Glime, J. M. 2017. Terrestrial Insects: Holometabola – Coleoptera Biology and Ecology. Chapt. 12-9a. In: Glime, J. M. Bryophyte Ecology. Volume 2. Bryological Interaction. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 19 July 2020 and available at <http://digitalcommons.mtu.edu/bryophyte-ecology2/>.

CHAPTER 12-9a TERRESTRIAL INSECTS: HOLOMETABOLA – COLEOPTERA BIOLOGY AND ECOLOGY

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Figure 1. ***Ptychomitrium*** in the Neotropics with beetle navigating within the mat. Photo by Michael Lüth, with permission.

COLEOPTERA – BEETLES

I opened my email one morning to see one subject labelled "Catching Beetles." Upon investigation, I found this was an advertisement for a new book, 320 pages, all directed toward the various methods for catching beetles in the myriad of habitats they occupy and the families you might encounter (Julio 2011). This large book attests to the huge number of species, sizes, and wide range of habitats of beetles. The picture of a car with large fine-mesh funnel nets on the top and sides struck me as a symbol of their **ubiquitous** (found everywhere) nature.

It seemed like every time I looked up information on a beetle species, I found three more beetle species that inhabited mosses during part of the life cycle. At some point I had to stop and ignore or this volume would never get past the beetle chapter. Hence, I know there are more records that are out there, but these are adequate to show the wide range of families, uses, habitats, and adaptations.

Among the insects, the **Coleoptera**, those hard-winged insects known as beetles, are the largest group of organisms on the planet, and are likewise abundant within the shelter of bryophytes. A renowned biochemist and friend of the entomologist E. O. Wilson, J. B. S. Haldane, when asked by a theologian what the natural world had taught him about the Creator, replied that he has "an inordinate fondness for beetles." It is unclear whether Haldane is the one who coined the phrase because many variants of it appear in the literature (Farrell 1998).

With such large numbers, it is not surprising that we find some of them among mosses. For example, **Parnidae** and **Elmidae** are common in ***Sphagnum*** peatlands (Figure 2) (Leng 1913). That means that they can become unwitting passengers on harvested mosses, travelling around the world with them (Reich 1974; Peck & Moldenke 1999).

Figure 2. ***Sphagnum*** lawn, home for some members of **Parnidae** and **Elmidae**. Photo from Creative Commons.

Moss-dwelling beetles have been known for a long time (for example, Douglas 1871; Waterhouse 1871). Ferguson (1901) enumerated many species of beetles among mosses in the Clyde area of the British Isles, listing the most in the families **Curculionidae** (weevils) and **Staphylinidae** (rove beetles). Day (1907) reported several species from mosses in Cumberland, England. Brown (1972) considered that some seek mosses to maintain their moisture.

Des Callaghan (pers. comm. 3 February 2012) relayed to me his experience with grubs he thought might be beetle larvae. He had saved a sample of ***Micromitrium tenerum*** (Figure 3) for photography, but when he was ready for the photography all he found was soil covered by capsules! He later observed the grubs eating the leaves of the moss.

Figure 3. ***Macromitrium tenerum***, a species for which clumps can be completely devoured by beetle grubs. Photo by Jan-Peter Frahm, with permission.

Bryophagids – Eating and Being Eaten

As seen above, a surprising number of beetles feed on mosses. A variety of small beetles eat mosses and use them as their homes (Drozd *et al*. 2007).

A number of genera in the **Byrrhidae** occur among mosses, use them for egg laying, or eat them. ***Exomella pleuralis*** (Figure 4) can be found in ***Racomitrium heterostichum*** (Figure 5), and adults both feed and oviposit on ***Eurhynchium oreganum*** (Figure 6) (Russell 1979). ***Curimopsis albonotata*** (Figure 7) and ***C. brevicollis*** are limited to higher elevations in the Pacific Northwest; ***C. brevicollis*** from northern Idaho had moss in its gut. ***Lioligus nitidus*** (Figure 8) and ***L. striolatus*** feed on a variety of mosses in the lab: ***Eurhynchium oreganum***, ***Hylocomium splendens*** (Figure 9), ***Hypnum circinale*** (Figure 10), ***Plagiothecium undulatum*** (Figure 11), ***Racomitrium heterostichum***, ***Rhytidiadelphus loreus*** (Figure 12), and ***R. triquetrus*** (Figure 13). One specimen was reared from an egg to an adult on the leafy liverworts ***Diplophyllum plicatum*** (Figure 14) and ***Scapania bolanderi*** (Figure 15). On the other hand, adults refused to eat ***S. bolanderi*** and other liverworts or ***Metaneckera menziesii*** (Figure 16).

Figure 4. ***Exomella pleuralis*** adult, a species that feeds on ***Eurhynchium heterostichum*** and oviposits there. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 5. ***Racomitrium heterostichum*** with capsules, home for ***Exomella pleuralis***. Photo by Kristian Peters, with pernission.

Figure 6. ***Eurhynchium oreganum***, home, food, and site for oviposition for ***Exomella pleuralis***. Photo by Matt Goff <http://www.sitkanature.org/>, with permission.

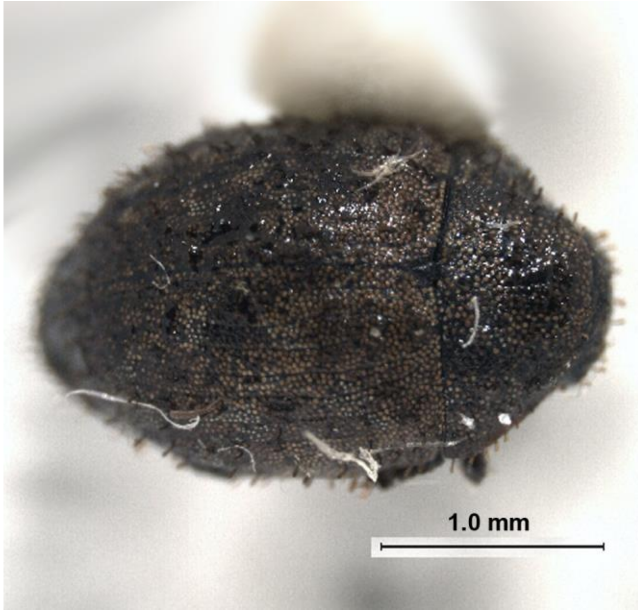

Figure 7. ***Curimopsis albonotata*** adult, a moss consumer at higher elevations. Photo by CNB-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 8. ***Lioligus nitidus***, a species that eats a variety of mosses. Photo by Matt Goff <http://www.sitkanature.org/>, with permission.

Figure 9. ***Hylocomium splendens***, food for ***Lioligus striolatus***. Photo by Chmee2, through Creative Commons.

Figure 10. ***Hypnum circinale***, food for ***Lioligus striolatus***. Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 11. ***Plagiothecium undulatum***, food for ***Lioligus striolatus***. Photo by David T. Holyoak, with permission.

Figure 12. ***Rhytidiadelphus loreus***, food for ***Lioligus striolatus***. Photo by Hermann Schachner, through Creative Commons.

