CHAPTER 12-9c
TERRESTRIAL INSECTS: HOLOMETABOLA – COLEOPTERA FAMILIES

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CHAPTER 12-9c TERRESTRIAL INSECTS: HOLOMETABOLA – COLEOPTERA FAMILY

Figure 1. **Curculionidae** on moss and litter in Ecuador. Photo by Andreas Kay, through Creative Commons.

POLYPHAGA cont.

Chrysomeloidea

Chrysomelidae – Flea Beetles, Leaf Beetles

This family of 35,000 species ranges 1-18 mm in length (Wikipedia 2015c). They are distributed everywhere except the high Arctic and the Antarctic (Benisch 2015a). All the species have wings, although some are slightly shortened so that the tip of the abdomen is visible (Wikipedia 2015c). And most are serious agricultural pests. But some are moss dwellers.

Among the earliest records of the **Chrysomelidae** from mosses is ***Plateumaris sericea*** (**Donaciinae**; Figure 2). Beare (1899) found several of these in his collecting in Surrey, UK.

Figure 2. ***Plateumaris sericea*** mating, a species that lives among mosses in the UK. Photo by Hedwig Storch, through Creative Commons.

One of the most frequently reported bryobionts is ***Mniophila muscorum*** (Figure 3), the moss flea beetle (Champion 1871; Kühnelt 1976; Cox 1997; Konstantinov & Lourdes Chamorro-Lacayo 2006). Its name says it all – a moss-loving moss dweller. It is a true **bryobiont**, living among the "litter" and feeding on mosses (Kühnelt 1976). And it has the typical small size of a moss dweller (1.1-1.6 mm for the genus), is globose, and has reduced hind wings (Nadein 2009). A shiny black elytra is common among small moss-dwelling beetles and is likewise characteristic of these. These characters are shared by ***Mniophilosoma***, ***Apteropeda*** (Figure 4), ***Minota*** (Figure 5), ***Clavicornaltica*** (Figure 6), and ***Kiskeya*** (Figure 40).

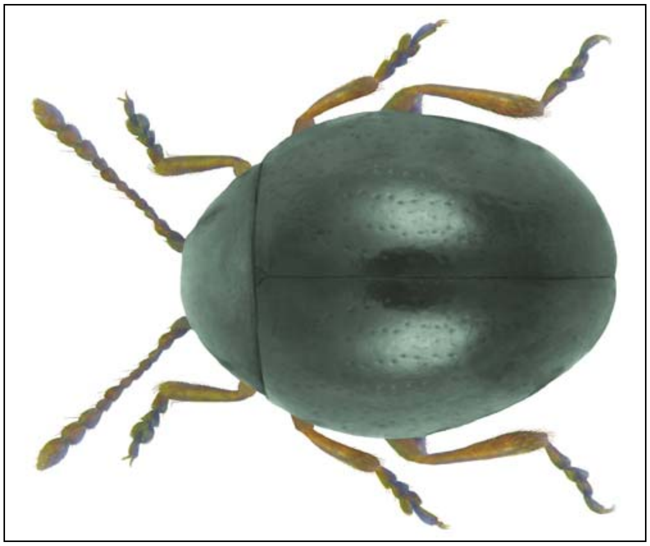

Figure 3. ***Mniophila muscorum***, the common moss dweller known as the moss flea beetle. Photo by Udo Schmidt, with permission.

Figure 4. ***Apteropeda globosa*** adult with moss. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

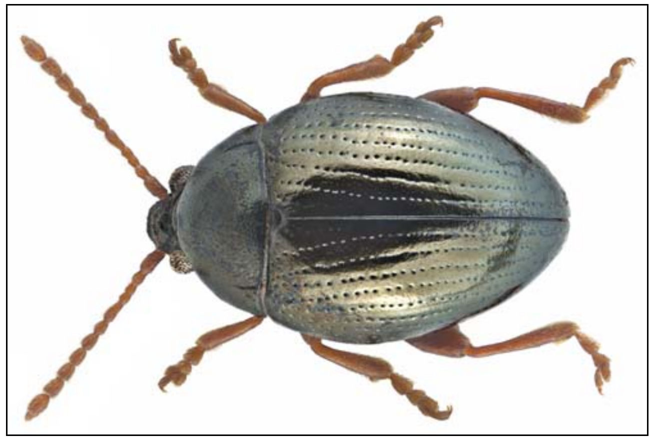

Figure 5. ***Minota obesa***, a shiny black and minute moss dweller. Photo by Udo Schmidt, with permission.

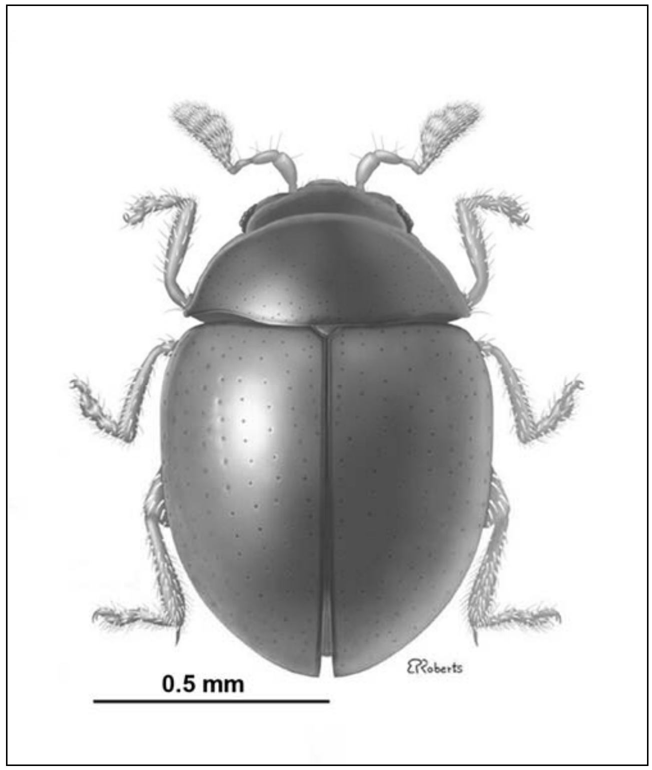

Figure 6. ***Clavicornaltica dali***, a common moss dweller. Image by Sasha Konstantinov, with permission.

Unlike many members of the family, ***Mniophila muscorum*** (Figure 3) is not a leaf miner (Cox 1997). Instead, both larvae and adults occur on mosses, the latter including ***Rhytidiadelphus loreus*** (Figure 7), ***R. triquetrus*** (Figure 8), and ***Eurhynchium striatum*** (Figure 9), all of which grow in a variety of habitats and on a variety of substrates (log stumps, fallen trees, tree branches, rocks, walls, and chalky slopes). They are also known from a number of other bryophyte species of both ground, boulders, and tree boles, including liverworts (Nadein 2009). Their substrate preference seems to depend on elevation. Those on vertical surfaces are usually restricted to thicker mats and cushions. And at least the first instar larvae are surface feeders on mosses. Nadein (2009) described the new species ***Mniophila taurica***, ***M. transcaucasica***, and ***M. caucasica*** from mosses in the Crimean Mountains. ***Mniophila taurica*** is known from the mosses ***Brachythecium glareosum*** (Figure 10), ***Homalothecium philippeanum*** (Figure 11), and ***Plagiomnium rostratum*** (Figure 12). The genus ***Mniophila*** seems to prefer fresh mosses – not dry or sopping wet. The beetles may be on the surface or within the moss colony.

Figure 7. ***Rhytidiadelphus loreus***, home for larvae and adults of ***Mniophila muscorum***. Photo by Hermann Schachner, through Creative Commons.

Figure 8. ***Rhytidiadelphus triquetrus*** Canyon Falls, MI, home for larvae and adults of ***Mniophila muscorum***. Photo by Janice Glime.

Figure 9. ***Eurhynchium striatum*** with capsules, a species of a wide variety of habitats, serving as a home for ***Mniophila muscorum***. Photo by J. C. Schou <www.biopix.com/>, with permission.

Figure 10. ***Brachythecium glareosum***, home to some ***Mniophila taurica***. Photo by Michael Lüth, with permission.

Figure 11. ***Homalothecium philippeanum***, home to some ***Mniophila taurica***. Photo by Michael Lüth, with permission.

Figure 12. ***Plagiomnium rostratum***, home to some ***Mniophila taurica***. Photo by Michael Lüth, with permission.

Let's return to those look-alikes for ***Mniophila*** (Figure 3). Gillerfors (1986) described ***Mniophilosoma obscurum*** from ***Sphagnum*** (Figure 13) and other substrata in the Azores. ***Mniophilosoma laeve*** occurs among mosses and other substrata in Europe (Wollaston 1857). Despite the generic name, which translates to moss-loving body, this genus often lives under bark. ***Apteropeda orbiculata*** (Figure 14-Figure 15) and ***A. globosa*** (Figure 4) both occur on mosses (Tomlin 1913). Tomlin also described ***Phaedon tumidulus*** (Figure 16-Figure 17), which occurs among mosses in Great Britain (Tomlin 1913). ***Cassida viridis*** (Figure 18-Figure 19) occasionally overwinters among mosses.

Figure 13. ***Sphagnum russowii***, a potential home for many species of beetles. Photo by Andrew Hodgson, with permission.

Figure 14. ***Apteropeda orbiculata*** larva, a moss dweller. Photo by Willem Ellis, with permission.

Figure 15. ***Apteropeda orbiculata*** adult, a moss dweller. Photo through Creative Commons.

Figure 16. ***Phaedon tumidulus*** larva, a resident among mosses at times. Photo by Keith Edkins, through Creative Commons.

Figure 17. ***Phaedon tumidulus*** adult, a sometimes moss resident. Photo by Keith Edkins, through Creative Commons.

Figure 18. ***Cassida viridis*** larva, a species that occasionally overwinters among mosses. Note the shed exuvia that the larva is carrying on its back. This is an unusual habit that may have a role in avoiding predation. Photo by James K. Lindsey, with permission.

Figure 19. ***Cassida viridis*** adult, a species that occasionally overwinters among mosses. Photo by Roger S. Key, with permission.

The adult of ***Minota*** (Figure 5) occurs among mosses or litter in northern Eurasia (Medvedev 1997). But ***Minota nigropicea*** feeds on the ferns *Dryopteris erythrosora* (Figure 20), *Pteridium aquilinum* (Figure 21), and *Cyrtomium fortunei* (Figure 22) (Kimoto 1984; Kato 1991). Thus, being tiny, globose, shiny black, and having reduced hind wings adapts these flea beetles for not only mosses, but also for life on ferns and under bark.

Figure 20. ***Dryopteris erythrosora***, food for ***Minota nigropicea***. Photo by Megan Hansen, through Creative Commons.

Figure 21. ***Pteridium aquilinum*** habitat at edge of forest, food for ***Minota nigropicea***. Photo by Rasback, through Creative Commons.

Figure 22. ***Cyrtomium fortunei***, food for ***Minota nigropicea***. Photo by Harum.Koh, through Creative Commons.

