

# CHAPTER 12-16

## TERRESTRIAL INSECTS:

### HOLOMETABOLA – MECOPTERA

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Figure 1. *Boreus hyemalis*, female, among *Polytrichum piliferum*, Thetford Warren Lodge, Norfolk, UK. Photo by Brian Eversham, with permission.

#### MECOPTERA – SCORPIONFLIES

The **Mecoptera** comprise a small order of about 550 known species (Wikipedia 2016), 9 families, and 32 genera (Byers & Thornhill 1983). They were more abundant in the Permian, Mesozoic, and Tertiary periods, with 348 species in 87 genera and 34 families known. They are known as scorpionflies because of the position of the

Scorpionfly larvae (Figure 2) are among those that live in mosses (as well as damp soil) (Miall 1902). It is interesting that many of the relatively few **bryophagous** animals (including arthropods) often show unusually high levels of winter activity. Larvae of snow scorpionflies (**Mecoptera: Boreidae**) are active **ONLY** in the winter in temperate regions, hopping about and even mating on the snow (Figure 3). Some insects, including gall aphids, move from a summer angiosperm host to a winter moss host. Could these snow scorpionflies and gall aphids, and probably other insects, be sequestering compounds from mosses that allow them to remain active at sub-freezing temperatures? Aside from chemistry, the correlation

between bryophagy and cold weather could be explained by the simple fact that mosses remain green throughout the winter, and therefore might become a more attractive host plant during this period. Or do the winter-active fauna simply have the right enzymes or gut pH to permit them to gain nutrients from mosses and survive by being active at a time of year when predators are limited in their activity?



Figure 2. *Panorpa* sp. larva, genus that lives among bryophytes. Photo by Pierre-Marc Brousseau, with permission.





Figure 3. *Boreus westwoodi* mating on snow. Photo by hrasiranta, with online permission.

## Choristidae

Tillyard (1926) was among the early reporters on the relationship of the **Mecoptera** with bryophytes. He considered the Australian *Choristes* to be both a bryophyte resident and a **bryophage** (eats bryophytes). However, this genus name has been pre-empted by other phyla (the genus *Choristes* is a sea snail in the Gastropoda) and was changed to *Chorista* (Figure 4) in the **Mecoptera** (see <<http://direct.biostor.org/reference/80557.text>>).



Figure 4. *Chorista australis* adult, a bryophyte dweller and bryophage. Photo by John Tann, through Creative Commons.

*Chorista* is a small genus of only two apparent species. Its family, the **Choristidae**, lives among mosses as larvae (Wikipedia 2015). The larvae are unusual among holometabolous insects in having **compound eyes** with ommatidia, a trait shared by the scorpionflies *Neopanorpa* (Figure 93) and *Panorpa* (Figure 94), both in the **Panorpidae** and also bryophyte dwellers (Ramel 2016). Compound eyes are best at detecting motion. Could it be that living among bryophytes selects for these compound eyes in an environment where there is limited light and many of the inhabitants tend to blend in until they move?

The food of *Chorista* (Figure 4) seems to be contested, or perhaps just wide ranging. Tillyard (1926) considered them to eat mosses. On the other hand, in the lab both larvae and adults fed on dead insects, fresh fruit, strained carrots, and beef (Bush 1967; Byers & Thornhill 1983).

Members of *Chorista* (Figure 4) oviposit loose clusters of eggs, using pre-existing cavities in moist soil (Miyake 1912; Tillyard 1926; Byers 1963; Riek 1970). We need to look for the eggs among or under the bryophytes as well. If the larvae feed on bryophytes, surely the eggs must be near the host plants.

## Boreidae

The family **Boreidae** has only three genera (Cannings & Scudder 2005). *Boreus* (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27) has 14 known species in Eurasia and 12 in North America; only two of these are in the eastern USA. *Hesperoboreus* (Figure 89) has only two species, confined to western North America from Washington to California. *Caurinus* (Figure 28-Figure 30, Figure 38-Figure 39) has two species, one occurring only in Oregon and Washington, USA, and another in Alaska. Both larvae and adults of the **Boreidae** feed exclusively on bryophytes (Russell 1979a, b). Because of their small size and clandestine habitat, it is likely that more species await our discovery.