Figure 13. ***Rhytidiadelphus triquetrus***, food for ***Lioligus striolatus***. Photo by Eric Schneider, with permission.

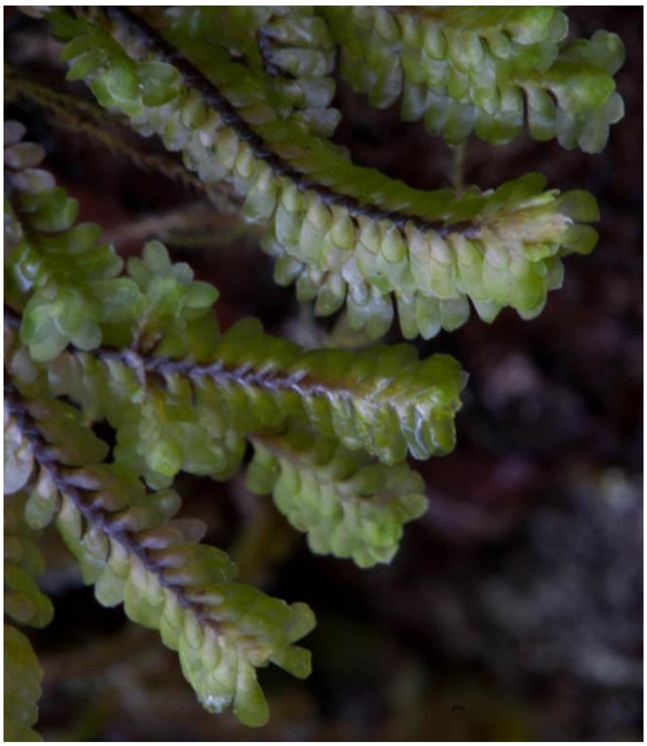

Figure 14. ***Diplophyllum plicatum***, food for larvae of ***Lioligus striolatus***. Photo by Martin Hutten, with permission.

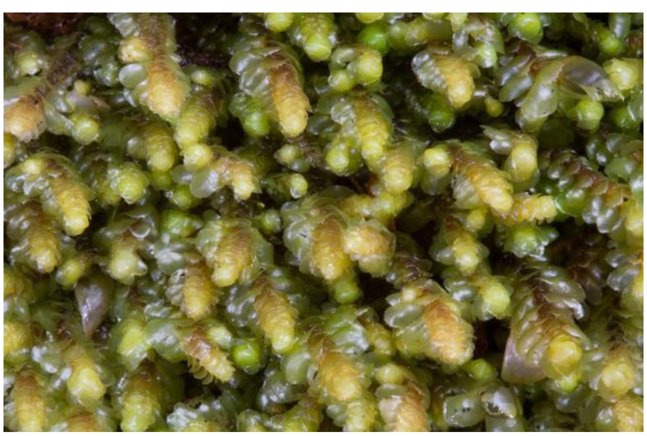

Figure 15. ***Scapania bolanderi***, food for larvae of ***Lioligus striolatus***. Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 16. ***Metaneckera menziesii***, a moss the adults of ***Lioligus striolatus*** refuse to eat. Photo by Dale Vitt, with permission.

Adults of ***Lioon puncticeps*** and ***L. simplicipes*** (Figure 17) live among many kinds of mosses (Russell 1979). In the laboratory, ***Lioon puncticeps*** adults and larvae both feed on ***Dicranum fuscescens*** (Figure 18), ***Rhytidiadelphus loreus*** (Figure 12), ***Antitrichia curtipendula*** (Figure 19), ***Eurhynchium oreganum*** (Figure 6), and ***Plagiothecium undulatum*** (Figure 11). On ***Polytrichum commune*** (Figure 20), they eat only lamellae and leaf tips while avoiding the tougher parts.

Figure 17. ***Lioon simplicipes*** adult, a species that lives among many kinds of moss. Photo by Joyce Gross, with permission.

Figure 18. ***Dicranum fuscescens***, food for ***Lioon puncticeps***. Photo by Michael Lüth, with permission.

Figure 19. ***Antitrichia curtipendula***, food for ***Lioon puncticeps***. Photo by Dale Vitt, with permission.

Figure 20. ***Polytrichum commune***, food for ***Lioon puncticeps***. Photo by Michael Lüth, with permission.

Listemus acuminatus (Figure 21) and ***L. formosus*** grow among mosses on soil, rocks, and logs, but not among epiphytes (Russell 1979). In the lab they feed on ***Eurhynchium oreganum*** (Figure 6), ***Hypnum circinale*** (Figure 10), and ***Plagiothecium undulatum*** (Figure 11). Larvae occur in mats of the leafy liverworts ***Gyrothyra underwoodiana*** (Figure 22) and ***Nardia scalaris*** (Figure 23), but they may only feed on associated mosses.

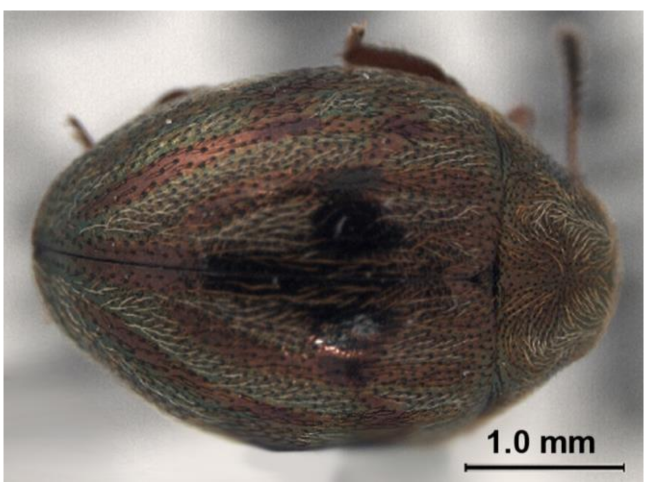

Figure 21. ***Listemus acuminatus***, a species that lives among mosses on soil, rocks, and logs, but does not venture up the boles of trees. Photo from CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

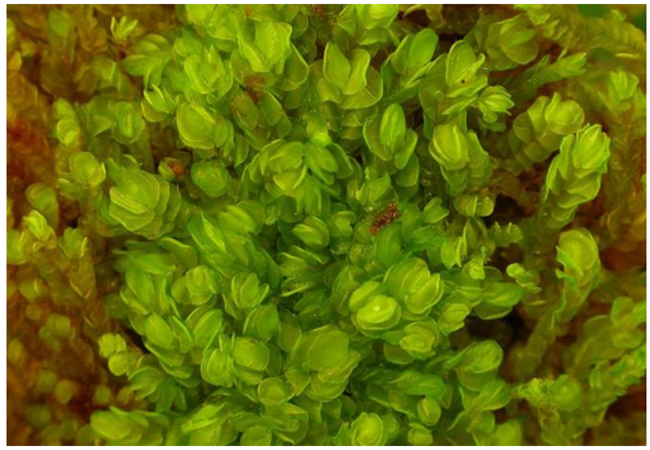

Figure 22. ***Gyrothyra underwoodiana***, a home that doesn't seem to be eaten by ***Listemus acuminatus***. Photo by Li Zhang, with permission.