In a Cornish *Calluna* heath (Figure 23), Brown (1991) noted that the young larval stages of the heather beetle, ***Lochmaea suturalis*** (Figure 24), are dependent on the moisture of the moss layer. They are only found in older *Calluna* heaths, where ***Pleurozium schreberi*** (Figure 25) has had time to develop. When there is no moss layer present, these larvae have a density of about 0.4 per sample compared to 25 per sample when a moss layer is present. The mosses are essential to the larvae (Garvey 2011). Adults are destructive of the *Calluna*. This destruction initiates a complex series of events (Scandrett & Gimmingham 1991). The ***Sphagnum plumulosum*** (Figure 26) and ***Hypnum jutlandicum*** (Figure 27) increase, while ***Sphagnum compactum*** (Figure 28) and ***Pleurozium schreberi*** decrease. The *Calluna* is able to regenerate through layering, no doubt facilitated by the moisture-holding mosses, and by seedling development, especially in the ***Sphagnum***.

Figure 23. Heathland, home of the heather beetle, ***Lochmaea suturalis***, where the beetle larva lives among the moss ***Pleurozium schreberi***. Photo by Willow, through Creative Commons.

Figure 24. ***Lochmaea suturalis*** adult, a species whose larvae require the moisture of moss mats. Photo by Niels Sloth <www.biopix.dk>, through Creative Commons.

Figure 25. ***Pleurozium schreberi***, home for ***Lochmaea suturalis*** in heathlands. Photo by J. C. Schou <www.biopix.com/>, with permission.

Figure 26. ***Sphagnum subnitens***, a species that increases when ***Lochmaea suturalis*** damages the *Calluna* and increases light penetration. Photo by Michael Lüth, with permission.

Figure 27. ***Hypnum jutlandicum***, a species that increases when ***Lochmaea suturalis*** damages the *Calluna* and increases light penetration. Photo by Janice Glime.

Figure 28. ***Sphagnum compactum***, a species that decreases when ***Lochmaea suturalis*** damages the *Calluna* and increases light penetration. Photo by Michael Lüth, with permission.

In the heathland, ***Lochmaea suturalis*** (Figure 24) oviposits at the base of the *Calluna* (Figure 23), usually among ***Sphagnum*** (Beagan 2015). The larvae crawl up the *Calluna* to eat the leaves, developing to as much as 2 cm in length. The mature larvae return to the mosses, where they spend 4 weeks to pupate. Then adults return to eat the *Calluna* leaves again, but once more return to ground level to spend the winter.

Recently, Sasha Konstantinov and associates have entered the picture, specializing in the tiny tribe of **Alticini**, among which are many previously ignored moss dwellers. The tiny size and time-consuming process of separating these beetles from their moss cushions seems to have discouraged most coleopterists. After all, this is the largest order of insects, and there were many much easier beetles to study.

The elusive ***Phaelota*** beetles living among mosses are typically small, with lengths about 2-3 mm, and are flightless (Prathapan & Konstantinov 2009). Among collections of six new species in the genus ***Phaelota*** from India, three were from mosses and a fourth moss dweller (***P. semifasciata***) was not new but was longer (up to 5 mm). The new moss-dwelling species include ***Phaelota saluki*** (Figure 29) from the moss ***Forsstroemia thomsonii***, ***P. maculipennis*** (Figure 30), and ***P. viridipennis*** (Figure 31) from moss on tree trunks and rocks. The two groups of species are separated by their ability to fly – those living on ferns are capable of flight, but the moss-dwelling species are flightless. This flight restriction may be an adaptation to protect them from the windy mountain habitat (> 1470 m) where they reside in Southern India. In India they occur in the humid tropical evergreen forests of the Western Gats at 1000-2600 m asl (Konstantinov *et al*. 2013). ***Phaelota kerzhneri*** (Figure 32) from Borneo, like other flightless members of ***Phaelota***, is probably also an inhabitant of moss (Prathapan & Konstantinov 2008).

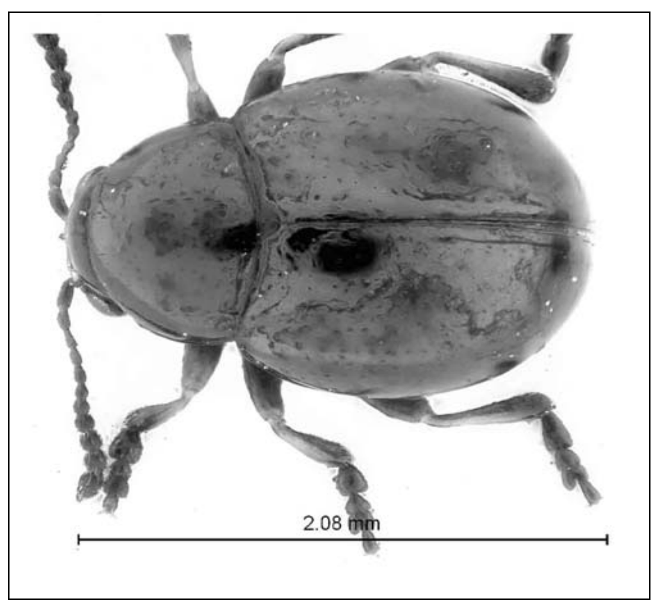

Figure 29. ***Phaelota sakuli*** adult, a moss dweller in India. Photo courtesy of Sasha Konstantinov.

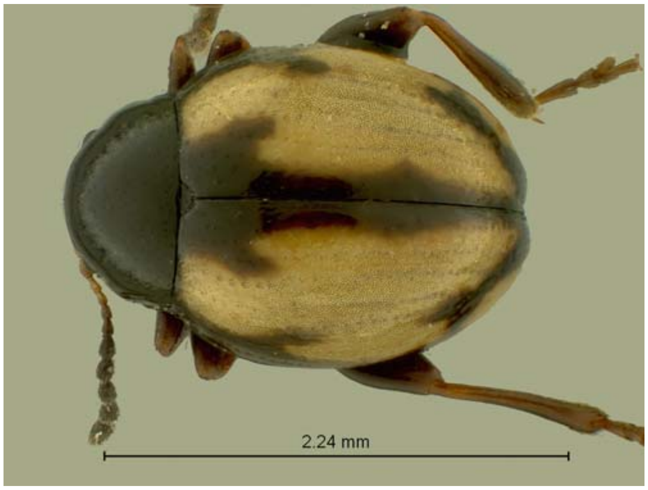

Figure 30. ***Phaelota maculipennis*** adult, a moss dweller in India. Photo courtesy of Sasha Konstantinov.

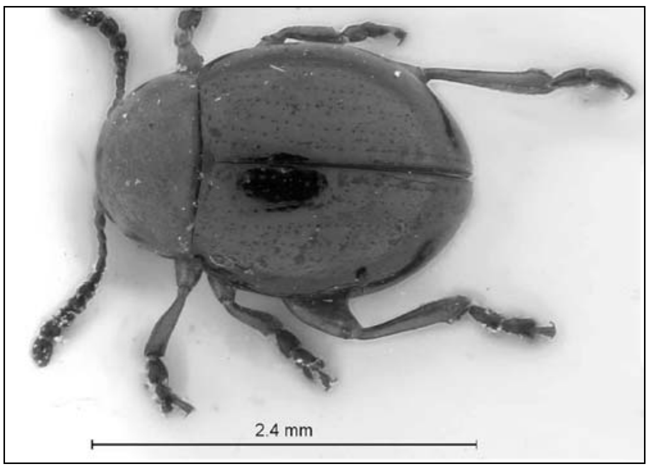

Figure 31. ***Phaelota viridipennis*** adult, a moss dweller in India. Photo courtesy of Sasha Konstantinov.

Figure 32. ***Phaelota kerzhneri*** adult, a probable moss dweller from Borneo. Image by Sasha Konstantinov, with permission.

Both Indian species in the genus ***Ivalia*** are moss dwelling, but their selection of host plants is not related to a loss of flight – their flightlessness apparently evolved before their choice of mosses for food (Prathapan & Konstantinov 2009). Recently, Duckett *et al*. (2006) found both adults and larvae of the new species ***Ivalia korakundah*** (Figure 33) on mosses in southern India by sifting mosses from the trunks of large pine trees. ***Ivalia korakundah*** also feeds on mosses. In one case, adults were found on the moss ***Isopterygium*** sp. (Figure 34). This genus seems to prefer more humid environments of the tropical evergreen forests, especially at altitudes of 1000 to 2600 m asl in the Western Ghats (Konstantinov *et al*. (2013).

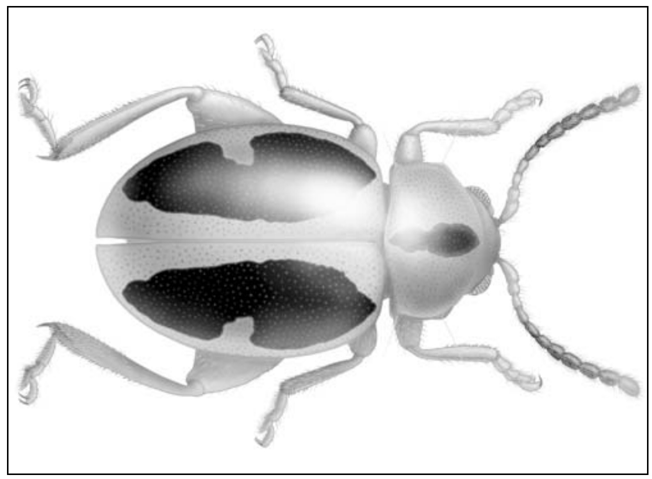

Figure 33. ***Ivalia korakundah***, a moss dweller from pine trees in India. Image by Sasha Konstantinov, with permission.

Figure 34. ***Isopterygium elegans***, potential home, and probably food, for ***Ivalia korakundah***. Photo by Robin Bovey, with permission from Dale Vitt.

In China, Konstantinov *et al*. (2013) described the new genus and species ***Cangshanaltica nigra*** (Figure 35-Figure 36) from the moss cushions of ***Hypnum*** (Figure 27). Unlike findings in most of the studies on such tiny beetles, Konstantinov and coworkers were able to find ***Hypnum*** in the guts of these beetles. These likewise are among the smallest leaf beetles; they have round bodies with robust appendages, reduced hind wings, highly simplified and shortened meso- and metathorax, and their antennae have "more or less" enlarged apical antennomeres.

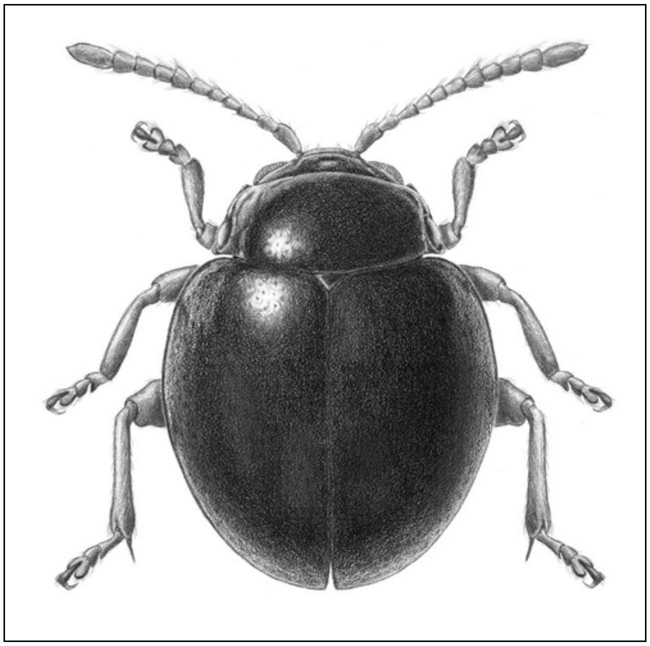

Figure 35. ***Cangshanaltica nigra*** adult, a species that lives among ***Hypnum*** in China. Image courtesy of Sasha Konstantinov.

