119)] to eat. However, this was an isolated success – other adult members of *Lioligus* would not feed on *Scapania* or other liverworts in cultures.



Figure 111. *Lioligus nitidus* adult female, a species that eats both mosses and liverworts. Photo by Louisiana State Arthropod Museum, through Creative Commons.



Figure 112. *Hylocomium splendens*, a suitable food for species of *Lioligus*. Photo by Andrew Spink, with permission.

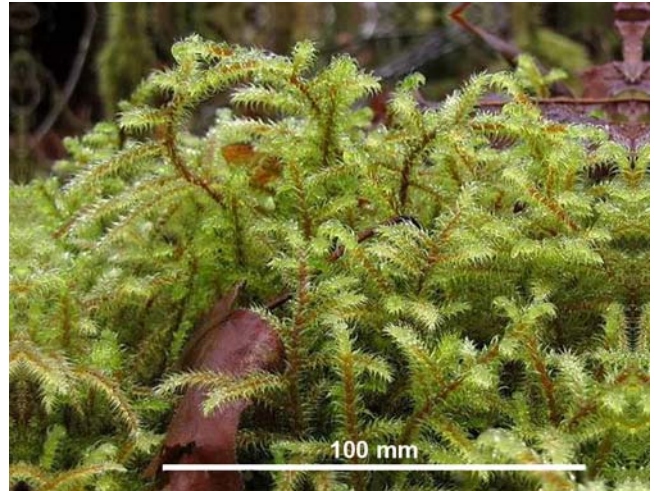


Figure 115. *Rhytidiadelphus loreus*, a suitable food for species of *Lioligus*. Photo by Andrew Spink, with permission.



Figure 113. *Hypnum circinale* with capsules, a suitable food for species of *Lioligus*. Photo by Tab Tannery, through Creative Commons.



Figure 116. *Rhytidiadelphus triquetrus*, a suitable food for species of *Lioligus*. Photo by Janice Glime.



Figure 114. *Plagiothecium undulatum*, a suitable food for species of *Lioligus*. Photo by Kristian Peters, with permission.



Figure 117. *Metaneckera menziesii*, a potential food that was refused by species of *Lioligus*. Photo by Michael Lüth, with permission.





Figure 118. *Diplophyllum plicatum*, a suitable food for *Lioligus striolatus*. Photo by Martin Hutten, with permission.

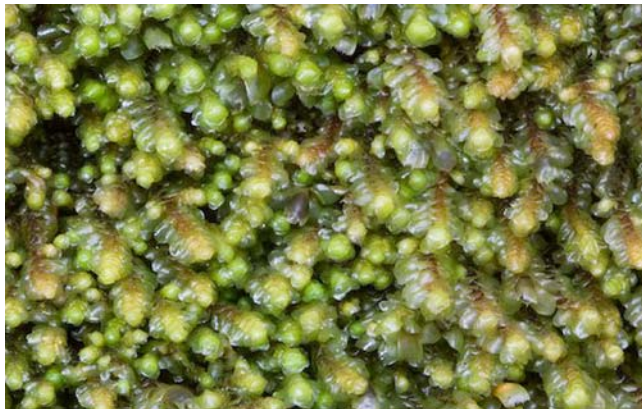


Figure 119. *Scapania bolanderi*, a suitable food for *Lioligus striolatus* in the lab, but not for other members of the genus. Photo by Matt Goff <[www.sitkanature.org](http://www.sitkanature.org)>, with permission.

### **Liolon**

*Liolon puncticeps* and *L. simplicipes* (Figure 120) are closely related species in the coastal coniferous forests of western USA (Loren Russell & Paul Johnson, pers. comm. 21 March 2012). Larvae and adults have a wide range of mossy habitats, ranging from wet, boggy soil to dry epiphytes. Like *Lioligus* (Figure 111), they accept a wide range of host mosses, including *Antitrichia curtispindula* (Figure 121), *Dicranum fuscescens* (Figure 122), *Eurhynchium oregonum* (Figure 110), *Plagiothecium*

*undulatum* (Figure 114), and *Rhytidiadelphus loreus* (Figure 115) for *L. puncticeps*. They also eat leaf tips and leaf lamellae of *Polytrichum commune* (Figure 123), but they leave the tougher parts such as the stems.