Figure 23. ***Nardia scalaris*** with capsules, a home but not food for ***Listemus acuminatus***. Photo by J. C. Schou <http://www.biopix.com/>, with permission.

Byrrhus americanus (Figure 24), ***B. concolor*** (Figure 25), and ***B. kirbyi*** (Figure 26) have been found with mosses in their guts (Russell 1979). Hradílek and Boukal (2003) reported **Polytrichaceae** cells from the gut of ***Byrrhus luniger***. These were lamellae with papillae on the terminal cells (Figure 28, Figure 30), suggesting either ***Pogonatum urnigerum*** (Figure 27-Figure 28) or ***Polytrichastrum alpinum*** (Figure 29-Figure 30).

Figure 24. ***Byrrhus americanus*** adult, a moss feeder. Photo by Tom Murray, through Creative Commons.

Figure 25. ***Byrrhus concolor***, a moss feeder. Photo by Tom Murray, through Creative Commons.

Figure 26. ***Byrrhus kirbyi*** adult, a moss consumer. Photo by Tim Loh, with permission.

Figure 27. ***Pogonatum urnigerum***, probable food for ***Byrrhus luniger***. Photo by David T. Holyoak, with permission.

Figure 28. ***Pogonatum urnigerum*** lamellae showing papillae on the terminal cells like those in the gut of ***Byrrhus luniger***. Photo by Kristian Peters, with permission.

Figure 29. ***Polytrichastrum alpinum***, probable food for ***Byrrhus luniger***. Photo by Andrew Hodgson, with permission.

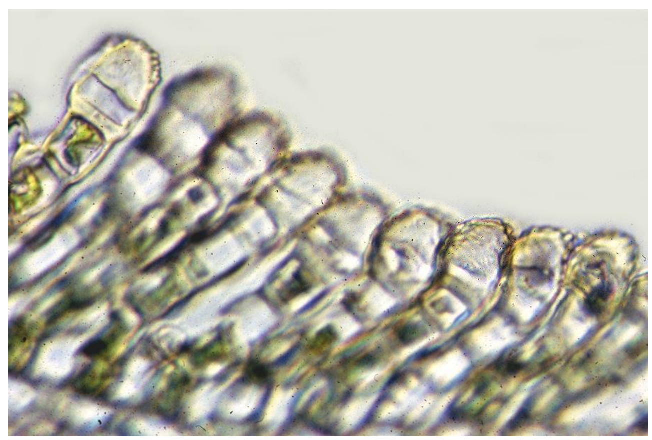

Figure 30. ***Polytrichastrum alpinum*** lamellae showing papillae on the terminal cells like those in the gut of ***Byrrhus luniger***. Photo by Janice Glime.

It appears that all North American species of the **Artematopodidae** might be bryophagids (Russell 1979). Adults of ***Macropogon*** (Figure 31) and larvae of ***Eurypogon*** (Figure 32) in western Washington and Oregon usually occur on trees or shrubs near moss-covered rocks, but some larvae have been collected under the moss ***Ceratodon purpureus*** (Figure 33).

Figure 31. ***Macropogon testaceipennis*** adult, a North American bryophagid. Photo by Joyce Gross, with permission.

Figure 32. ***Eurypogon niger*** adult, a North American bryophagid. Photo by Tom Murray, through Creative Commons.

Figure 33. ***Ceratodon purpureus***, habitat for larvae of ***Eurypogon***. Photo by Jiří Kameníček <BioLib, Obázek>, with permission.

A beetle in the family **Lagriidae** in the Afromontane forest of South Africa feeds on both living and dead parts of the moss ***Braunia secunda*** (**Hedwigiaceae**; Figure 34-Figure 35), as evidenced by gut analysis (Chown 1993), but whether it is specific to this food is not known. Among the weevils (**Curculionidae**) in the sub-Antarctic Prince Edward Islands, ***Antarctonesiotes elongatus***, ***Bothrometopus randi***, ***Ectomnorrhinus marioni***, ***Mesembriorrhinus brevis***, and ***Palirhoeus eatoni*** (**Brachyceridae**) all feed on cryptogams, including bryophytes (Chown & Scholtz 1989a). Similar relationships are known from Marion Island in the Antarctic (Smith 1977), where ***Mesembriorrhinus brevis*** and ***Ectomnorrhinus marioni*** prefer bryophytes over flowering plants (Chown & Scholtz 1989a). ***Ectomnorrhinus similis***, a weevil (**Curculionidae**), consumed 1.67 mg per day of ***Brachythecium rutabulum*** (Figure 36) on an Antarctic island. On the other hand, mosses and lichens consumed by microfauna in two other Antarctic moss communities were less than 0.2 g m^{-2} yr^{-1}.

Figure 34. ***Braunia secunda*** wet, food and home for a member of the **Lagriidae**. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 35. ***Braunia secunda*** dry, food and home for a member of the **Lagriidae**. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 36. ***Brachythecium rutabulum***, food and home for a member of the **Lagriidae**. Photo by Michael Lüth, with permission.

Lazarenko *et al*. (1960) reported the use of mosses as food for flax flea beetles (**Chrysomelidae**). Wallin *et al.* (1999) examined the food habits of beetles inhabiting ***Sphagnum*** (Figure 2) mosses as a possible cause of mandibular wear. The species that exhibited the greatest mandibular wear was not the one with the highest consumption of mosses. Rather, they found that mandibular wear in the carabid beetles ***Chlaenius costulatus*** (Figure 37) and ***C. sulcicollis*** (Figure 38) appeared to be caused by their activities in biting and burrowing into ***Sphagnum***-hummocks.

Figure 37. ***Chlaenius costulatus*** adult, an inhabitant of a protected bog in Sweden. Photo by Tim Faasen, with permission.

Figure 38. ***Chlaenius sulcicollis*** adult, a species that suffers mandibular wear from biting and burrowing into ***Sphagnum***. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

Chown (1990) found that even in the presence of the abundant grass *Agrostis magellanica* (see Figure 39), some larvae of the weevil ***Ectemnorhinus*** (see Figure 40) in the sub-Antarctic feed on bryophytes, primarily the leafy liverwort ***Blepharidophyllum densifolium***. The smaller of the two species found by Chown and Scholtz (1989b), ***E. marioni***, lives among the mosses, feeding on them at all stages and having a generation time of one year or less. By contrast, the larger species, ***E. similis***, feeds on detritus as larvae and flowering plants as adults. It has a generation time of more than one year and has more instars. The advantage to ***E. marioni*** of a bryophyte diet appears to be that the bryophytes are both abundant and available year-round. Furthermore, they contrast with the flowering plants in their seasonal N distribution. The seed plants have the highest concentrations in spring, whereas the mire bryophytes have the highest concentrations in autumn. It is interesting that the bryophytes have high concentrations of polyphenolic lignin-like compounds that interfere with digestion, whereas the flowering plants lack these.