Figure 36. ***Cangshanaltica nigra*** habitat. Photo courtesy of Sasha Konstantinov.

Figure 37. ***Hypnum cupressiforme***, a genus that provides homes for ***Cangshanaltica nigra*** in China. Photo by Michael Becker, through Creative Commons.

The members of ***Cangshanaltica*** (Figure 35) are small (0.8.-.2 mm) and rounded (Konstantinov & Duckett 2005). The elytra covers the abdomen, but the bodies are fragile and easily broken. The genus is distinctive in having **clavate** antennae (thicker at apex, like a club).

The additions of moss-dwelling species continue. Damaška and Konstantinov (2016) added another species of ***Cangshanaltica siamensis*** (Figure 38) from Thailand. In this case, the beetles are able to survive the dry season in the moss cushions.

Figure 38. ***Cangshanaltica siamensis***, a moss dweller from Thailand. Photo by Sasha Konstantinov, with permission

Konstantinov and Duckett (2005) found ***Clavicornaltica dali*** (Figure 39) at 3300 m in China under mosses. The tiny ***Clavicornaltica*** are distributed in Sri Lanka, Vietnam, and Thailand, despite their wingless males and mostly wingless females. This new species is among the first known for the genus in China and raises the question of dispersal mechanisms. Could they be distributed with the mosses they inhabit?

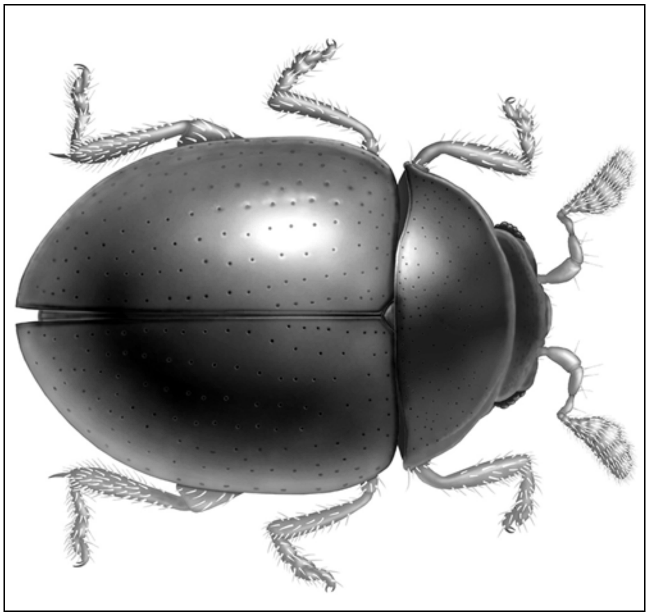

Figure 39. ***Clavicornaltica dali***, an Asian species that lives under mosses. Image by Alexander Konstantinov, with permission.

Benedictus (Figure 53), a moss inhabitant in Asia, is not present (or hasn't been discovered) in the New World (Sprecher-Uebersax *et al*. 2009). In fact, it seems that the Eastern and Western Hemispheres have distinct genera.

As is common for the **Alticini** bryophyte dwellers, new species and even genera are lurking in these neglected habitats, and this seems especially true for the Western Hemisphere. Konstantinov and Lourdes Chamorro-Lacayo (2006) sieved moss samples in forests of the Dominican Republic and were able to describe the new genus ***Kiskeya*** (Figure 40), small, rounded beetles at 1.06-1.10 mm long, with two species, ***K. baorucae*** (Figure 40) and ***K. neibae***. ***Kiskeya baorucae*** was collected from mosses in forests where they were growing on rocks, dangling as pendent mosses, and growing on the boles of trees. ***Kiskeya neibae*** was collected in forests from mosses growing on rocks, tree stumps, boles, and branches (Figure 41). Using a Berlese funnel, the researchers also extracted ***Aedmon*** sp. (**Alticini**; Figure 42) from the mosses.

Figure 40. ***Kiskeya baorucae***, a species that lives on mosses in forests – on rocks, tree boles, and pendent mosses. Photo by Alexander Konstantinov, with permission.

Figure 41. ***Kiskeya neibae*** habitat. Photo courtesy of Sasha Konstantinov.

Figure 42. ***Aedmon ferruginea*** adult, a moss dweller in the Dominican Republic. Photo by Celeigher Piñango, through Creative Commons.

Again in 2011, Konstantinov and Konstantinova found a new genus (***Borinken***) and three new species of moss dwellers in Puerto Rico by sifting mosses. ***Borinken elyunque*** (Figure 43) is a tiny (1.08-1.18 mm) beetle from the forest, living in mosses on rocks, tree stumps, tree boles, and branches. ***Kiskeya elyunque*** (Figure 44), an even smaller species (0.81-0.92 mm), lives in similar habitats. By comparison, ***Ulrica eltoro*** (Figure 45) is much larger (1.94-2.16 mm) and likewise lives among mosses in similar locations, whereas ***Ulrica iviei*** (Figure 46), also a new species, is thus far known only from leaf litter.

Figure 43. ***Borinken elyunque***, a moss dweller in Puerto Rico. Photo courtesy of Sasha Konstantinov.

Figure 44. ***Kiskeya elyunque*** adult, a moss dweller in Puerto Rico. Photo courtesy of Sasha Konstantinov.

Figure 45. ***Ulrica eltoro*** adult, a moss dweller in Puerto Rico. Photo courtesy of Sasha Konstantinov.

Figure 46. ***Ulrica iviei*** adult, a litter species in the Dominican Republic. Photo by Sasha Konstantinov, with permission.

The moss-inhabiting ***Kiskeya*** (Figure 40, Figure 44) is known elsewhere in the Neotropics. There are three species in the West Indies, two in the Dominican Republic, and one in Puerto Rico (Konstantinov & Konstantinova 2011).

Konstantinov *et al*. (2013) described ***Cangshanaltica nigra*** from Yunnan Province in China.

Konstantinov *et al*. (2015) have recently added five new species of ***Monotalla*** in the West Indies. Of these, ***Monotalla maierae*** is a new species that occurs in mosses and litter and ***M. viridis*** is a new species from epiphytic mosses.

Figure 47. ***Monotalla maierae*** adult, a moss dweller in the West Indies. Photo by Sasha Konstantinov, with permission.

Figure 48. ***Monotalla viridis*** adult, a species from epiphytic mosses in the West Indies. Photo by Sasha Konstantinov, with perission.

As is clear by these examples, the Western Hemisphere moss inhabitants have remained almost unexplored. Konstantinov *et al*. (2009) found another new genus in Nicaragua. ***Nicaltica selvanegra*** (Figure 49), a species similar to ***Kiskeya***, likewise lives among mosses there. In Bolivia, Konstantinov *et al*. (2014) discovered another new genus of moss and litter dwellers; ***Stevenaltica normi*** (Figure 50) and ***S. erronis*** (Figure 51) both include mosses as well as leaf litter as their habitats.

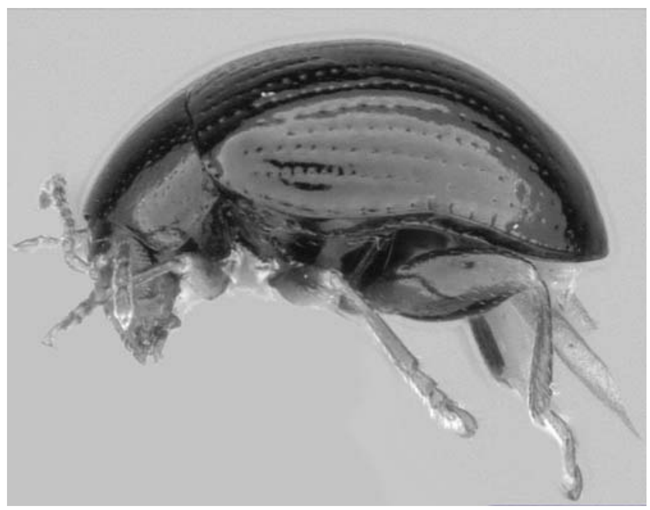

Figure 49. ***Nicaltica selvanegra*** male, a moss dweller in Nicaragua. Photo courtesy of Sasha Konstantinov.

Figure 50. ***Stevenaltica normi*** adult. a moss and leaf litter dweller in Bolivia. Photo courtesy of Sasha Konstantinov.

Figure 51. ***Stevenaltica erronis***. a moss and leaf litter dweller in Bolivia. Photo courtesy of Sasha Konstantinova.

Distigmoptera borealis (Figure 52) eats mosses in North America (Konstantinov, pers. comm. 26 June 2016). And that's it! Other records for North America are lacking. This species is known from North Dakota (Fauske 2014) and Oklahoma (Palmer 2016).

Figure 52. ***Distigmoptera borealis***, the only moss-dwelling genus known in North America. Photo from BIO Photography group, Biodiversity Institute of Ontario, through Creative Commons.

As of 2013, of the 14 known genera of moss-dwelling **Alticini**, only six were true **bryobionts** [***Kiskeya*** (Figure 40), ***Borinken*** (Figure 43), ***Cangshanaltica*** (Figure 35), ***Mniophila*** (Figure 3), ***Nicaltica*** (Figure 49), and ***Ulrica*** (Figure 45)] (Konstantinov *et al*. 2013). The remaining eight are **bryophiles** [***Benedictus*** (Figure 53), ***Clavicornaltica*** (Figure 39), ***Ivalia*** (Figure 33), ***Monotalla*** (Figure 47-Figure 48), ***Minota*** (Figure 5), ***Paraminota*** (Figure 54), ***Paraminotella*** (Figure 55), and ***Phaelota*** (Figure 29-Figure 32)]. By 2016, the number of known moss-inhabiting **Alticini** genera in the world grew to 15 and the number of species to 30 (Damaška & Konstantinov 2016).

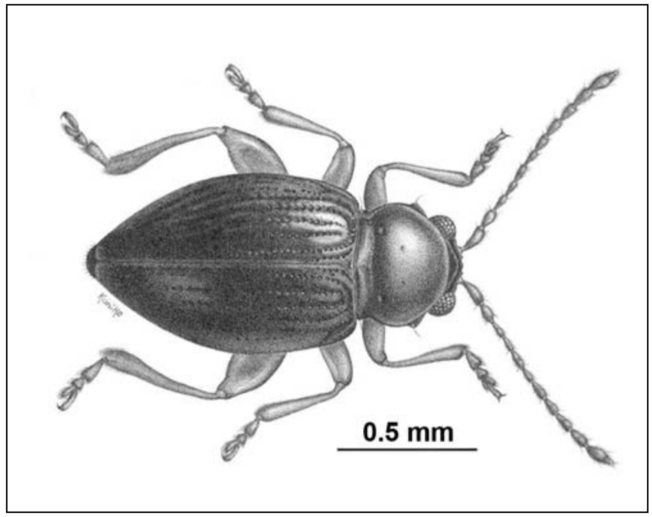

Figure 53. ***Benedictus shivalayanicus*** adult, Sasha Konstantinov.