The **Boreidae** are small (2-5 mm), dark-colored mecopterans and are most easily seen when they are on the snow (Figure 5) (Byers 2002). They resemble fleas, but use their legs to propel them. When they land, they tuck their legs against their bodies (Figure 6) and resemble a bit of dirt on the surface of the snow. The dark body color (Figure 5-Figure 13) may help them to maintain sufficient temperature when they are bouncing around on snow (Cannings & Scudder 2005).



Figure 5. *Boreus brumalis* on snow. Photo by J. Mihuc, through Creative Commons.





Figure 6. *Boreus brumalis* adult, showing the legs tucked against the body as they are when the adults land after a hop. Photo by Tom Murray, through Creative Commons.

The **Boreidae** are boreal, with the adults appearing in winter or at high elevations. They are sufficiently different from other **Mecoptera** that some systematists consider them to be a separate order, the **Neomecoptera** (Cannings & Scudder 2005). The larvae lack both abdominal prolegs and conspicuous dorsal setae. They have lateral eyes and usually have three **ommatidia** (units of the compound eye) per eye.

Several researchers have provided lists of moss species from which boreids have been collected or on which they have been reared (e.g. Svensson 1972; Cooper 1974; Penny 1977). Both larvae and adults in the **Boreidae** feed on mosses (Svensson 1972; Cooper 1974; Penny 1977; Byers & Thornhill 1983). But Brauer (1863 in Carpenter 1931) found that they also feed on other small animals that live among the moss rhizoids. And Penny (2006) stated that they feed on leaves of mosses, club mosses (*Selaginella*?), and liverworts as adults, but feed on the rhizoids of these same plants as larvae. They seem to require little food (Withycombe 1926), but need "a great deal of moisture" (Penny 2006). Penny (1977) concluded that **Boreidae** prefer mosses that form low, compact cushions with their rhizoids tightly matted. The loose mats, which had fewer **Boreidae**, may have more predator **Carabidae** beetles. Or they may lose moisture too quickly.

In contrast to *Chorista* (Figure 4), the **Boreidae** oviposit single eggs or small clusters in the soil surrounding moss rhizoids (Cooper 1974; Penny 1977; Byers & Thornhill 1983). Some deposit eggs among epiphytic bryophytes (Russell 1979a; Byers & Thornhill 1983).

As one might guess for a boreal species that hops about on the snow, temperature is an important parameter in the niche of **Boreidae** (Byers & Thornhill 1983), even more important than light (Cooper 1974). Nevertheless, the minimum temperature for adult activity is close to 0°C (Sauer 1966; Svensson 1966; Penny 1977; Byers & Thornhill 1983). When their mossy habitat becomes dry,

the boreid larvae may go as much as 20 cm down into the soil below the mosses to attain suitable humidity (Strübing 1950).

Scorpionfly larvae [*Boreus* (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27), *Caurinus* (Figure 28-Figure 30, Figure 38-Figure 39)] feed on moss cushions on trees in damp woodlands (Penny 1977; Russell 1979a, b; Shorthouse 1979), making mosses their principal food. Adults of the family **Boreidae** are well known for their moss diet (Cooper 1974; Penny 1977).

### **Boreus**

Although *Boreus* (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27) seems always to be associated with mosses, its distribution is clearly not limited by its host mosses, but rather by some other parameter of its environment that is more restrictive (Cooper 1974). I suggest that limitation is moisture, combined with bryophytes that are suitable food. Both larvae and adults of *Boreus* eat mosses (Withycombe 1922; Fraser 1943; Strübing 1950; Svensson, 1966; Hågvar 2010).