On Heard Island, Chown and Klok (2001) found that the weevil species complex of ***Ectemnorhinus viridis*** feed on both tracheophytes and bryophytes. Cryptogams, including both lichens and bryophytes, serve as a primary source of energy and nutrients for 5 of the 6 species of weevils on the sub-Antarctic Marion Island (Crafford & Chown 1991).

Figure 39. *Agrostis curtisii*, a relative of *Agrostis magellanica*, which is ignored as food by ***Ectemnorhinus*** that eats bryophytes in the same habitat of the sub-Antarctic. Photo by Malcolm Storey through <www.discoverlife.org>, through Creative Commons.

Figure 40. ***Ectemnorhinus vanhoeffenianus***; several members of this genus in the sub-Antarctic feed on bryophytes, primarily on the leafy liverwort ***Blepharidophyllum densifolium***. Photo by Alex Puzyr, with permission.

Carabid beetles also seem to find bryophytes, particularly in peat bogs, to be suitable habitats. Främbs (1994) found that the Swedish ***Agonum ericeti*** (Figure 41) and ***Pterostichus rhaeticus*** (Figure 42) use the damp lawns in the summer and migrate to drier hummocks for overwintering. Therefore, larger populations were restricted to areas with distinct hummock-hollow complexes (Figure 43).

Figure 41. ***Agonum ericeti*** in its summer habitat among moist ***Sphagnum*** leaves. Photo by Walter P. Pfliegler, with permission.

Figure 42. ***Pterostichus rhaeticus***, a species that requires a hummock-hollow complex in Swedish bogs. Photo by Niels Sloth <www.biopix.com/>, with permission.

Figure 43. Bohemian bog with ***Sphagnum cuspidatum***, ***S. denticulatum***, and other species creating a hummock-hollow complex. Photo by Jonathan Sleath, with permission.

Beetles in geothermal areas seek refuge from the heat of the soil by inhabiting the cooler bryophytes (Elmarsdottir *et al*. 2003). In turn, bears may eat the beetles, as suggested by their piles of feces (Figure 44) in the area (personal observation).

Figure 44. Bear dung at Ponponyama, Japan. Many beetles are present in this dung. The moss in the foreground is ***Campylopus japonicus***. Photo by Janice Glime.

Epichorius longulus and ***E. aucklandiae*** (**Byrrhidae**) live in the coastal rata (***Metrosideros***) forest (Figure 45) of Auckland Island, New Zealand (Farrell 1974). ***Epichorius longulus*** lives in the ground layer, whereas ***E. aucklandiae*** lives in the canopy. The former species was abundant in the liverwort ***Riccardia*** spp., but rarely occurred among ***Bazzania adnexa*** (Figure 46). When larvae were reared on the ***Riccardia*** (Figure 47), they gained more weight than on ***Bazzania adnexa***. The adults of ***E. longulus*** sought shelter under the leaf litter in the daytime but moved about to feed on bryophytes at night.

Figure 45. Coastal rata forest where ***Epichorius*** lives among liverworts. Photo by James Russell <islandconservation.auckland.ac.nz>, with permission.

Figure 46. ***Bazzania adnexa***, rarely a home for ***Epichorius aucklandiae*** in the rata canopy in New Zealand. Photo by Andy Hodgson, with permission.

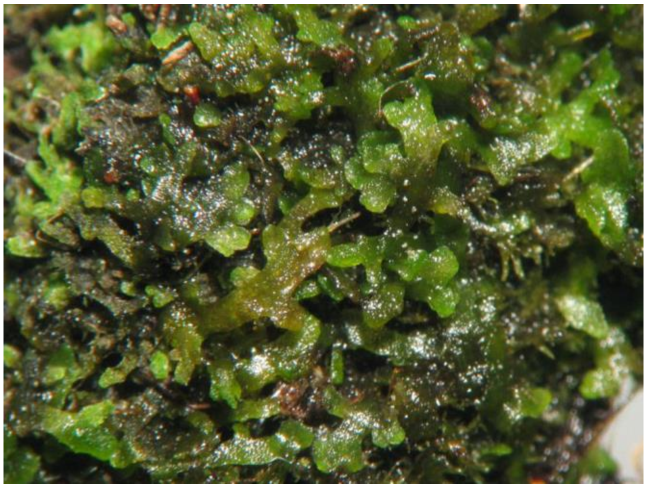

Figure 47. ***Riccardia chamedryfolia***, a genus that is home and food for ***Epichorius aucklandiae*** in the New Zealand. Photo by Kristian Peters, with permission.

Some bryophytes apparently are eaten unintentionally by animals searching for food, including the beetle fauna. The carnivorous salamander ***Phaeognathus hubrichti*** (Red Hills Salamander; Figure 48) typically has a diet that is nearly 70% arthropods, including beetles (Gunzburger 1999). But also in the gut and feces one can find moss fragments, most likely consumed as the salamanders forage for arthropods among the mosses.

Figure 48. ***Phaeognathus hubrichti***, a salamander that eats insects among mosses. Photo by Danté B. Fenolio, with permission.

Sampling

Most researchers have used the same sampling methods for bryophytes as they use for leaf litter. But bryophytes provide small spaces, and some insects never leave those small spaces. This behavior impacts the suitability of trapping methods.

Nelson and Hauser (2012) used both Berlese funnels and water sampling for bryophyte fauna, accounting for many small invertebrates that are usually not found in these associations. Nevertheless, small insects, including tiny beetles, might not have crawled out of the moist moss and into the funnels. The bias of sampling methods is demonstrated by the near absence of overlap between the two sampling methods.

Beetles (Coleoptera) are so common among the ***Sphagnum*** plants (Figure 2) (Brink 1983; Runtz & Peck 1994) that sifting through squeezed mosses can be the best method of collecting (Leiler 1983). Boháč and Bezděk (2004) once again emphasized the role of sampling method in determining the bryophyte fauna. This may be especially true for beetles, where a number of species are wingless and do little moving around. In the Mrtvy Luh peat bog they found that of 38 species in their traps, only 3 were found in both pitfall and light traps.

Boháč and Bezděk (2004) found that the light traps in the Czech Republic peat bog had more species, but many were accidental species that were not typical bog inhabitants. Among these the dominant species were species that are good fliers. Based on these findings, Boháč and Bezděk (2004) recommended that sifting and **trampling** (pressing the moss down to create a pool of water and causing the beetles to float) be included in the sampling strategies. But be aware that sifting and hand grabs are destructive and should be avoided in fragile systems or where repeated sampling is planned.

Leiler (1983) was particularly successful in finding beetle fauna by sifting squeezed wet ***Sphagnum***. Wallin *et al*. (1999) used pitfall traps that were connected with a gutter and embedded into large ***Sphagnum*** hummocks. Lindroth (1974) considered the ordinary insect sieve to be indespensible for sampling in leaf litter and "not too wet" moss, especially for hibernating insects. He suggested that litter samples could also be put under water to force the insects to the surface. For pitfall traps, he suggested adding a few drops of detergent to the formalin to break the surface tension.