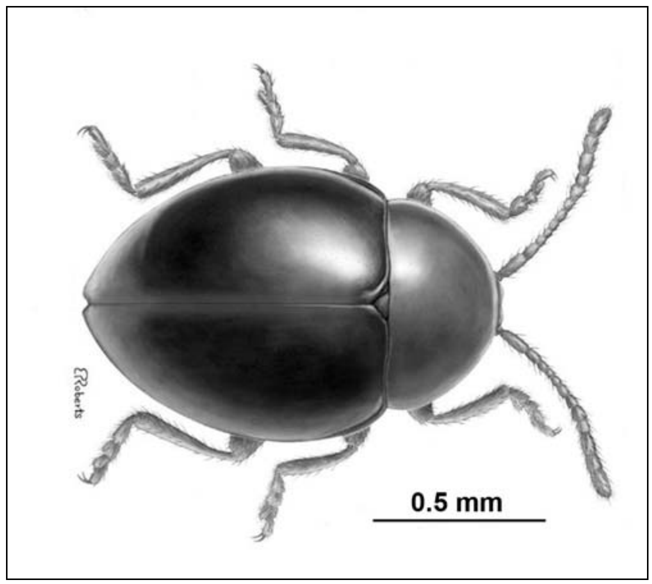

Figure 54. ***Paraminota lauribina***, member of a moss-dwelling genus. Image permission from Sasha Konstantinov.

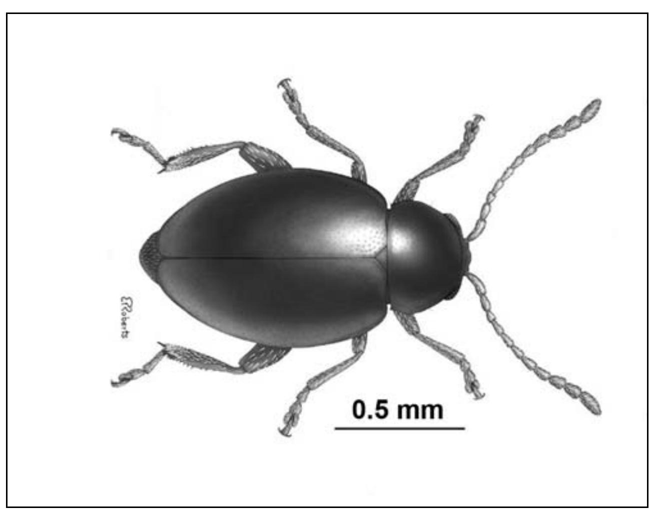

Figure 55. ***Paraminotella nigrita*** adult, member of a moss-dwelling genus. Image permission from Sasha Konstantinov.

There is good reason why so many new beetle species remain to be found among bryophytes. Many of these bryophyte dwellers are flightless. Furthermore, their moisture requirements are somewhat specific. Many are mountain-dwellers, living only above certain elevations. This combination makes it difficult for the beetles on one mountain to mix with those on another. When one or a few do disperse to a new mountain, both the **founder principle** (small population arrives in a new area and does not represent the genetic frequencies of its parent population) and **genetic drift** (random changes in gene frequencies that are common in small populations) are likely to play a role. As time passes, original and new populations diverge genetically, and over geologic time – or less – they can become separate species. When a single individual arrives in a new location, perhaps carrying fertilized eggs or for some beetles being **parthenogenetic** (reproducing from an unfertilized egg), this individual does not represent the middle of the curve of variation and produces offspring that are recognizably different from most of the individuals at the source. Do they pass the test of reproductive isolation? As long as they are separated by a valley, yes. Could they interbreed if they were joined? That remains to be tested.

Cucujoidea

Latridiidae – Minute Brown Scavenger Beetles

These small (0.8-3 mm) beetles number 1000 species (McClarin 2005). Most are associated with leaf litter, but around habitation they associate with other rotting vegetable matter. They are elongate with sculptured thorax and outer wings. Aside from their small size, they are not well adapted for bryophytes, although their coloration is usually dull and may be mottled. The sculpturing may also help to disguise them.

Some **Latridiidae** (Figure 58) take advantage of moss inhabitants for food. This family of beetles feeds on **Myxomycetes** (slime molds; Figure 56-Figure 57) (Dudka & Romanenko 2006), and these are often found among bryophytes. Decaying logs provide good habitats for slime molds and for mosses. And the slime molds often invade the space of the bryophytes. The mosses may also improve the habitat for the slime molds by increasing the moisture retention. Hence, the bryophytes on these logs provide protected sites where the **Latridiidae** can feed on the slime molds.

Dudka and Romanenko (2006) found 13 species of slime molds on 9 species of mosses and 3 of liverworts at the Crimean Nature Reserve. Most of these slime molds occur on non-bryophyte substrates as well, but some, like ***Physarum cinereum*** (Figure 56-Figure 57), occur predominantly on bryophyte substrates. Dudka and Romanenko (2006) found that ***Enicmus*** (Figure 58) and ***Dienerella*** (Figure 59) were the most common **Latridiidae** on moss-dwelling slime molds. The beetles not only use the slime molds for food, but also for oviposition and cover.

Figure 56. ***Physarum cinereum*** plasmodium, a bryophyte-inhabiting slime mold that feeds slime-mold-eating **Latridiidae**. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 57. ***Physarum cinereum*** with fruiting bodies, a bryophyte-inhabiting slime mold that feeds slime-mold-eating **Latridiidae**. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

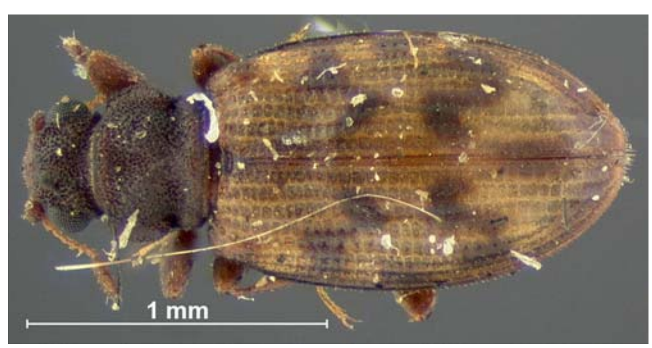

Figure 58. ***Enicmus maculatus*** adult, one of the most common **Latridiidae** genera that lives on moss-dwelling slime molds. Photo from Museum of Comparative Zoology Harvard, through Creative Commons.

Figure 59. ***Dienerella ruficollis*** adult, one of the most common **Latridiidae** genera on moss-dwelling slime molds. Photo by Tom Murray, through Creative Commons.

Curculionoidea

Atelabidae – Leaf-rolling Weevils

This family got its name because the female lays her eggs in leaves, then rolls the leaf around them. It is unlikely that these are regular moss dwellers. It is more likely that these are one of many of the beetles that traverse mosses simply because they are there. Although the mosses can provide moisture and a home for prey items, many species of beetles may arrive there without actually choosing to be in a mossy habitat. Such may be the case for the atelabid ***Eugnamptus angustatus*** (Figure 60), a 4.8 mm beetle Stephen Cresswell found walking on a moss in West Virginia, USA. Or it may have been searching there for food or replenishing body moisture. Behavioral studies on beetles associated with bryophytes are greatly needed.

Figure 60. ***Eugnamptus angustatus*** on moss – does it live there, or is it just visiting? Photo by Stephen Cresswell, with permission.

Curculionidae – Weevils

These are the cute little beetles with long "snouts" (Figure 61), somewhat resembling a miniature aardvark. A number of species have been discovered on bryophytes, eat them [Chown (1993) reported records of 35 species eating bryophytes], and some weevils even carry mosses around as camouflage.

Figure 61. ***Cionus hortulanus*** adult showing long snout with antennae on it. Photo by Lukas Jonaitis, through Creative Commons.

It seems that most beetles treat mosses as if they were litter, much like many soil biologists do. ***Ceutorhynchus erysimi*** (Figure 62), a species of Europe and invasive in the US, lives among mosses and forest litter around rhododendrons (in The Netherlands) (USDA 1950). ***Cryptorhynchus lapathi*** (Figure 63) lays its 1 mm long eggs mostly at stem bases, but also high in the crowns of large trees, under soil, or in the moss layer (Broberg 1997).

Figure 62. ***Ceutorhynchus erysimi*** adult among mosses, a species that lives among mosses and forest litter. Photo by Mick E. Talbot, through Creative Commons.

Figure 63. ***Cryptorhynchus lapathi*** adult, a species that sometimes lays eggs on mosses. Photo by Gyorgy Csoka, through Creative Commons.

I have been finding the best records of bryophyte-dwelling insects among those of the UK, especially the old records. For example, Moncreaff (1871) reported ***Baridius lepidii***, ***Phytobius waltoni*** (=*Pelonomus waltoni*; Figure 64), and ***Litodactylus leucogaster*** (=*Phytobius leucogaster*) from mosses in Portsea, British Isles. ***Bagous laticollis*** was abundant in mosses. Tomlin (1913) was able to find ***Liosoma ovatulum*** among mosses in Glamorgan, Wales, year round.

Figure 64. ***Phytobius waltoni*** adult, a moss dweller in the British Isles. Photo by Stefan Schmidt, through Creative Commons.

Dyer and Nijholt (2016) reported finding adults of ***Pseudohylesinus sericeus*** (Figure 65) and ***P. grandis*** (Figure 66), both pests on conifers in the western part of North America (USDA 2016), hibernating in thick mosses that grew on the trunks of oak trees in Oregon, USA. But in British Columbia, ***P. granulatus*** (Figure 67) instead penetrated the mosses on the amabilis fir and once there bored into the bark.

Figure 65. ***Pseudohylesinus sericeus*** adult, a conifer pest that hibernates among mosses. Photo by Javier Marcado, USDA APHIS ITP, Bugwood.org, through Creative Commons.

Figure 66. ***Pseudohylesinus grandis*** adult, a conifer pest that hibernates among mosses. Photo by Tim Loh, with permission.

Figure 67. ***Pseudohylesinus granulatus*** adult, a species that enters mosses to bore into the amabilis fir bark. Photo by Steven Valley, USDA APHIS ITP, Bugwood.org, through Creative Commons.

Some beetles only use bryophytes in part of their life cycle. Larvae of the weevil ***Palirhoeus eatoni*** (syn. =***Mesembriorrhinus eatoni***) develop in tufts of algae (Doyen 1976). But when it is time for pupation, the larvae in Antarctic waters move above the high water line to pupate in clumps of the moss ***Grimmia amblyophylla***. Mosses are often a safe haven for Antarctic arthropods in winter.

On the Austral Islands of the South Pacific, a number of new, hence **endemic**, species of ***Miocalles*** (Figure 68) were located by fogging mosses in the rata forest (Englund 2003). These included ***M. albolineatus***, ***M. akao***, ***M. carinatus***, ***M. hemata***, ***M.*** cf ***irregularis***, ***M. perau***/***maii***, ***M. pusillus***, ***M. setifer***, ***M.*** cf ***silvestris***, ***M.*** nr ***varians***, ***M.*** nr ***sanctijohni***.