Figure 120. *Liolon simplicipes* adult, a species that lives among mosses in a wide range of habitats in western USA. Photo by Joyce Gross, with permission.

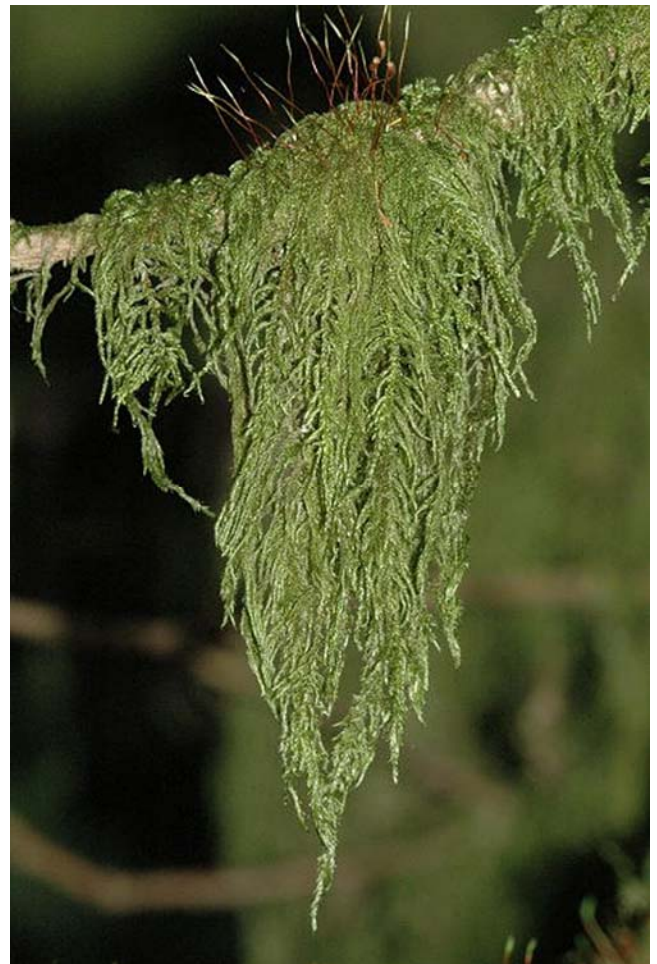


Figure 121. *Antitrichia curtispindula*, a host species for *Liolon puncticeps*. Photo by James K. Lindsey, with permission.



Figure 122. *Dicranum fuscescens*, a host species for *Lioon puncticeps*. Photo by Michael Lüth, with permission.



Figure 123. *Polytrichum commune* habit, common home and food for beetles, including *Lioon puncticeps*. Photo by Sten Porse, through Creative Commons.

### Listemus

*Listemus* is a small genus with three species in northwestern North America. These include *L. acuminatus* (Figure 124) and *L. formosus* (Russell 1979; Loren Russell & Paul Johnson, pers. comm. 21 March 2012). They are restricted to mesic coniferous forests of the Pacific Northwest, USA, but differ from *Lioligus* (Figure 111) and *Lioon* (Figure 120) in being restricted to mosses on soil, rocks, or logs and are not known from epiphytic bryophytes. In the lab both adults and larvae of *Listemus acuminatus* can survive on *Eurhynchium oregonum* (Figure 110), *Hypnum circinale* (Figure 113), and *Plagiothecium undulatum* (Figure 114). In the field one can find larvae of *L. acuminatus* in nearly pure mats of the leafy liverworts *Gyrothyra underwoodiana* (Figure 125) and *Nardia scalaris* (Figure 126), but there is no evidence that these beetles feed on them. It is possible that they feed on the occasional mosses that grow with the liverworts.



Figure 124. *Listemus acuminatus* adult, a species among mosses on the ground, rocks, or logs. Photo by Joyce Gross, with permission.



Figure 125. *Gyrothyra underwoodiana*, home for larvae of *Listemus acuminatus*, but apparently not suitable food. Photo by Tab Tannery, through Creative Commons.



Figure 126. *Nardia scalaris* with capsules, home for larvae of *L. acuminatus*, but apparently not suitable food. Note the accompanying mosses. Photo by J. C. Schou <[www.biopix.com](http://www.biopix.com)>, with permission.