Based on the differences seen among these methods, I once again recommend hand picking using a dissecting microscope if an unbiased, quantitative sampling is desired. Some insects move too slowly to get away from a heat source before they die. Some may burrow deep into the mat without vacating it. In any case, not all insects will enter traps equally.

Habitat Relations

The bryophytes are different in different habitats, and so are the beetles. But the correlations are likely to be secondary, with both of them correlating with moisture and bryophytes also with light and suitable substrate availability.

Forests

Pavel *et al*. (2007) found the **Coleoptera** to be the most abundant of the insect taxa in a forest study in the Czech Republic. Pitfall traps were used in three sites to compare those in ***Polytrichum*** cushions (Figure 49) with those at least 10 m away with no moss. Of the 56 species found, ~25% were found only among the mosses. These, combined with those also found in other parts of the forest floor, demonstrated a higher species richness among the mosses. Nevertheless, only one of these species (***Symplocaria*** sp., **Byrrhidae**) was a **bryophage** (one that eats bryophytes). Monte-Carlo permutation tests suggest that the beetles are correlated with moisture and the mosses just happen to provide the right moisture conditions. Those beetle species in dry habitats tend to be restricted to moss cushions, making them strict **bryobionts** (living only on bryophytes).

Figure 49. ***Polytrichum*** cushions that form habitat islands for ***Cytilus sericeus*** and other beetles, providing moisture in exposed areas. Photo by James K. Lindsey, with permission.

Nelson and Hauser (2012) surveyed the epiphytic bryophyte communities at the Tryon Creek State Natural Area in Oregon, USA. Among the five phyla represented, insects were among the top five taxonomic sub-groups (except for the recently ousted **Collembola**). In addition to the five more dominant insect taxa, **Diptera** and **Coleoptera** were present. Hence, beetles were not represented in proportion to their prominence among species numbers on Earth.

Hitch-hikers

Peck and Moldenke (1999) were concerned about the export of potential pest insects in commercial harvests of bryophytes in Oregon, USA. They likewise used the Berlese funnel extraction for arthropods on 200 samples of harvestable mosses. They compared the invertebrate populations at the bases and tips of shrubs of the vine maple (*Acer circinatum*; Figure 50). The base mosses had substantially higher species richness and total abundance overall. For **Coleoptera**, the bases had greater numbers of individuals than did the tips of the shrubs. Mites were the most common arthropods at the base, whereas spiders (**Micryphantidae**) and ***Sminthurus*** (**Collembola**) were the predominant taxa in mosses at the tips.

Figure 50. ***Acer circinatum***, home for **Coleoptera** in mosses at base and on branches. Photo by Ken Gilliland, through Creative Commons.

Forest Disturbance and Recovery

The carabid beetle ***Agonum fuliginosum*** (Figure 51) in Europe seems to have a generalist approach to canopy closure, but it does depend on the presence of ***Sphagnum*** (Figure 2) mires in the forest (Koivula 2002a, b; Koivula & Niemela 2002; Koivula *et al.* 2002). Even small islands of ***Sphagnum*** within a clear-cut forest will permit it to remain, presumably providing needed moisture. ***Patrobus assimilis*** (**Carabidae**; Figure 52) likewise requires the presence of ***Sphagnum*** to survive in forests (Koivula 2002b). On the other hand, ***Agonum mannerheimii***, despite being a mire specialist, is unable to survive in remaining mires if the forest is clearcut (Niemelä *et al.* 1993a, b). It can take 50-60 years for a spruce mire (Figure 53) to recover its forest cover after clearcutting, but it takes longer if there is serious disturbance of the ground layer (Koivula *et al*. 2002).

Figure 51. ***Agonum fuliginosum***, a species that seems to depend on ***Sphagnum*** for moisture in exposed or disturbed forest sites. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 52. ***Patrobus assimilis***, a species that requires mosses to survive in forests. Photo by Roy Anderson ©Roy Anderson <www.habitas.org.uk>, with permission.

Figure 53. ***Picea mariana*** forest in Northern Alberta, Canada, with ***Pleurozium schreberi*** and ***Hylocomium splendens***. Photo by Richard Caners, with permission.

Species of beetles in old-growth forests (Figure 54) are especially affected by logging (Figure 55) (Niemelä 1997). Microhabitats such as coarse woody debris, large deciduous trees, and patches of wet swamp forest and mires may disappear or be greatly reduced. These disturbances tend to cause the old-growth specialists to disappear, including those of beetles. Instead, species richness may increase as generalists remain and numerous open-habitat species invade. This trend is especially true for the ground beetles, which include moss dwellers.

Figure 54. Old Growth in Cathedral Grove, British Columbia, Canada, showing moss-covered logs (dead wood) and low-light plants. Photo by Sang Trinh, through Creative Commons.

Figure 55. Clearcut forest patches at Lewis and Clark River, Oregon, USA. Photo by Walter Siegmund, through Creative Commons.

Niemelä *et al*. (1993b) concluded that retaining habitat diversification on a regional scale was the best management strategy for retaining diversity of ground-dwelling arthropods, including beetles. Hence, retaining moss corridors for those species like the flightless ***Agonum mannerheimii*** may be necessary to permit these species to disperse and to retain the original species richness in the stand (Hoyle & Gilbert 2004). On the other hand, Jonsson and Jonsell (1999) showed that the occurrences of bryophytes are not good predictors for the species richness of beetles. Djupström *et al*. (2010) found only a weak positive correlation between beetles and bryophytes in Swedish boreal forests, and none between beetles and lichens. Like Jonsson and Jonsell, they found that the tested taxa did not provide reliable surrogates. On the other hand, dead wood diversity (Figure 54) represented both **saproxylic** (those that eat dead wood) beetles and bryophytes better than did random samples.

Effects of Beetles on Forest Bryophytes

Clear cutting (Figure 55) removes shade, changes the temperature, and eliminates many kinds of microhabitats. But bark beetles can also have an impact on the forest, removing cover and permitting the sun to raise the temperature. Nevertheless, a bark beetle outbreak in the Central European mountain spruce forests did not have the devastating effect on bryophytes that was experienced under clear cutting (Jonášová & Prach 2008). The latter causes a loss of forest floor bryophytes and the invasion of open habitat pioneers. The beetle outbreak left standing dead (Figure 56) that permitted the bryophytes to remain. Instead of promoting pioneer invasions, the beetle attack left the forest in a state that was more likely to avoid the pioneer stage and to promote a direct forest recovery, including the bryophytes.

Figure 56. Spruce bark beetle damage to the spruce forest in Rio Grande National Forest, USA. Standing dead spruce trees still provide shade, permitting bryophytes to survive. Photo from US Forest Service, through Public Domain.

Dunes

Following habitat restoration of dry dunes (Figure 57) on the Belgian coast, several dune-living ground beetles increased in population size (Maelfait *et al*. 2007). The researchers concluded that the rapid development of the ground vegetation, including both bare sand and moss patches, contributed to the rapid improvement of the insect fauna.

Figure 57. Sand dune in Belgium, where the invasive ***Campylopus introflexus*** is becoming a problem. Photo through Creative Commons.