The weevils are among the unique fauna of the Antarctic region. The genus ***Bothrometopus*** has several members that live among rocks on Marion Island, including ***B. randi***, ***B. parvulus***, and ***B. elongatus*** (Van der Merwe *et al*. 1997). All three of these species occur on rock surfaces, in crevices, and within the rock-dwelling bryophytes. On Heard Island, ***Bothrometopus brevis*** and ***B. gracilipes*** both feed on cryptogams (Chown & Klok 2001).

Figure 68. ***Miocalles*** adult, a genus with a number of new endemic bryophyte-dwelling species on the Austral Islands. Photo by April Yang, through Creative Commons.

Bryophagy and Evolution

Bryophagy is known in at least 35 species of **Curculionidae** from the sub-Antarctic (Kuschel 1964, 1971; Chown & Scholtz 1989a). Chown and Scholtz (1989a) suggest that a specialized moss herbivory, rare among **Curculionidae**, may have evolved in response to the adverse conditions during Pleistocene glaciations when bryophyte species were more likely to survive than their tracheophyte counterparts. Let's examine a few examples and then return to the evolution of this bryophyte-curculionid herbivory relationship.

Dichotrachelus stierlini (Figure 69) is a moss-eating weevil, known from 3350 m in the Alps (Thaler 1999). It is easily collected in alpine regions by sieving mosses (Barbara Thaler-Knoflach, pers. comm. 9 June 2011). As seen in Figure 69, this weevil has numerous protuberances that give it texture similar to that of a moss. A shiny weevil would be much more obvious among the mosses.

Figure 69. ***Dichotrachelus stierlini***, a curculionid beetle (weevil). Note how this highly textured beetle would blend with the similarly highly textured bryophytes. Photo by Barbara Thaler-Knoflach, with permission.

Smith (1977) examined the consumption of ***Ectemnorrhinus similis*** (formerly ***Dusmoecetes similis***) adults on sub-Antarctic Marion Island. These weevils reached densities up to 220 m^{-2}, representing a biomass of about 1 g m^{-2}. Their diet included 14% of their body weight per day of *Acaena magellanica* (flowering plant in Rosaceae; Figure 70) and 37% per day of the moss ***Brachythecium rutabulum*** (Figure 71). In fact, it appears that nearly all members of the tribe **Ectemnorhinini** are cryptogam feeders, especially on bryophytes (Chown & Scholtz 1989a). This is unusual in the **Curculionidae**, a family that predominantly feeds on tracheophytes.

Figure 70. *Acaena magellanica*, part of the diet of ***Ectemnorrhinus similis***. Photo by El Grafo, through Creative Commons.

Figure 71. ***Brachythecium rutabulum***, home and food for ***Ectemnorrhinus similis***. Photo by J. C. Schou <www.biopix.com>, with permission.

Chown (1989) suggests that the near absence of flowering-plant feeders in the **Ectemnorhinini** is due to the previous climatic conditions, claiming that they would preclude flowering plant herbivory. What we know about the habitat use, diet, and species morphology supports this view (Table 1; see also Chown & Klok 2001). Using ***Ectemnorhinus*** (see Figure 72) in the sub-Antarctic as an example (Chown & Scholtz 1989b; Chown 1990), Chown and Scholtz showed feeding and morphological differences between the larger species, ***E. similis***, that feeds on angiosperms [but also on bryophytes (Grobler *et al*. 2006)], as adults and detritus as larvae, and the smaller species, ***E. marioni***, that feeds on bryophytes in all its life cycle stages. Both of these species are found on ***Azorella selago*** (see Figure 74), but ***E. marioni*** feeds exclusively on the epiphytic bryophytes, whereas ***E. similis*** only eats bryophytes when the quality of the tracheophytes deteriorates (Chown & Scholtz 1989b).

Table 1. Feeding strategies of the tribe **Ectemnorhinini** of **Curculionidae** from sub-Antarctic Marion and Prince Edward Islands. % of cryptogams (**crypt**) and bryophytes (**bryo**) represent the percentage of individuals examined that fed on each of these groups. Note that bryophytes are included in cryptogams. Data were gathered from field observations and gut analyses. The bryophyte associations are defined by Gerson (1982) with **bryobionts** occurring exclusively in association with bryophytes, **bryophiles** usually living on bryophytes but also occurring elsewhere, **bryoxenes** regularly spending part of their life cycle on bryophytes, and **occasionals** spending part of their time on bryophytes but not dependent on them. n = number in sample. Modified from Chown and Scholtz 1989a.

Species	Stage	n	food % crypt	% bryo	bryo assn
Palirhoeus	larvae	17	100	6	bryoxene
eatoni	adults	40	100	0	occasional
Bothrometopus	larvae	38	100	16	bryoxene
randi	adults	46	100	2	occasional
Antarctonesiotes	larvae	28	100	18	bryoxene
elongatus	adults	62	100	7	occasional
Mesembriorrhinus	larvae	50	100	61	bryophile
brevis	adults	116	98	21	bryoxene
Ectemnorhinus	larvae	67	97	97	bryobiont
marioni	adults	1314	88	88	bryobiont
Ectemnorhinus	larvae	82	9	9	occasional
similis	adults	1037	38	38	bryoxene

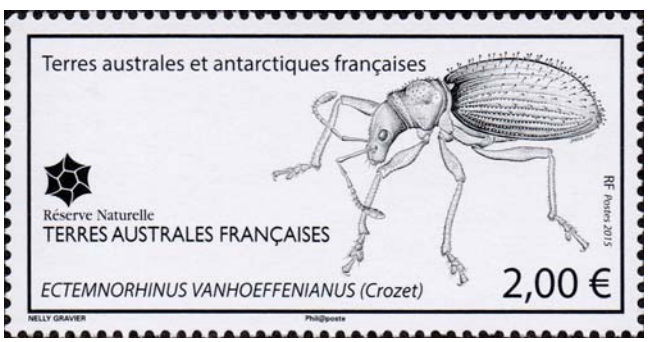

Figure 72. ***Ectemnorhinus vanhoeffenianus*** on French stamp. Photo by Alex Pozyr, with permission.

Figure 73. ***Ectemnorhinus vanhoeffianus***. Photo by Alex Pozyr, with permission.

In a later publication, Crafford and Chown (1991) cast doubt on the thesis that a colder climate would preclude these weevils from feeding on flowering plants due to energy constraints. Although five of the six species of weevils in the **Ectemnorhinini** on the sub-Antarctic Marion Island feed on cryptogams, temperature does not seem to be involved. They tested the consumption rate and approximate digestibility for the two native species of ***Ectemnorhinus*** (Figure 72) and found that the digestibility of the leafy liverwort ***Blepharidophyllum densifolium*** and dry mass differed little between 5°C and 10°C. Similar results were present for ***E. similis*** adults fed *Azorella selago* (see Figure 74). On the other hand, the performance ratios for ***E. similis*** feeding on *Azorella selago* was greater at 5°C than that for ***E. marioni*** feeding on bryophytes at either temperature. Crafford and Chown (1991) modified their interpretation to suggest that moss feeding more likely evolved in response to an absence of angiosperms during glacial periods, rather than because of a nutritional advantage associated with bryophagy at low temperatures. This is supported by studies on these beetles on islands. These feeding habits constrain species in their habitat distributions in the South Indian Ocean Province Islands where they seem to have been a result of climatic forcing (Chown 1994).

Figure 74. ***Azorella compacta*** from Tierra del Fuego, a flowering pant that resembles a moss. ***Azorella selago*** serves as food for ***Ectemnorhinus similis*** and ***E. marioni***. Photo by Heretiq, through Creative Commons.

In *Agrostis* (Figure 75) mires the genus ***Ectemnorhinus*** (Figure 72) feeds exclusively on bryophytes, mostly the leafy liverwort ***Blepharidophyllum densifolium***, even in the presence of the grass *Agrostis magellanica*. Chown (1990) considers the bryophytes to be a relatively poor food source, but they have the advantage of being available year-round. Another factor is that flowering plants have their highest nitrogen concentrations in the spring, whereas the bryophytes have their highest in autumn. Only the bryophytes have secondary compounds that serve as dietary inhibitors, resulting in the bryophyte feeders being smaller than the flowering-plant feeders. In fact, Chown suggests that the differences in feeding strategies lead to both size differences in the beetles and spatial separations between the two feeding groups. These differences keep the species groups from interbreeding.

Figure 75. *Agrostis*, a common genus in mires, but ***Ectemnorhinus*** species there feed mostly on leafy liverworts. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Bryophytes are well known for their insecticidal properties. Abay *et al*. (2012) demonstrated that extractions of the cosmopolitan moss ***Hypnum cupressiforme*** (Figure 76) had high levels of contact activity against the granary weevil *Sitophilus granarius*. This research was expanded to include the mosses ***Dicranum scoparium*** (Figure 77), ***Polytrichastrum formosum*** (Figure 78), ***Homalothecium lutescens*** (Figure 79), and the thallose liverwort ***Conocephalum conicum*** (Figure 80) (Abay *et al*. 2013). Using *Sitophilus granarius* in their bioassays, Abay and coworkers determined that hexane extracts of ***Polytrichastrum formosum*** exhibited the highest insecticidal activity (70.3%). Mortality was highest (53.34%) from the fatty acid **myristic acid**. **Palmitic acid** resulted in 17.75% mortality and **lauric acid** 4.32%. Abay and coworkers consider liverworts to be preferred foods nutritionally because of the presence of oil bodies (Kang *et al*. 2007; Abay *et al*. 2013). Yet there seem to be few reports of insects feeding on liverworts.

Figure 76. ***Hypnum cupressiforme***, a species known to have contact insecticidal properties against some beetles. Photo by J. C. Schou <www.discoverlife.org>, with permission.

Figure 77. ***Dicranum scoparium***, a species known to have contact insecticidal properties against some beetles. Photo by Janice Glime.

Figure 78. ***Polytrichastrum formosum***, a species known to have contact insecticidal properties against some beetles. Photo by Alexander Klink, through Creative Commons.

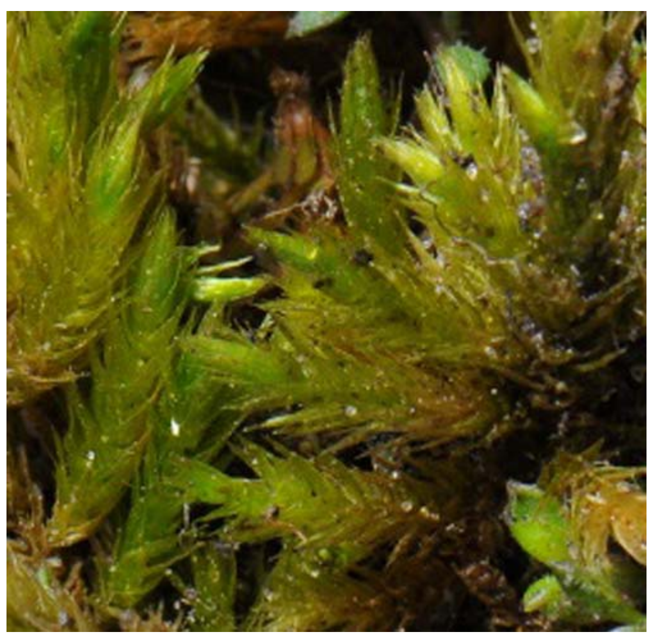

Figure 79. ***Homalothecium lutescens***, a species known to have contact insecticidal properties against some beetles. Photo by J. C. Schou <www.biopix.com>, with permission.