### Nothochaetes

*Nothochaetes howensis* (see Figure 127), a new genus and species, lives among mosses on trees in Australia (Lawrence *et al.* 2013).

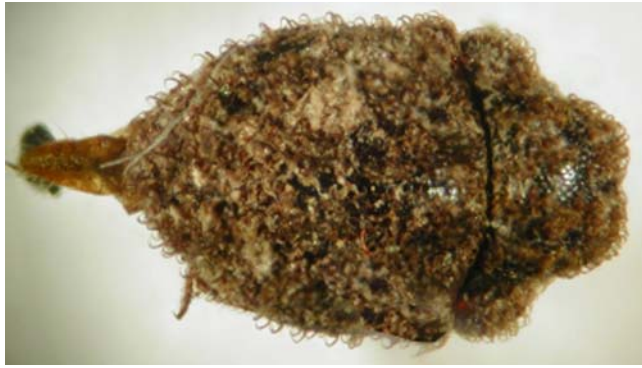


Figure 127. *Nothochaetes fasciculatus* adult. *Nothochaetes howensis* lives among mosses on Australian trees. Photo by Lynne Forster, with permission.

### Notolioon

Lawrence *et al.* (2013) described six new genera from the **Byrrhidae** in Australia (Figure 128-Figure 129) and made nomenclatural changes in how some of the existing species are classified. This study suggests that many more **Byrrhidae** might be found around the world if more bryophytes are searched.

*Notolioon nodipennis* (Figure 128-Figure 129), a member of the most water-loving of the Australian **Byrrhinae**, occurs in the wet forests of southeastern Australia and Tasmania (Lawrence *et al.* (2013). Both adults and larvae appear to be adapted to feeding on mosses and liverworts, based on their lack of digging legs in the adult and the occurrence in the larvae of a well-sclerotized dorsal cuticle that has defensive glands.



Figure 128. *Notolioon nodipennis* among mosses, a species newly described in 2013. Photo by Kristi Ellingsen, Insects of Tasmania, with permission.



Figure 129. *Notolioon nodipennis* among mosses, demonstrating its ability to play dead by pulling its legs against its body. Photo by Kristi Ellingsen, Insects of Tasmania, with permission.

### Simplocaria

In western Europe one can find *Simplocaria metallica* (Figure 130) in the lower part of the alpine zone. In this alpine area it lives among mosses in sandy places, often close to water courses or lakes, attesting to the importance of water in its habitat. It also occurs in the sub-alpine region, but it is rarely found in conifer forests (Böcher 1988). In Greenland, it is typically associated with the mosses *Polytrichum commune* (Figure 123) and *Aulacomnium* sp. (Figure 131), but also with the lichen *Peltigera* sp. (Figure 132) and the flowering plant *Cerastium alpinum* (Figure 133). Johnson (1990) found it with different mosses (*Bryum*?; Figure 134) on sandy gravel in boulder fields. These larvae, like those of *Byrrhus* (Figure 74, Figure 76-Figure 81), burrow into the moss mats (Böcher 1988).



Figure 130. *Simplocaria metallica* adult, a moss dweller in alpine and subalpine zones in Europe. Photo from Louisiana State Arthropod Museum, through Creative Commons.



Figure 131. *Aulacomnium palustre*, home for *Simplocaria metallica*. Photo by Janice Glime.



Figure 132. *Peltigera canina*, a lichen genus that is one of the habitat choices for *Simplocaria*. Photo by J. C. Schou <[www.biopix.com](http://www.biopix.com)>, with permission.



Figure 133. *Cerastium alpinum*, alternate host of *Simplocaria metallica*. Photo by Meneerke Bloem, through Creative Commons.



Figure 134. *Bryum algovicum*, in a genus that can serve as host for *Simplocaria metallica*. Photo by David T. Holyoak, with permission.