Heathland

Beetles seem to prefer some mosses and to avoid others. In the *Empetrum* heathlands (Figure 58), beetles avoid the moss ***Pleurozium schreberi*** (Figure 59), but in the *Calluna* heath (Figure 60), with different bryophytes, the beetles were much more common (Barkman 1979, p. 138, in van Tooren 1990).

Figure 58. Dune heath with ***Calluna*** and ***Empetrum***. In ***Empetrum*** heaths, beetles avoid the ***Pleurozium schreberi***. In the ***Calluna*** heaths, beetles live among the different moss species there. Photo by Pat Doody, National Coastal Consultants, UK, with permission.

Figure 59. ***Pleurozium schreberi***, a moss that is avoided by beetles in *Empetrum* heathlands. Photo by J. C. Schou <www.biopix.com/>, with permission.

Figure 60. Heath with *Calluna vulgaris* (pink flowers) and *Ulex europaea* (yellow flowers), where bryophytes seem to be an important part of the habitat for beetles. Photo by Magnus Manske, through Creative Commons.

In a wet heathland in Scotland, the heather beetle ***Lochmaea suturalis*** (**Chrysomelidae**; Figure 61) is a herbivore on ***Calluna*** (Figure 62) (Scandrett & Gimingham 1991). The result of this herbivory is that cover decreases and the mosses ***Sphagnum plumulosum*** (Figure 63) and ***Hypnum jutlandicum*** (Figure 64) increase. The increases in these mosses is concurrent with the decline of ***Sphagnum compactum*** (Figure 65) and ***Pleurozium schreberi*** (Figure 59), thus improving the habitat for bryophyte-dwelling beetles. The ***Calluna*** regenerates mostly by layering, with only limited restoration through seedlings that germinate in the moist ***Sphagnum***.

Figure 61. ***Lochmaea suturalis*** adult, a herbivore on ***Calluna***, causing an increase in ***Sphagnum plumulosum*** (Figure 63) and ***Hypnum jutlandicum*** (Figure 64) as light increases. Photo by James K. Lindsey, with permission.

Figure 62. ***Calluna vulgaris*** – food source for ***Lochmaea suturalis***. Photo by Janice Glime.

Figure 63. ***Sphagnum plumulosum*** (= ***S. subnitens***), a species that increases when cover decreases. Photo by J. C. Schou <www.biopix.com/>, with permission.

Figure 64. ***Hypnum jutlandicum***, a species of mosses that increases in dunes following herbivory by ***Lochmaea suturalis***. Photo by Andrew Spink, with permission.

Figure 65. ***Sphagnum compactum***, a species that declines when ***Sphagnum plumulosum*** and ***Hypnum jutlandicum*** increase following loss of cover due to herbivory by ***Lochmaea suturalis***. Photo by Andrew Hodgson, with permission.

In the ***Racomitrium lanuginosum*** heaths (Figure 66), the Dotterel ***Charadrius morinellus*** (Figure 67) adults eat a large number of beetles (Galbraith *et al*. 1993). Both chicks and adults prefer habitats where both montane bogs and ***Racomitrium lanuginosum*** heaths are available to meet the feeding requirements of both adults and chicks. Overgrazing by sheep has endangered these suitable habitats.

Figure 66. ***Racomitrium lanuginosum*** hummocks in the UK. Photo by Alan Silverside, with permission.

Figure 67. ***Charadrius morinellus*** male, a forager for beetles in ***Racomitrium lanuginosum***. Photo by Helwig Brunner, through Creative Commons.

Bogs and Wetlands

Boháč and Bezděk (2004) found that in the Mrtvy Luh, Czech Republic, peat bog the species of **Staphylinidae** differed significantly between the bog margin and the center. Only 1 **tyrphophilous** (bog affiliate) species occurred in the marginal peat, whereas there were no **tyrphobionts** (species living only in bogs) or **tyrphophiles** (bog affiliates, breeding in bogs and elsewhere) in the center. Rather, the center of the bog was home to ***Drusilla canaliculata*** (Figure 68), a staphylinid that eats ants.

Figure 68. ***Drusilla canaliculata*** adult male, a bog dweller that eats ants. Photo by Christoph Benisch <www.kerbtier.de>, with permission.

Likewise, Bordoni (1972) found 179 species of Coleoptera, representing 25 families) in a Tuscan fen. Many were generalists and few were bryophilous. On the other hand, the Staphylinidae were the best represented and are moss feeders (Mani 1962). And ***Cretinis punctatostriata*** (**Hydrophilidae**) spends its entire life cycle in ***Sphagnum***, making it a true **bryobiont** (Matthey 1977). Its eggs are deposited in the ***Sphagnum*** and its pupation cell is constructed from bryophytes. On the other hand, many of the **bryophilous** mosses do not feed on the mosses, but rather feed on the epiphytic algae (LeSage & Harper 1976).

Using yellow pan traps and emergence traps, Runtz and Peck (1994) found 5734 beetles, representing 30 families, in a mature spruce-***Sphagnum*** bog (fen?) (Figure 69) in Algonquin Park, Ontario, Canada. Among these, members of the **Ptiliidae** were the most abundant and **Staphylinidae** was the most taxonomically diverse family. The **Carabidae** were also important, ranking second in diversity and third in abundance. But, as in many other studies, there are few beetle species specific to the bog. Most of the species in the bog are from adjacent habitats.

Figure 69. Boreal forest fen with spruce (***Picea mariana***) and ***Sphagnum fuscum***, home for many **Ptiliidae** and **Staphylinidae**. Photo by Richard Caners, with permission.

Kvamme (1976) found similar relationships to these in mires at Eidskog, Norway. He trapped (pitfall) 18 species of **Carabidae** and 4 of **Curculionidae** in thirteen mire habitats there. Only ***Agonum ericeti*** (Figure 41) seemed to be a true **tyrphobiont** (restricted to bog and mire habitats). Six species if **Carabidae** were **tyrphophiles** (typical in bogs and mires but not restricted to them). The greatest number of species occurred in the transition zone between the mire and the forest.

On the other hand, bogs are habitats where rare species occur. Wallin *et al*. (1999) found the rare carabid ***Chlaeniu***s ***costulatus*** (Figure 37) in a protected bog in central Sweden. Wallin *et al.* (2000) likewise found the rare ***Chlaenius sulcicollis*** (Figure 38). ***Chlaenius costulatus*** overwinters in the bog; larvae (Figure 70) and newly emerged adult beetles appeared in pitfall traps, suggesting that they have surface activity during all developmental stages.

Figure 70. ***Chlaenius*** sp. larva, a rare bog dweller. Photo by Tom Murray, through Creative Commons.

Carabid beetles have specific requirements within the bog that determine their distribution. The development of that fauna is closely related to the presence of a mosaic of hummocks and hollows (Främbs 1994). On the Swedish Ryggmossen ***Agonum ericeti*** (Figure 41) and ***Pterostichus rhaeticus*** (Figure 42) use damp ***Sphagnum*** lawns (Figure 2) for summer activities but migrate to drier hummocks for overwintering, accounting for the need for the mosaic. The rare carabid ***Chlaenius sulcicollis*** (Figure 38) was discovered in Sweden in a bog dominated by large ***Sphagnum*** hummocks (Wallin *et al*. 1999, 2000). Severe mandible wear in this beetle could be caused by intensive biting and burrowing needed to navigate the ***Sphagnum*** hummocks.