*Boreus brumalis* (Figure 7, Figure 13) includes the mosses *Dicranella heteromalla* (Figure 8-Figure 9) and *Atrichum angustatum* (Figure 10-Figure 11) in its diet in Illinois, USA (Webb et al. 1975) and New England, USA (Maier 1984).

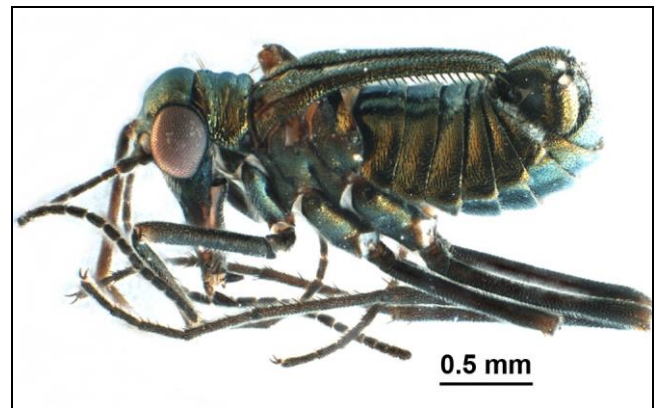


Figure 7. *Boreus brumalis* male showing modified wings that are used to clasp the female. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 8. *Dicranella heteromalla* on soil bank – food for *Boreus brumalis*. Photo by Janice Glime.





Figure 9. *Dicranella heteromalla* with capsules – food and home for *Boreus brumalis*. Photo by Michael Lüth, with permission.



Figure 10. *Atrichum angustatum*, home and food for *Boreus brumalis*. Photo by Michael Lüth, with permission.



Figure 11. *Atrichum angustatum*, home and food for *Boreus brumalis*. Photo by Michael Lüth, with permission.

Desiccation can be a problem, and the moss habitat would seem to be ideal for these organisms. It typically stays moist longer than other kinds of plants, it provides cover against not only desiccation but also many kinds of predators, and it is a food source. Furthermore, being flightless, it is an advantage to have your food and cover in the same place.

This genus has a somewhat different mating behavior from that of other **Mecoptera** (Byers 2002). The male has slender, hardened wings that he uses to grasp the female (Figure 7). He manipulates her to a position above his back (Figure 12) with the lower part of her ovipositor inserted into his ninth (genital) segment (Figure 12) (Cockle 1908).



Figure 12. Mating pair of the snow scorpionfly, *Boreus westwoodi*. Note the female is on top of the male, held by two wings of male. Photo by Barbara Thaler-Knoflach, with permission.

*Boreus brumalis* (Figure 7, Figure 13) feeds primarily on bryophytes (Gerson 1982). Shorthouse (1979) determined that both larvae and adults of *Boreus brumalis* (Figure 13) in Ontario, Canada, eat the bryophytes in the winter under the snow.



Figure 13. *Boreus brumalis* female adult on snow. Photo by Tom Murray, through Creative Commons.

*Boreus hyemalis* (Figure 1, Figure 14), an inhabitant of heaths and moors, is well known for its habitation of mosses (Plant 1994; Winnall 2009). Nevertheless, because of this seclusion, it is often overlooked (Whitehead 2010). This insect is flightless (Hågvar 2010) and can be seen moving about on the snow in exposed locations. Carpenter



(1931) reported that adults could be seen in spring and early summer among moss rhizoids and under stones, but that their activity is confined to winter. On sunny winter days they hop on the snow, as far as 15 cm in a single leap.



Figure 14. *Boreus hyemalis* in moss at Ellerburn Beck, UK. Photo by Roger S. Key, with permission.

Bingham (2012) found that the typical habitat for *Boreus hyemalis* (Figure 1, Figure 14) in Wyre Forest (UK) seemed to be oak woodlands or other open woodlands with sparse ground flora to compete with the mosses, mostly *Polytrichastrum formosum* (Figure 15) and *Dicranum scoparium* (Figure 16). He also perceived a possible connection between acid woodland and the presence of *B. hyemalis*.