*Simplocaria semistriata* (Figure 135) is a native of Europe, but it has become widespread in North America (McClarín 2006). It grazes on the pioneer moss *Dicranella heteromalla* (Figure 85) and in Scotland on *Mnium hornum* (Figure 84) (Johnson 1990). Like *Chaetophora spinosa* (Figure 83), *Simplocaria semistriata* appears to be an invasive species in North America (Johnson 1990). Here it feeds, mates, and oviposits on mats of *Dicranella heteromalla*. At the same time, both larvae and adults avoid feeding on intermixed *Atrichum angustatum* (Figure 136) in both the field and laboratory. Since *Mnium hornum* is abundant in North America, but in more moist sites than those of *D. heteromalla*, it is likely that *Simplocaria semistriata* will be found on that host in North America as well. Nate Schoonover (BugGuide 2015) reports that this species plays dead when disturbed. His 3 mm adults appeared in his terrarium among "cushion mosses" collected in Dover, New Hampshire, USA.



Figure 135. *Simplocaria semistriata* (Coleoptera: Byrrhidae), a North American invasive moss dweller shown here on mosses. Photo by Vítězslav Plášek, with permission.



Figure 136. *Atrichum angustatum*, a moss that is avoided as food by *Simplocaria semistriata*. Photo by Michael Lüth, with permission.

## Chelonariidae – Turtle Beetles

This family, mostly tropical (Harpootlian 2006), was presumed to be aquatic, but Spangler (1980) discovered that it included a number of terrestrial larvae in *Chelonarium* (Figure 137). The adults are larger than most moss dwelling beetles (2.5-10 mm) and have the oval shape and somewhat flattened body typical of swimming beetles. But these lack gills and in the tropics they are associated with roots of a number of species of orchids and a few other epiphytes. Although the larvae have been reported from aquatic habitats, Brown (1972) suggested that these larvae might have been living on damp mosses near the streams and occasionally were washed into streams.



Figure 137. *Chelonarium lecontei* adult. Some members of this genus that have terrestrial larvae associated with mosses near water. Photo by Mike Quinn, through Creative Commons.

## Limnichidae – Minute Marsh-loving Beetles

This is a relatively small family (~400 spp.), as beetles go, but it nevertheless has worldwide distribution (Harpootlian 2005). It is small (~2 mm) and rounded and, in the word of Harpootlian, otherwise "unremarkable" (Figure 138). This family is primarily riparian, living streamside, on emergent plants, on wood, or in windrows of debris. The larvae live in damp soil near water. Little is known about their food – they are presumed to be herbivorous.



Figure 138. *Eulimnichus* adult showing the nondescript appearance of the **Limnichidae**. Photo by Tom Murray, through Creative Commons.

Although little is known about the biology of the **Limnichidae**, some are known to feed on algae and mosses (Pütz 1998). Jim McClarin (pers. comm. 30 August 2014) finds **Limnichidae** with bryophytes in the cloud forest zone of eastern Ecuador.

Pütz (1998) reported on members of this family in China. There one can find *Cephalobyrrhus sichuanensis* on algae and mosses of sandy river banks. Champion (1925) earlier reported *Cephalobyrrhus gibbicollis* running over wet mosses on river banks in India.

### Summary

The **Carabidae** are the only members of **Adephaga** I have found to associate with bryophytes. The **Carabidae** among bryophytes lack any special adaptations for that habitat. Some are there to feed, including fungi, bacteria, detritus, and various invertebrates. Bryophytes themselves do not seem to serve as a food source for them. Nevertheless, the diversity of **Carabidae** among bryophytes is large. Some use the mosses as a summer refuge where they can find moisture or a place to spend the winter. Some, often rare species, inhabit bogs. *Sphagnum* mires in forests serve as a refuge for carabid species following cutting.

Some members of **Artematopidae** live among bryophytes as larvae.

The **Byrrhidae** are well known as moss-dwelling beetles. They are typically tiny and rounded. Some are able to play dead when disturbed and can retract their legs into grooves on the lower surface. Most of them also eat bryophytes, including a wide range of species, and some are known to eat liverworts. Some burrow into *Sphagnum*. The ability of these beetles to survive at high altitudes and latitudes may be due to the **arachidonic acid** from their bryophyte diet. The family is ancient and worldwide. Because of the difficulty of sampling these tiny moss inhabitants, and their inability to disperse far, one is likely to encounter new species if venturing into an unexplored region. Other species are invasive as passengers with their moss habitat when it is used commercially.

Other moss-dwelling members of **Byrrhoidea** include some species in the **Chelonariidae** and **Limnichidae**.

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