Hydroporus morio (Figure 71) has a similar topography requirement (Jackson 1956). This member of the **Dytiscidae** lives in bog pools, but when the pools dry out in summer it bores small, round holes in the deep ***Sphagnum***. There it **aestivates** (spends hot or dry period in prolonged state of torpor or dormancy) until the rain returns.

Figure 71. ***Hydroporus morio*** adult, a species that bores into ***Sphagnum*** when the bog pools dry out. Photo by Niels Sloth <www.biopix.dk>, with permission.

The genus ***Sphaerius***, a member of the family **Sphaeriusidae**, has members that live among mosses in bogs (Wikipedia 2015). The bog dwellers are able to store air under the **elytra** (hardened outer wings). ***Sphaerius acaroides*** is a minute scavenger beetle that occurs in moss and plant litter at the edge of slumping cliff seepages (Boyce 2002). Other scattered records exist from sites throughout England, including other wetland habitats such as fens.

It appears that some carrion beetles may be specific to peatlands (Beninger & Peck 1992). ***Nicrophorus*** carrion beetles (Coleoptera: Silphidae; Figure 72-Figure 73) utilize small mammal carcasses; some are able to spend their entire lives in the bog, using the bog carrion for reproduction, whereas others migrate to the nearby forest to reproduce (Beninger & Peck 1992). In the genus ***Nicrophorus*** (Coleoptera: **Silphidae**), the proportion of dead mice (***Mus musculus*** – house mouse; Figure 74) utilized in the peatland as a resource did not differ from that of the nearby forest. ***Nicrophorus*** buries its carrion under mosses and leaf litter (Eggert & Müller 1997). However, ***N. vespilloides*** (Figure 72) reproduced exclusively in the ***Sphagnum***, whereas ***N. defodiens*** (Figure 73) reproduced exclusively in the nearby mixed forest. Furthermore, three other species in the genus rarely occurred on bog carrion but were common on forest carrion. In other cases, it is the larvae of the beetles that live among the mosses (LeSage 1983).

Figure 72. ***Nicrophorus vespilloides*** adult, a species that reproduces in ***Sphagnum***. Photo by Holger Gröschl, through Creative Commons.

Figure 73. ***Nicrophorus defodiens*** adult, a species that leaves the ***Sphagnum*** to reproduce in the forest. Photo by John and Jane Balaban, through Creative Commons.

Figure 74. ***Mus musculus***, a mouse that provides small carrion for reproduction of some species of ***Nicrophorus***. Photo by Ozwildlife, through Creative Commons.

Parthenogenesis (reproduction from an egg without fertilization) is common in bogs, and ***Ptiliopycna moerens*** is one such species in the beetle family **Ptiliidae** (Dybas 1978). These featherwing beetles live mostly in ***Sphagnum*** bogs and similar habitats in swamp forests in eastern North America. In addition, ***Acrotrichis*** (Figure 75), ***Bythinopsis tychoides***, and ***Ptinella mekura*** are all small beetles in these bogs and all are parthenogenetic there.

Figure 75. ***Acrotrichis discolorides*** adult, member of a genus of small, parthenogenetic beetles of ***Sphagnum*** bogs. Photo through Creative Commons.

Antarctica and Antarctic Islands

Beetles are one of the groups of organisms that are able to survive in the harsh conditions of the Antarctic (Figure 76). On this icy continent, the **Curculionidae** exhibit two feeding groups – those that feed on flowering plants and those that feed on cryptogams (algae, lichens, and bryophytes). These feeding constraints result in habitat constraints. For example, on Heard Island, ***Ectemnorhinus viridis*** lives from sea level to 600 m, where it feeds on tracheophytes and bryophytes (Chown & Klok 2001). ***Candonopsis sericeus*** likewise feeds on these two plant groups, but in a narrower altitudinal range. Further details of Antarctic feeding habits in this family are discussed in the sub-chapter on Coleoptera Families.

Figure 76. Mosses in Antarctica, a safe refuge for beetles. Photo by Sharon Robinson, through Creative Commons.

Home for Rare Species

Bryophytes can often hold surprises, species that have been considered rare or were previously unknown. Such was the case when a group of British entomologists were forced to abandon collecting due to very cold, wet weather on the Isle of Wight (Appleton 1986). In a last furtive effort to make the trip worthwhile, the entomologists grabbed handfuls of moss to sample at home. As they sieved through them, they found three individuals of ***Baris analis*** (**Curculionidae**; Figure 77), unknown for a century, from mosses that had grown on low cliffs. Shepard and Barr (1991) were able to describe the larva of ***Atractelmis*** (**Elmidae**; Figure 78) from a bryophyte habitat. In Sweden, several red-listed ***Chlaenius*** (**Carabidae**; Figure 38) species inhabited the mosses (Wallin *et al.* 2000).

Figure 77. ***Baris analis*** adults mating, a rare species known from mosses. Photo by Roger Key, with permission.

Some moss beetles have been even more elusive. Duckett *et al*. (2006) described ***Ivalia korakundah*** (**Chrysomelidae**) as a new species from the Doddabetta Valley, India, where it inhabits mosses. On rocks, adults of this species occur among the branches of the moss ***Isopterygium*** sp. (Figure 79). Both adults and larvae were found by sifting mosses from large pine tree trunks.

Figure 78. ***Atractelmis*** larva, a bryophyte inhabitant. Photo by Joseph Fortier, through Creative Commons

Figure 79. ***Isopterygium elegans***, home for ***Ivalia korakundah*** on rocks. Photo by Kristian Peters, with permission.

In addition to rare species, new species are likely to be lurking among the mosses, and until more collecting is done in these habitats, these will seem rare. For example, Konstantinov and Duckett (2005) found a new member of **Chrysomelidae** – ***Clavicornaltica dali*** (Figure 80) – in Asia. Its type locality is in Yunnan, China, where it was found under a moss. This is a tiny, rounded beetle (1.13-1.24 mm) and the only known species of ***Clavicornaltica*** that has wingless males – a possible adaptation for moss-dwelling that can reserve more space and energy for developing the gut or other structure. In the same collection in China they found a new species of ***Benedictus*** together with ***Clavicornaltica dali*** (Konstantinov & Lourdes Chamorro-Lacayo 2006). No moss-inhabiting weevils were known from the New World until 2006 when these same researchers found the new genus ***Kiskeya*** (**Chrysomelidae**; Figure 81) and named two new species in the Dominican Republic.