Figure 15. *Polytrichastrum formosum*, home of *Boreus hyemalis*. Photo by David T. Holyoak, with permission.



Figure 16. *Dicranum scoparium*, home for *Boreus hyemalis*. Photos from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

*Boreus hyemalis* (Figure 1, Figure 14) lays its eggs among mosses and the larvae make tunnels between the moss and the substrate – soil, logs, walls (Russell 1979a). Although many entomologists have reported this species from the mosses, only Fraser (1959) has identified the moss used for oviposition as *Polytrichum commune* (Figure 17). Most likely other species of bryophytes are also used. Carpenter (1931) observed that the larvae eat both moss "roots" and liverworts.



Figure 17. *Polytrichum commune*, home and oviposition site for *Boreus hyemalis*. Photo by Michael Lüth, with permission.



*Boreus* in Norway takes advantage of mosses to provide protective space. This is a safe space in which they lay their eggs (Hågvar 2001). And it appears that mosses might be a site of copulation (Figure 12), an event rarely observed on the snow (Figure 3). The chambered air spaces most likely also provide space for this winter-active scorpionfly to move about in safety. Adults of *B. elegans* (Figure 18) and *B. californicus* (Figure 19-Figure 20) feed on *Racomitrium heterostichum* (Figure 21); larvae and pupae of *B. elegans* can be found under *Brachythecium* (Figure 22) and other mosses (Russell 1979a). Russell (1979a) has found *B. elegans* on mosses on a north-facing roadcut, in mosses near a hillside spring, and among mosses on logs in a coastal forest in the Pacific coastal states, USA. Both larvae and pupae were present under a mat of *Brachythecium* sp. and other mosses.



Figure 20. *Boreus californicus* on one of the compact mosses it calls home. Photo by Baldo Villegas <[www.discoverlife.com](http://www.discoverlife.com)>, through Creative Commons.



Figure 18. *Boreus elegans* adult, a species that feeds on *Racomitrium heterostichum*. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 21. *Racomitrium heterostichum*, food for *Boreus californicus* and *B. elegans*. Photo by Michael Lüth, with permission.



Figure 19. *Boreus californicus* male, a species that lives in compact mosses such as *Grimmia*. Photo by BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 22. *Brachythecium rutabulum*, home for *Boreus elegans*. Photo by Michael Lüth, with permission.

*Boreus californicus* (Figure 19-Figure 20) occurs primarily east of Cascade Mountain (Russell 1979a). In western Oregon, it seems to occur in more open, rocky sites than *B. elegans* (Figure 18), but in some sites both species occur. Larvae of *B. californicus* also occur in soil under mosses in crevices of jointed basalt and under moss among grasses in deep sandy loam on a stream bank. In California, Penny (2006) found *B. californicus* on the tightly compacted *Grimmia* (Figure 23).





Figure 23. *Grimmia longirostris*, exhibiting the compact cushion character of many **Grimmiales**. Photo by Hermann Schachner, through Creative Commons.

*Boreus reductus* (Figure 24) is likewise east of the Cascades, but in semi-arid regions of the Northwest (Russell 1979a, b). Although the larvae usually inhabit mosses (Russell 1979a, b), they can also occur in mats of *Selaginella* (Figure 25-Figure 26), a moss look-alike that is related to club mosses (tracheophytes) (Penny 1977).