Figure 80. ***Conocephalum conicum***, a species known to have contact insecticidal properties against some beetles. Photo by Li Zhang, with permission.

Wahedi *et al.* (2013) expanded on the research on the effects of bryophyte compounds with *Sitophilus zeamais*. They tested powders from ***Calymperes afzelli*** (Figure 81), ***Thuidium gratum***, ***Bryum coronatum*** (Figure 82), and ***Semibarbula lambarenensis***. All four species were effective in reducing oviposition and F_1 progeny emergence rate, prolongation of pre-adult duration, and having toxicity. The order of efficacy in toxic effects was ***B. coronatum*** > ***T. gratum*** > ***C. afzelli*** > ***S. lambarenensis***, although the symptomatic effects were different among these. The bryophyte powders were so effective that the authors suggested using them as insecticides against the weevils in maize.

New compounds are constantly being discovered in the bryophytes (You *et al*. 2007; Jockovic *et al*. 2008). Many of these are phenolic acids, often unique with the bryophytes. Others are flavonoids or unique or scarce fatty acids. The research on the effects of these compounds on herbivory are limited, especially for mosses. And we don't know if any of these are inducible or if they are always present at similar levels. Likewise, we don't know how they are affected by seasons. Understanding these phenomena could help to explain some of the seasonal food choices of part-time bryophages.

Figure 81. ***Calymperes afzelli***, a species that can reduce oviposition and cause other toxic reactions in powder from on at least some beetles. Photo by Scott Zona, with permission.

Figure 82. ***Bryum coronatum***, a species with antibiotic properties against at least some beetles. Photo by Michael Lüth, with permission.

Impacts on Ecosystems

The weevils can play important roles in ***Sphagnum*** (Figure 13, Figure 83, Figure 128) habitats. For example, warming trends have an interesting way of increasing spruce bark beetles in ***Sphagnum*** fens (Figure 84), ultimately resulting in more frequent fires. Beetles in the Kenai Peninsula of Alaska typically take two years to develop in their ***Sphagnum*** habitat, but during recent warming the fen increased in temperature (Berg 2008). These longer, warmer summers reduced the life cycle to one year and caused exponential growth in the spruce bark beetle. The beetles declined ultimately as a result of destruction of their food source. At the same time, the warmer summers dried the fens and reduced their role as firebreaks, causing invasion of woody shrubs and white spruce. Instead of being fire breaks, the spruce and woody shrubs became fuel bridges. A 400-600-year fire interval was reduced by the beetles to one of 50 years. The warming and beetle invasion makes the lowland areas more vulnerable to fire, whereas the upland areas are likely to change toward grasslands and hardwoods with lower fire potential.

Figure 83. Spruce, Denali National Park, showing an advancing front of bark beetle damage (**right** and **distance**). Photo from National Park Service, through public domain.

Figure 84. Spruce beetle damage, Denali National Forest, Alaska. Photo by Davyd Betchkal, NPS, through public domain.

Another example of the role of these beetles, albeit indirect, is the role of bark beetles following logging (Jonášová & Prach 2008). In the Central European mountain spruce forests (*Picea abies*; Figure 85), logging had a greater impact on the bryophyte cover than did forest damage by bark beetles. Rather, the mountain spruce forests will recover from a bark beetle outbreak without intervention.

Figure 85. ***Picea abies*** forest, trees that provide cover for bryophytes even when damaged by bark beetles, but not when logging occurs. Photo by Crusier, through Creative Commons.

Camouflage

What better way to look like a bryophyte than to grow them on your back! Weevils of the moss forests of New Guinea "cultivate" the mosses (Gressitt *et al.* 1965, 1968; Gerson & Seaward 1977) and one liverwort species (Gerson 1969) as camouflage. The large moss forest weevils may even have special secretions that encourage the growth of the mosses on their backs (Gressitt *et al.* 1965).

Gressitt *et al.* (1968) reported mosses growing on a ***Gymnopholus*** weevil (Figure 86). These moss garden weevils seem to be restricted to high moss forest ridges and moist summits of New Guinea. Two of the involved genera are endemic there. These garden transporters include not only ***Gymnopholus***, but ***Pantorhytes*** (Figure 87) and some of the cryptorhynchine weevils. The weevils provide a favorable environment for the mosses and the mosses provide a protective cover and possibly a chemical predator deterrent for the weevils.

Figure 86. The moss ***Daltonia angustifolia*** living epizootically on the weevil ***Gymnopholus reticulatus***. Photo courtesy of Rob Gradstein.

Figure 87. ***Pantorhytes*** adult with epizootic lichens. Photo by Alex Riedel, with permission.

The leaf-eating weevils ***Gymnopholus*** (Figure 86) and ***Pantorhytes*** (Figure 87) have pits in their carapaces and these pits are colonized by algae, lichens, liverworts, and mosses (Gressitt *et al.* 1965, 1968; Gressitt & Sedlacek 1967). Some weevil species (*e.g.* ***Gymnopholus reticulatus***, Figure 86) seem to be moss specialists, especially the moss ***Daltonia angustifolia*** (Figure 86) (Gradstein *et al.* 1984), and others are lichen specialists. Tiny mites live among these epizootic mosses and may serve as moss dispersal agents to new hosts. The epizootic mosses take advantage of the soft substrate of the beetle. The small branches of montane rainforest trees seem to provide the sources for the mosses and the humidity keeps the garden growing. ***Daltonia angustifolia*** (see Figure 88) matures quickly, further supporting its suitability for its mobile, short-lived habitat.

Figure 88. ***Daltonia*** cf ***longifolia*** from the Neotropics. Photo by Michael Lüth, with permission.

It appears that the weevils have gained sufficient benefit from their gardens that their evolution has preserved characters that encourage the camouflage growth. In addition to secretions mentioned earlier (Gressitt *et al*. 1965), the genus ***Gymnopholus*** (Figure 86) provides depressions and grooves on its outer wings, along with specialized scales and hairs (Gressitt 1966). The bryophytes grow on the fused **elytra**, but often also grow on the pronotum. ***Symbiopholus*** likewise is modified to encourage cryptogamic growth. It has depressions, pits, and grooves. The dorsal surface is rough and may have specially modified hairs or scales. It likewise has secretions that seem to encourage growth of its garden. It appears that the hairs and scales are modified in ways that encourage growth of the flora, and these are the locations where the bryophytes and lichens begin their growth (Gressitt & Sedlacek 1970). The species of ***Gymnopholus*** that do not have plant associations have normal, flat scales or have a smooth, hairless body surface.

The latest member of this family to be described with attached bryophytes is ***Lithinus rufopenicillatus*** (Figure 89) from Madagascar. Paul Bertner and his associates are studying this unusual weevil, so look for more information in the future.

Figure 89. ***Lithinus rufopenicillatus*** with liverworts and mosses in its "backpack." Photo by Paul Bertner, with permission.

But do these gardens help the beetles? Using a reduviid bug, Jackson and Pollard (2007) demonstrated that carrying natural objects such as moss bits or dead ants does indeed reduce predation on the camouflaged bugs. However, such experiments remain to be performed on the camouflaged weevils.

Travelling Ecosystems

Some of these elytral moss gardens are moving microecosystems. Aoki (1966) found an epizootic symbiosis in which the oribatid mite ***Symbioribates papuensis*** lived on lichens on the backs of weevils in Papua, New Guinea. Gressitt (1970) likewise found epizootic mites in the plant growth on three members of the weevil genus ***Gymnopholus*** (Figure 86), a genus that lives on leaves of woody plants in moss forests and on alpine shrubs (Gressitt 1966).

Not only were mites part of this travelling ecosystem, but also lichens, fungi, rotifers, nematodes, diatoms, and other microorganisms (Gressitt 1966; Gressitt & Sedlacek 1967). Psocopterans even feed on the plants growing on the weevils. One individual of ***Gymnopholus acarifer*** had 60 oribatid mites among the resident fungi. The absence of flight in ***Gymnopholus*** (Figure 86) has resulted in different species evolving on different ridges in New Guinea. This mountain-valley system of geographic separation has resulted in 47 such specialists recognized in ***Gymnopholus*** in New Guinea (Gressitt & Sedlacek 1967).

Of the 850 ***Symbiopholus*** specimens examined, 675 had plant growth on their backs (Gressitt 1966). These included the liverworts ***Metzgeria*** (Figure 90) and members of the epiphytic/epiphyllous family **Lejeuneaceae** (Figure 91). Mites, only 0.2 mm long, were abundant among the fungal growth on the ***Symbiopholus***. The mites are able to spread to other weevils when the weevils mate, and the spores of the fungi may likewise spread that way as well as being carried on the bodies of the mites. The mites are absent from three of the weevil species that have hairy-sided, flat-bottomed pits.

Elateroidea

Lampyridae – Fireflies

This family was one of those nice surprises one can find while browsing the internet. I was searching for images on insects on mosses when I found one of eggs of the Japanese firefly on mosses. The eggs of ***Luciola cruciata*** (Figure 92) were nestled among the apical portions of mosses, and one video image shows a tiny larva crawling about. Another short video shows the emerging larva getting its first view of its larval moss home <http://www.gettyimages.com/detail/video/closeup-shot-moment-of-firefly-hatch-stock-video-footage/505766040>. But does the larva stay there and eat the mosses?

Figure 90. ***Metzgeria conjugata***, in a genus that is eaten by ***Symbiopholus***. Photo by David T. Holyoak, with permission.

Figure 91. ***Colura vitiensis*** growing on a leaf in the Fiji Islands. Species in this family can colonize members of **Curculionidae**. Photo courtesy of Tamás Pócs.

Figure 92. ***Luciola cruciata*** larva, a species that can lay eggs on mosses in Japan. Photo by Keisotyo, through Creative Commons.

This species flashes, using luciferase to activate the light (Tatsumi *et al*. 1989). The frequency of the light is dependent on temperature, with more frequent flashes at lower temperatures (Iguchi 2010).

Lycidae – Net-winged Beetles

The **Lycidae** are larger beetles, 10-15 mm long (Wikipedia 2015d). They are protected from predators by their toxicity. The larvae live under bark or in leaf litter and are predaceous.

This family is unusual in that the females are **neotenous**, whereas the males go through full metamorphosis of larvae, pupae, and adults (Masek & Bocak 2014). **Neotenous** refers to reaching sexual maturity at an immature morphological stage. In this case, the females are sexually mature as mature larvae and never change into pupae and adults.

Platerodrilus paradoxus (syn. = *Duliticola paradoxa*) (trilobite beetle; Figure 93) seems to be an exception to the carnivorous habit, but perhaps it is just hunting for prey. Nevertheless, the prey must be small.

Figure 93. ***Platerodrilus paradoxus*** (larval trilobite beetle) foraging on moss from Borneo. Note the tiny head protruding from the triangular prothorax at the bottom of the picture. Photo by Nick Garbutt, with permission.