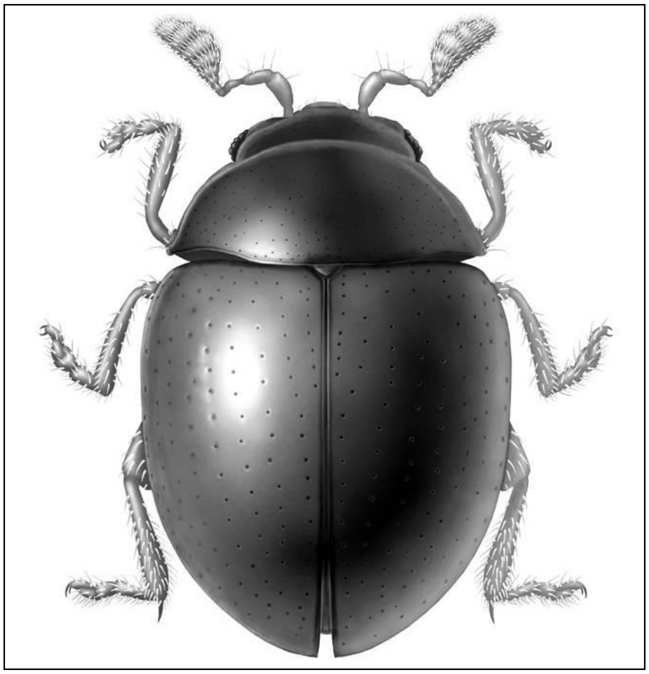

Figure 80. ***Clavicornaltica dali***, a moss-inhabiting flea beetle. Photo by Alexander Konstantinov; permission pending.

Figure 81. ***Kiskeya baorucae***, a moss-inhabiting flea beetle. Photo by Alexander Konstantinov; permission pending.

Invasive Bryophytes

We know that ***Curimopsis*** (**Byrrhidae**; Figure 7) eats the invasive moss ***Campylopus introflexus*** (Figure 82) (Brian Eversham, pers. comm.). On the other hand, Schirmel *et al*. (2011) found that the invasion of ***Campylopus introflexus*** into acidic coastal dunes (grey dunes; Figure 83) at the southern Baltic Sea shore coincided with a reduction among plant-eating beetles in **Carabidae** compared to those in native dune habitat. They considered this reduction to be the result of reduced food supply of arthropod food items in areas with dense carpets of this invasive moss. This is concerning because the dunes are home to many endangered species of arthropods.

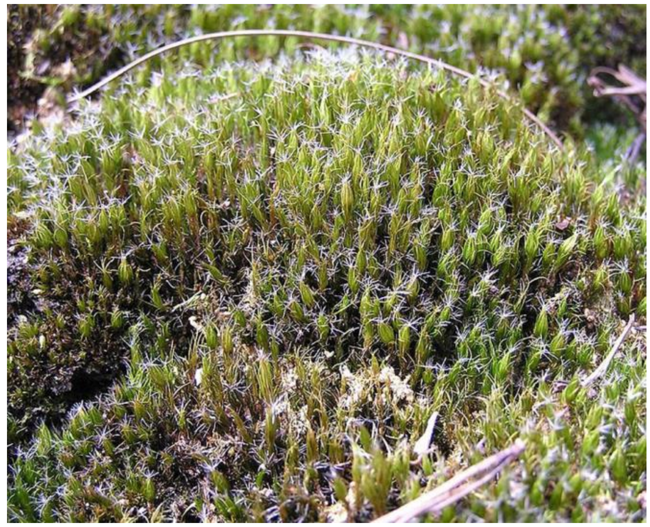

Figure 82. ***Campylopus introflexus***, an invasive moss in Europe that is food for ***Curimopsis***. Photo by Michael Becker, through Creative Commons.

Figure 83. ***Campylopus introflexus*** invading sand dunes. Photo from BIOSOS, permission pending.

Campylopus introflexus (Figure 82) forms dense carpets in these acidic coastal dunes, replacing native vegetation. Using pitfall traps, Schirmel and Buchholz (2013) compared trait composition of beetles and spiders. They found that this invasive moss caused body size and feeding preference of the **Carabidae** to shift. The species examined were smaller in the native habitats, perhaps because percentages of web-building spiders decreased in the sites of moss invasion. But the plant-eating beetles were reduced as well. Hence, the functional diversity of the **Carabidae** was likewise reduced. The functional diversity of spiders increased in the invaded dunes, but that of the carabid beetles decreased.

On South Georgia Island, introduced reindeer reduced the native grass vegetation of ***Poa flabellata*** (Christie 2010). This grass, home of ***Hydromedion sparsatum*** (**Perimylopidae;** Figure 84-Figure 87), was replaced by short grass ***Poa annua***, moss carpets, bare soil, and other unsuitable substrata for ***Hydromedion sparsatum***. As a result, this abundant beetle was reduced from more than 33% of the invertebrate fauna to 7-9%.

Figure 84. ***Hydromedion sparsatum*** larva, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.

Figure 85. ***Hydromedion sparsatum*** pupa, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.

Figure 86. ***Hydromedion sparsatum*** adult, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.

Figure 87. ***Hydromedion sparsatum*** adult, a species whose abundance is reduced by invasion of mosses on South Georgia. Photo by Roger Key, with permission.

Summary

Beetles comprise the largest order of insects and live in almost every imaginable habitat. Their membranous wings are protected by the outer hardened **elytra**, but many of the bryophyte dwellers are flightless. The greatest numbers among bryophytes are **Curculionidae** and **Staphylinidae**, both very large families, but some, like the **Byrrhidae**, are moss specialists, living mostly in bryophytes and eating them.

The moss-dwelling beetles are typically tiny and rounded. Some are able to play dead (**Byrrhidae**) and can retract their legs into grooves on the lower surface. This family, and others, lay their eggs among the mosses. Some live in water as larvae and adults, but come to land to pupate among the mosses. Some migrate up and down in ***Sphagnum*** hummocks to adjust to changing moisture conditions or to overwinter.

Many beetles not only live among mosses, but also eat them. A wide range of mosses seem to be suitable for food, but some are refused. Few beetles, however, seem to eat liverworts. In geothermal areas, the mosses provide a moist and warm refuge in these polar climates.

In forests, bryophytes provide a more moist refuge following a disturbance that opens the canopy. In other cases, the beetles may attack the forest canopy, exposing the bryophytes and causing species changes. Many forest species are likely to be transported around the world as hitch-hikers among horticultural mosses.

In dunes, the invasion of the moss ***Campylopus introflexus*** is changing the kinds of species of beetles occurring there, reducing the beetle functional diversity. Different kinds of heathlands differ in kinds of bryophytes and their beetle fauna.

Bogs are often home to rare beetle species, and some are tiny, wingless, and parthenogenetic, hence poorly dispersed. Here, and elsewhere, sampling bias can miss these tiny, immobile beetles. Hand sorting is the only reliable, albeit time-consuming, method for finding all the species.

On one hand, bryophytes often harbor rare or unknown species. On the other hand, invasive bryophytes can cause reductions in the number of beetle species or their abundance due to replacing food plants.

Acknowledgments

I appreciate all the photographers who have given me permission or placed their images on the web with a Creative Commons license. As usual, Bryonetters have helped me find images when I was unable to find ones I needed. Thank you to Gerhard Winter for helping me find that tramling was meant to be trampling, getting an explanation from the second author, A. Bezděk.

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