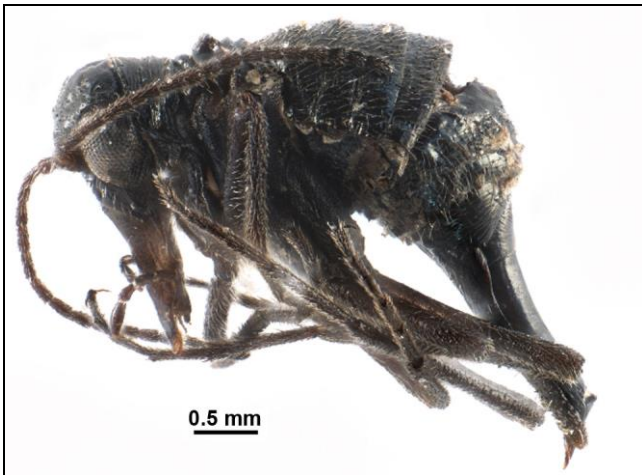


Figure 24. *Boreus reductus* female, a species east of the Cascades that eats mosses and *Selaginella*. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.



Figure 25. *Selaginella wallacei* in its epiphytic habitat where one might find *Caurinus dectes*. Photo by Paul Slichter, with permission.



Figure 26. *Selaginella wallacei*, home for *Caurinus dectes*. Photo by Paul Slichter, with permission.

In Fennoscandia, *Boreus westwoodi* (Figure 3, Figure 12, Figure 27) and *B. hyemalis* (Figure 14) larvae develop in the soil that occurs among the mosses (Hågvar 2010). The adults hatch in autumn before the new snow becomes established. Each adult migrates in its own separate and fixed direction by continuous jumping, achieving 1.2 m per minute (Hågvar 2001). The adults spend most of winter below the snow, among the mosses. On warmer days when the temperature is just above freezing, they climb tree trunks to reach the snow surface where they hop about. Jumping about on sunny, cloudless days may be risky because the temperature is likely to drop rapidly as the sun sets.



Figure 27. *Boreus westwoodi* adult female on one of the mosses where it lives. Photo by Petr Kočárek, with permission.

These adults lay eggs throughout the winter (Hågvar 2001) and *Boreus hyemalis* (Figure 14) is able to produce a maximum of 320 eggs per female (Steiner 1937). They oviposit in mosses in the **subnivean** (beneath snow) air spaces (Hågvar 2001), laying 1-2 eggs at a time (Withycombe 1922; Strübing 1950; Svensson 1966; Cooper 1974). Larvae develop there, feeding on the mosses, and continue to feed on them as adults.



### **Caurinus**

I was delighted when, in January of 2008, David Wagner sent me a note about his former student who had studied a small boreid, *Caurinus dectes* (Figure 28-Figure 30) (Russell 1979a, b, 1982). Unlike *Boreus* (Figure 1, Figure 3, Figure 5-Figure 14, Figure 18-Figure 20, Figure 24, Figure 27), this insect feeds primarily on liverworts! Wagner helped me contact his former student, Loren Russell, who has been very helpful in providing me with further information. Russell learned how to find his study insect by a change in the branching pattern of the leafy liverwort, *Scapania bolanderi* (Figure 31), the preferred food of the boreid (David Wagner, pers. comm. January 2008). It chewed the tender tips, which caused the liverwort to branch, causing a fluffy appearance that is in evidence even from a distance! The larvae feed on the liverwort in mines or galleries constructed there (Penny 2012).



Figure 28. *Caurinus dectes* female, a liverwort dweller. Photo courtesy of Loren Russell.



Figure 29. *Caurinus dectes* male. Photo courtesy of Loren Russell.



Figure 30. *Caurinus dectes* larva on a species of the leafy liverwort *Scapania*. Photo courtesy of Loren Russell.



Figure 31. *Scapania bolanderi*, a common home for *Caurinus dectes*. Photo by Matt Goff, with permission.

Fabian *et al.* (2015) took advantage of this knowledge of food choice to locate larvae of *Caurinus dectes* (Figure 28-Figure 30) for their study on larval morphology. Penny (2012) used heat to cause adults of this species to drop from the epiphytic liverworts (*Porella navicularis*; Figure 32) on vine maple (*Acer circinatum*). Penny noted that the most common mosses associated with these vine maple stems are *Rhytidiadelphus loreus* (Figure 33), *Metaneckera menziesii* (Figure 34-Figure 35), and *Neckera douglasii* (Figure 36-Figure 37). Nevertheless, its favorite food is *Porella navicularis*. Penny contends that *C. dectes* breeds in these epiphytes.