Platerodrilus paradoxus (Figure 93) has only been observed in copulation twice, but that proves that mating does occur. Crew (2014) described the mating process of *Platerodrilus ruficollis* (syn. = *Platerodrilus hoiseni*), based on research by Wong (1998). One can only guess if it is similar in ***P. paradoxus***. The female of *Platerodrilus ruficollis* arches her abdomen upward to expose her gonopore. The male, which is much smaller (about 10% the size of the female) climbs onto the female and attaches to the gonopore. About three hours after copulation is completed, the male drops dead. The female incubates the eggs for about three days, then places them among leaf litter. Then she too dies a few weeks later.

Bupestroidea

Bupestridae – Jewel Beetles

Trachys troglodytes (Figure 94-Figure 95) is a species that likes high humidity. It is widespread and lives in damp, grassy places and ***Sphagnum*** bogs (Smith & Freeman 1987). As an adult, it hibernates among ***Sphagnum***.

Figure 94. ***Trachys troglodytes*** larva, a species that occurs in ***Sphagnum*** bogs. Photo by Steve Wullaert, through Creative Commons.

Figure 95. ***Trachys troglodytes*** adult, a hibernator in ***Sphagnum*** bogs. Photo by Boris Loboda, through Creative Commons.

Hydrophiloidea

Helophoridae – Water Scavenger Beetles

This is a family of small insects (2-9 mm) with only one genus. They are mostly **Holarctic** (zoogeographical region comprising Nearctic and Palaearctic regions combined), but a few occur in the tropics. ***Helophorus brevipalpis*** (2-3.5 mm; Figure 96) is ubiquitous and common, often occurring far from water in mosses (Stenhouse 2007).

Figure 96. ***Helophorus brevipalpis*** adult, a member of an aquatic family, but it can live far from water among mosses. Photo by James K. Lindsey, with permission.

Some members of the genus are flightless, but ***Helophorus brevipalpis*** (Figure 96) always has functioning flight "apparatus" (Landin 1980). This flight ability permits this mostly aquatic species to travel great distances. It is interesting that it rarely has food in its gut when it is flying, suggesting that mosses may provide it with moisture but probably do not provide food.

Hydrophilidae – Water Scavenger Beetles

This family, widespread in Europe, is generally considered to be aquatic. Some of these beetles are amphibious, but require a very moist environment. For example, ***Chaetarthria simillima*** (Figure 97) is a tiny water beetle, but it has been found among mosses growing beside a lake in the Outer Hebrides (Bratton 2012).

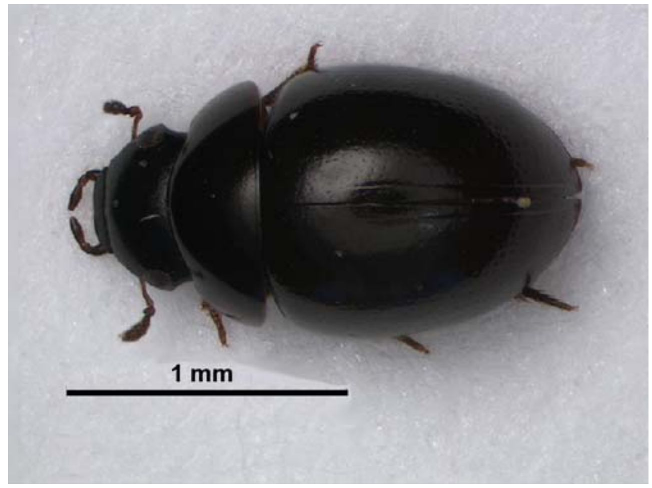

Figure 97. ***Chaetarthria seminulum*** adult, an aquatic beetle that can live among mosses near water on land. Photo from Naturalis, Biodiversity Centre, through Creative Commons.

Crenitis punctatostriatus (Figure 98) is a true bryobiont. It spends its entire life among ***Sphagnum*** (Matthey 1977).

Figure 98. ***Crenitis punctatostriatus*** adult, a ***Sphagnum*** dweller. Photo from SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

Scaraboidea

Scarabaeidae

Darwin reported ***Pinotus torulosa*** from mosses (Smith & Freeman 1987). This name has apparently been superseded and I can't find its current name or any further information.

Staphylinoidea

Leiodidae – Round Fungus Beetles

This worldwide family (1.2-7 mm long) seems to have dropped off the radar in recent studies. However, Sharp (1865) found ***Agathidium varians*** (Figure 99) to be abundant among mosses in Great Britain. Most are fungal feeders (Wikipedia 2015b), a food frequently available among mosses. Most of the members of this genus are known as slime mold beetles (Miller & Wheeler 2005) and their association with slime molds may explain the association of this species with mosses, often the substrate for slime molds.

Figure 99. ***Agathidium varians*** adult on moss, a once-abundant moss dweller in Great Britain. Photo by Tim Faasen, with permission.

Darwin reported several members of this family from mosses, including ***Nargus anisotomoides*** (Figure 100), ***N. wilkini*** (Figure 101), ***Ptomaphagus medius*** (Figure 102), and ***Choleva angustata*** (Figure 103), but none of these were bryobionts, having not only mosses but also dead leaves and other substrata among their choices (Smith & Freeman 1987).

Figure 100. ***Nargus anisotomoides*** adult, a species that includes mosses among its substrata. Photo by NSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 101. ***Nargus wilkinii*** adult, a species that includes mosses among its substrata. Photo by SNSB, Zoologische Staatssammlung Muenchen, through Creative Commons.

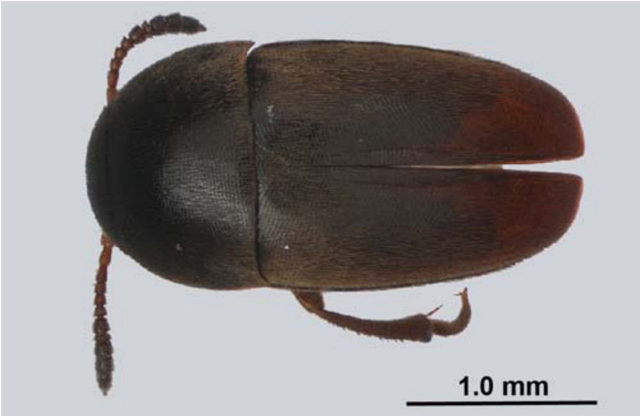

Figure 102. ***Ptomaphagus medius*** adult, a species that includes mosses among its substrata. Photo from Naturalis, Biodiversity Centre, through Creative Commons.

Figure 103. ***Choleva angustata*** adult, a species that includes mosses among its substrata. Photo by Stefan Schmidt, SNSB, through Creative Commons.

Pselaphidae – Short-winged Mold Beetles

This is a worldwide family, but it reaches its greatest diversity in the tropics (Benisch 2015b). More than 9000 species are known. Most prefer moist habitats such as the edges of bogs and marshes, under bark of dead trees, and especially in leaf litter and rotten wood. Like the **Staphylinidae**, they have a short elytra, leaving most of the abdomen exposed (Figure 104-Figure 105).

Ferguson (1901) reported three genera in this family living among mosses in the Clyde area of the British Isles: ***Bythinus*** (Figure 104), ***Bryaxis*** (Figure 105), and ***Pselaphus*** (Figure 106).

Figure 104. ***Bythinus macropalpus*** adult, member of a genus with moss dwellers. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 105. ***Bryaxis collaris*** adult, member of a genus with moss dwellers. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 106. ***Pselaphus heisei*** adult, a British moss dweller. Photo by Rudolf Macek, with permission.

Ptiliidae – Featherwing Beetles

Bogs provide another set of isolated habitats, and they seem to have more than their share of parthenogenetic females. For example, ***Ptiliopycna moerens*** is a minute (<1.0 mm) featherwing beetle in the northeastern USA and adjacent Canada (Dybas 1978). This moss dweller lives primarily in ***Sphagnum*** (Figure 84) bogs/poor fens and swamp forests. In most of its range, only females are known, thus making these populations parthenogenetic. Males are known only from the northern part of the range. Other parthenogenetic small beetles in bogs include species of ***Pteryx*** (Figure 107), ***Acrotrichis*** (Figure 108), and ***Ptinella*** (Figure 109) – all in **Ptiliidae**. Dybas surmised that the incidence of parthenogenesis in small beetles in relict bogs is unusually high. This is advantageous because it means they can remain in the safety of the mosses without having to venture farther and expend a lot of energy to find a mate, often unsuccessfully.

Figure 107. ***Pteryx suturalis*** adult, a moss dweller in bogs. Photo by Udo Schmidt, through Creative Commons.

Figure 108. ***Acrotrichis sitkaensis*** adult among mosses. Photo by Tim Faasen, with permission.

Figure 109. ***Ptinella pustulata*** adult, a parthenogenetic beetle in bogs. Photo by S.E. Thorpe, through Creative Commons.

Staphylinidae – Rove Beetles

This is a family of 58,000 species and thousands of genera, a family even larger than the **Carabidae**. They don't look like most of the other beetles because their hard, outer wings do not cover the abdomen, leaving more than half the abdomen exposed (Figure 110-Figure 111). Their size range is large (<1-35 mm). Even on mosses, the range is large. Like the **Carabidae**, these beetles are elongate and seem to lack morphological adaptations to a bryophyte habitat. They live in every imaginable habitat, including submersion at high tide (Frank & Ahn 2011), and eat almost anything, depending on the species.

The earliest records of occurrences of the **Staphylinidae** among mosses seem to be those of Champion (1871) and Waterhouse (1871). Waterhouse reported ***Anthophagus alpinus*** (Figure 110) from mosses in Scotland. Champion reported ***Syntomium aeneum*** (Figure 111) and ***Atheta tibialis*** (Figure 113) from mosses and ***Corticaria fuscula*** (see Figure 112) in peat mosses. Klimaszewski *et al*. (2015) found ***Atheta graminicola*** (Figure 114) in Saskatchewan and Newfoundland, Canada, where mosses near water provided a home for some adults.

Figure 110. ***Anthophagus alpinus*** adult, one of the early-reported moss dwellers from Scotland. Photo by Udo Schmidt, with permission.

Figure 111. ***Syntomium aeneum*** adult, one of the earliest species to be reported among bryophytes. Photo by Tim Faasen, with permission.

Figure 112. ***Corticaria foveola*** adult; ***C. fuscula*** lives among peat mosses. Photo by Marko Mutanen, University of Oulu, through Creative Commons.

Figure 113. ***Atheta tibialis*** adult, one of the earliest species to be reported among bryophytes. Photo from Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 114. ***Atheta graminicola*** adult with mosses. Photo by Tim Faasen, with permission.

Early records from the UK show that ***Gymnusa brevicollis*** (Figure 115) was a moss inhabitant (Beare 1899). Widespread and common species ***Atrecus affinis*** (Figure 116), ***Phloeocharis subtilissima*** (Figure 117), and ***Tachyporus obtusus*** (Figure 118) occur in mosses in the UK (Stenhouse 2007). ***Bythinus burrelli*** (Figure 119) occurs in mosses on the ground and on tree stumps (Stenhouse 2007). Others that have been found in mosses at least once include ***Aleochara funebris*** (female), ***Aleochara verna*** (female; Figure 120), ***Geostiba circellaris*** (female; Figure 121), ***Gyrohypnus fracticornis*** (Figure 122), ***Othius subuliformis*** (Figure 123), ***Oxypoda elongatula*** (female; Figure 124), ***Quedius nitipennis*** (female; Figure 125), and ***Stenus impressus*** (Figure 126).

Figure 115. ***Gymnusa brevicollis*** adult on moss. Photo by Tim Faasen, with permission.

Figure 116. ***Atrecus affinis***, a widespread species that lives among mosses in the UK. Photo by Udo Schmidt, with permission.

Figure 117. ***Phloeocharis subtilissima***, a widespread species that lives among mosses in the UK. Photo by Stefan Schmidt, through Creative Commons.

Figure 118. ***Tachyporus obtusus***, a widespread species that lives among mosses in the UK. Photo by Entomart, through Creative Commons.

Figure 119. ***Bythinus burrelli***, a widespread species that lives among mosses in the UK. Photo by Zoologische Staatssammlung Muenchen, through Creative Commons.

Figure 120. ***Aleochara verna***, a species that at least occasionally visits mosses. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 121. ***Geostiba circellaris***, a species that is at least an occasional visitor to mosses. Photo by Tim Faasen, with permission.

Figure 122. ***Gyrohypnus fracticornis***, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.

Figure 123. ***Othius subuliformis***, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.

Figure 124. ***Oxypoda elongatula***, a species that is at least an occasional visitor to mosses. Photo by Tim Faasen, with permission.

Figure 125. ***Quedius nitipennis***, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.

Figure 126. ***Stenus impressus***, a species that is at least an occasional visitor to mosses. Photo by Trevor and Dilys Pendleton <eakringbirds.com>, with permission.

Stenus (Figure 126-Figure 127), a moss visitor, has an unusual adult behavior. These species are predators on small invertebrates, including **Collembola** (Piper 2007). To catch their prey, they shoot out the **labium** using blood pressure. This narrow structure ends in a pad of bristles and hooks. Between the bristles are small pores that exude an adhesive that sticks to the prey.

Like some **Carabidae**, some of the **Staphylinidae** obtain their moisture from wet mosses. For example, ***Stenus kiesenwetteri*** (Figure 127) is a rare species living among very wet ***Sphagnum*** (Figure 128); ***Dianous coerulescens*** (Figure 129) lives where water trickles over mosses and liverworts (Butler 1886). And some are aquatic, as discussed in the **Coleoptera** subchapter on Aquatic Insect interactions.

Figure 127. ***Stenus kiesenwetteri***, a species that uses terrestrial mosses to create an aquatic habitat (**limnoterrestrial**). Photo by Udo Schmidt, with permission.

Figure 128. ***Sphagnum*** in flush, a potential home for the rare ***Stenus kiesenwetteri*** that prefers very wet ***Sphagnum***. Photo by Andrew Hodgson, with permission.

Figure 129. ***Dianous coerulescens*** adult on leafy liverworts. This is a species that uses terrestrial bryophytes to create an aquatic habitat. Photo by Malcolm Storey, through Creative Commons.

In Great Britain, ***Achenium humile*** (Figure 130) is widespread. This species is predatory and lives in broad-leaved woodlands, fields, sand dunes, coastal marshes, and alluvial flats (Hyman & Parsons 1994). It takes advantage of habitats under bark on dead wood, under stones, among mosses, at roots of grasses, muddy dykes, and clay banks. ***Bryophacis crassicornis*** (Figure 131) is more restricted, living in dry mixed woodlands among leaves, moss, and rotting fungi, but also in heathlands among the *Calluna* litter (Lindgren & Palm 2011).

Figure 130. ***Achenium humile*** adult on mosses, a widespread species with a wide range of habitats, including mosses. Photo by Tim Faasen, with permission.

Figure 131. ***Bryophacis crassicornis*** adult male, a species that includes mosses among its homes. Photo by Christoph Benisch <kerbtier.de>, with permission.

Philonthus nigrita (Figure 132) lives in high and transitional moors. It is most common in the ecotone between water bodies and peat "bogs," living in the partly submerged ***Sphagnum*** layer (Figure 133) (Burakowski *et al*. 1980; Koch 1989; Staniec & Pietrykowska-Tudruj 2008).

Figure 132. ***Philonthus nigrita*** adult on ***Sphagnum***. Photo by Christoph Benisch <kerbtier.de>, with permission.

Figure 133. Peatland in Alaska showing the wet ***Sphagnum*** that borders peatland pools, a potential habitat for ***Philonthus nigrita***. Photo by Vita Plasek, with permission.

There is little information regarding the specific eating habits of the moss dwellers among the **Staphylinidae**, but Mani (1962) reported that some staphylinids are moss feeders in high alpine areas.

In Canada, ***Trichiusa*** (Figure 134) species live in forest leaf litter and mosses, especially at the edges of streams and pools (Klimaszewski *et al*. 2015).

Figure 134. ***Trichiusa immigrata*** adult, member of a genus that sometimes lives among mosses. Photo by Veli-Matti Mukkala, in Public Domain.

Scydmaenidae – Ant-like Stone Beetles

This worldwide family (Figure 135) lives in moist forests where they often take advantage of the moisture they can find among mosses (O'keefe 2001, 2005). They feed primarily on mites (Wikipedia 2015a), perhaps contributing to their presence on bryophytes, where mites are common. They are closely related to the **Staphylinidae** and Grebennikov and Newton (2009) have proposed their inclusion in that family.

Figure 135. ***Microscydmus nanus*** (**Scydmaenidae**) adult among mosses. Photo by Tim Faasen, with permission.

The **Scydmaenidae** are frequently associated with ants. And they even resemble ants by having constrictions between the head and thorax and between the thorax and abdomen. O'Keefe (2000) reviewed all the published relationships between ants and these beetles. He suggested that they may occur in the same locations because of a common preferred food. If so, then we should expect some of these associations to be among mosses. Ants are common among a number of kinds of mossy locations, as will be seen in the chapter on **Hymenoptera**. It would be interesting to know just why there are so many members of this family associated with ants and what they gain from the relationship.

Tenebrionoidea

Perimylopidae (=Promecheilidae)

The Antarctic has beetle species that take advantage of the insulation and moisture available when living within the moss clumps. The **Perimylopidae** contribute some of these species. ***Perimylops antarcticus*** (Figure 136-Figure 137) seems to be well adapted by eating bryophytes (Worland *et al*. 1993) and has cold-adapted low-temperature respiration activation rates (Sømme *et al*. 1989). It lives among the moss ***Polytrichastrum alpinum*** (Figure 138) and lichens. Worland and coworkers tested **ice nucleation** in these insects – a process that causes ice crystals to form, expand, and ultimately damage cell membranes. They found that the gut freezes at 1°C lower than does the adult insect. The fecal material experiences ice nucleation at temperatures as high as -2°C and the insects themselves nucleate -3°C. The mosses nucleate at -4 to -5°C. They suggest that bacteria may be responsible for the nucleation proteins, since this food has a lower nucleation temperature than does the beetle.

Figure 136. ***Perimylops antarcticus*** larva on **Polytrichaceae**, South Georgia. Photo by Roger S. Key, with permission.

Figure 137. ***Perimylops antarcticus*** adult on South Georgia, a species that eats mosses. Photo by Roger S. Key, with permission.

Figure 138. ***Polytrichastrum alpinum***, home for ***Perimylops antarcticus***. Photo by Michael Lüth, with permission.

Lagriidae – Long-jointed Beetles

The **Lagriidae** (Figure 139) are medium-sized (Benisch 2015c). They are worldwide, but are concentrated in the tropics. Typical habitats are trees, shrubs, and herbaceous plants, with larvae in decaying wood or leaf litter. Chown (1993) found that **Lagriidae** from the Afromontane forest in South Africa fed on both live and dead parts of the moss ***Braunia secunda*** (Figure 140), based on both field observations and gut analysis. This unknown species is the only record of bryophagy in the family.

Figure 139. ***Lagria*** from a West Java mountain rainforest; at least one member of this family eats mosses. Photo by gbohne, through Creative Commons.

Figure 140. ***Braunia secunda***, food for an unidentified member of the **Lagriidae**. Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Nevertheless, ***Adelium alpicola*** (see Figure 141larvae are known from damp forest moss in Australia (Watt 1974). But there is no evidence that they eat the mosses – or that they don't.

Figure 141. ***Adelium pustulosum*** adult; ***Adelium alpicola*** larvae occur among damp forest mosses in Australia. Photo by Tamara Leitch, through Creative Commons.

Tetratomidae – Polypore Fungus Beetles

The **Tetratomidae** is a small Palaearctic and Nearctic family (~30 species) that is typically associated with fungi, especially wood-decay fungi and those on tree boles (Lawrence 1991; Pollock 2008, 2012). They are poorly known, both taxonomically and biologically.

Tetratoma fungorum (Figure 142) is not generally a moss dweller, as implied by its name. Nevertheless, it finds mosses to be suitable hiding places to survive the winter (Curtis 1823-1840).

Figure 142. ***Tetratoma fungorum*** adult with mosses, a species that overwinters under mosses. Photo by Tim Faasen, with permission.

Summary

There are probably more families of beetles among bryophytes than the ones represented here. Some of these are full-time bryophyte dwellers, some go to the bryophytes at specific times in the life cycle or for specific purposes, and others may simply traverse them while going from one point to another.

One of the largest families, **Staphylinidae**, has bryophyte dwellers among them. They range in size from tiny to large, even on mosses, and seem to have little specialization among the bryophyte dwellers. These include both casual visitors and those that spend part of their lives among mosses. Their lack of well-developed wings suggests they don't travel far. Some of these are bog dwellers. For many of them, mosses appear to be just more litter on the forest floor. The best and most common adaptations to living among bryophytes seems to be those of being small, roundish, smooth, and perhaps shiny and black, as seen in many of the **Chrysomelidae**.

There is some suggestion that bryophytes as food may provide a means to survive the cold, providing gut contents that have lower nucleation temperatures than the surrounding beetle.

Families like **Latridiidae** find suitable food among mosses, particularly slime molds.

The weevils (**Curculionidae**) are among the most abundant species among bryophytes. Their sizes vary; some seem to have camouflage. A few unique taxa have depressions in the elytra and bryophytes and lichens grow there, anchoring among hairs or spikes and being facilitated by a type of glue secreted by the beetle. A number of weevil species also eat bryophytes, sometimes on a seasonal basis when tracheophyte food becomes unavailable or unpalatable.

For those that eat bryophytes, suitable food includes a wide range of bryophyte species. Nevertheless, some bryophytes seem to be avoided. Liverworts may be eaten because of the rich food source in their oil bodies. Some beetles may take advantage of the fatty acids that remain fluid at low temperatures.

Sphagnum habitats often have rare species. They also provide places to survive forest disturbance or to survive the dry season (for those that can fly). Beetles can change the form of the habitat in ways that affect the mosses. In bogs, they can destroy the cover, causing the mosses to dry and more tolerant species to replace them. Bark beetles damage the spruce forests, but recovery of the forest, mosses, and moss-dwelling beetles is faster than it is from clear cutting.

Some terrestrial beetles in aquatic families use mosses as a limnoterrestrial habitat, maintaining their moisture because the moss remains damp.

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