Figure 32. *Porella navicularis*, an epiphytic liverwort where one can find *Caurinus dectes* larvae feeding on the liverwort. Photo by John Davis, with permission.





Figure 33. *Rhytidiadelphus loreus*, potential home for *Caurinus dectes*. Photo by Martin Hutten, with permission.



Figure 34. *Metaneckera menziesii*, potential home for *Caurinus dectes*. Photo by Dale Vitt, with permission.



Figure 35. *Metaneckera menziesii*, potential home for *Caurinus dectes*. Photo by Michael Lüth, with permission.



Figure 36. *Neckera douglasii*, one of the epiphytic mosses in areas where one can find *Caurinus dectes*. Photo by Kirill Ignatyev, through Creative Commons.



Figure 37. *Neckera douglasii*, potential home for *Caurinus dectes*, but refused as a food source. Photo by Dale Vitt, with permission.

*Caurinus dectes* (Figure 28-Figure 30) survives in a warmer climate than other members of the **Boreidae**. Its distribution is in Washington and Oregon, USA (Russell 1979a, b; Rood *et al.* 2015). It occurs in moist forests where mosses are abundant both on trees and on the ground. Knowing where to look often adds new species. In 2013, Sikes and Stockbridge described a new species, *Caurinus tlagu* (Figure 38) from Prince of Wales Island, Alaska, USA. Its habitat is different from the primary forested habitat of *C. dectes* (Figure 28-Figure 30), but *C. dectes*, like *C. tlagu*, also occurs in open rocky sites with the moss *Rhytidiadelphus loreus* (Figure 33). This moss species provides 20% of the cover at the Alaskan alpine tundra site where *C. tlagu* occurs.





Figure 38. *Caurinus tlagu*, a moss dweller in Alaska, USA. Photo by Derek Sikes, through Creative Commons.

Byers and Thornhill (1983) conjectured that *Caurinus* (Figure 28-Figure 30) probably pupates in damp mosses without making a cell (Russell 1979a). Russell (1982) pointed out that its larvae, unlike other **Mecoptera**, make a silk-lined cell or cocoon where pupation occurs. Pupation occurs in July to August in northwestern USA. The life cycle is **univoltine** (one generation per year), but two generations may overlap for a period.

Penny (2006) pointed out that in *Caurinus dectes* (Figure 28-Figure 30), the larvae (Figure 30) are almost legless. Furthermore, the adults lack hind wings (Figure 28-Figure 29). Hence, this small (1.4-1.9 mm) insect is not going to travel very far to escape unfavorable conditions of weather or other environmental change. It lives in moist forests where both epiphytic and terrestrial bryophytes are abundant. The adults feed on the epiphytic leafy liverwort *Porella navicularis* (Figure 32), but also occur on mosses (Russell 1979a). When females lay their eggs, the eggs are coated with black cement and they are attached to the bryophytes (Figure 39) (Russell 1982).



Figure 39. *Caurinus dectes* eggs on a leafy liverwort. Photo courtesy of Loren Russell.

Because other boreids are known to feed on mosses, Russell (1979a, b) provided his *Caurinus* (Figure 28-Figure 30) with several epiphytic moss choices: *Antitrichia curtispindula* (Figure 40-Figure 41), *Isoetecium spiculiferum* (Figure 43), *Metaneckera menziesii* (Figure 34-Figure 35), and *Rhytidiadelphus loreus* (Figure 33), all common on the trees in forests where *C. dectes* occurs. Although most of the larvae survived for three weeks, there was no evidence of feeding. He broadened their choices, providing *Rhizomnium glabrescens* (Figure 44), the foliose lichen *Peltigera canina*, the common mushroom *Agaricus campestris*, apple slices, and springtails. Again, nothing was eaten. Finally, when the leafy liverwort *Porella navicularis* (Figure 32) was presented, the boreids had dinner.



Figure 40. *Antitrichia curtispindula* growing epiphytically and providing a potential home, but not food, for *Caurinus dectes*. Photo by Michael Lüth, with permission.



Figure 41. *Antitrichia curtispindula* with snow, a potential refuge for *Caurinus dectes* under snow, but not eaten by them. Photo by Michael Lüth, with permission.





Figure 42. *Antitrichia curtispindula*, a species in the range of *Caurinus dectes*, but not eaten even when there is no other food choice. Photo by James K. Lindsey, with permission.



Figure 43. *Isoetecium spiculiferum*, potential home of *Caurinus dectes*, but not eaten by them. Photo by Ben Carter, through Creative Commons.

The boreid *Caurinus dectes* (Figure 28-Figure 30) apparently feeds only on leafy liverworts and completes its life cycle on *Scapania* (Figure 45), and several other liverwort epiphytes (Loren Russell, pers. comm. Jan. 2008). Among 11 liverwort taxa tested, the adults accepted about two-thirds of the species. *Scapania* serves as both

food and home for depositing eggs. Russell studied three other local species of boreids, but these three are all moss specialists, never feeding on liverworts.



Figure 44. *Rhizomnium glabrescens*, a moss not eaten by *Caurinus dectes* even when there is no other food choice. Photo by Paul Slichter, with permission.



Figure 45. *Scapania bolanderi*, food of *Caurinus dectes*. Matt Goff, with permission.

Russell (1979a) learned that *Caurinus dectes* (Figure 28-Figure 30) is an excellent liverwort taxonomist. In its various habitats, it recognized certain species to eat or to avoid, both as larvae and adults. On deciduous trees and shrubs, it readily accepted (as host and food) *Porella navicularis* (Figure 32) and *Frullania tamarsci* (Figure 46) (less so, and only if primary hosts were not available), but would not accept *Radula bolanderi* (Figure 47) or *Metzgeria conjugata* (Figure 48). On decaying logs and stumps with bark, it recognized a new array of species, accepting *Scapania bolanderi* (Figure 31) and *Bazzania tricenata* (Figure 49) and less preferentially (when given no choice) *Ptilidium californicum* (Figure 50), *Bazzania ambigua*, and *Lophocolea cuspidata*. Here *Lepidozia*



*reptans* (Figure 51) was not accepted, even under starvation conditions. On older logs and stumps that had lost their bark, it found *Calypogeia fissa* (Figure 52), *C. muelleriana* (Figure 53), *Kantius trichomanis*, *Scapania bolanderi*, *S. umbrosa* (Figure 54-Figure 55), and *Lophocolea heterophylla* (Figure 56) to be highly acceptable, whereas *Geocalyx graveolens* (Figure 57), *Lophozia incisa* (Figure 58), *Cephalozia bicuspidata* (Figure 59) (larvae only), *C. lunulifolia* (Figure 60) (adults only), *Calypogeia fissa*, *Jamesoniella autumnalis* (Figure 61), *Jungermannia atrovirens* (Figure 62), and *Riccardia latifrons* (Figure 63) were only secondary hosts, used when preferred choices were unavailable. *Cephalozia bicuspidata* (adults only), *C. lunulifolia* (larvae only), *Blepharostoma trichophyllum* (Figure 64), *Chiloscyphus pallescens* (Figure 65), and *Lepidozia reptans* were not accepted. Although refusing some members, *Caurinus deces* is apparently mostly a *Jungermanniales* specialist.



Figure 48. *Metzgeria conjugata*, a species that is not accepted as food by *Caurinus deces*. Photo by Michael Lüth, with permission.



Figure 46. *Frullania tamarisci*, an epiphytic liverwort that is eaten by *Caurinus deces* when the primary food (*Porella navicularis*) is not available. Photo by Bernd Haynold, through Creative Commons.

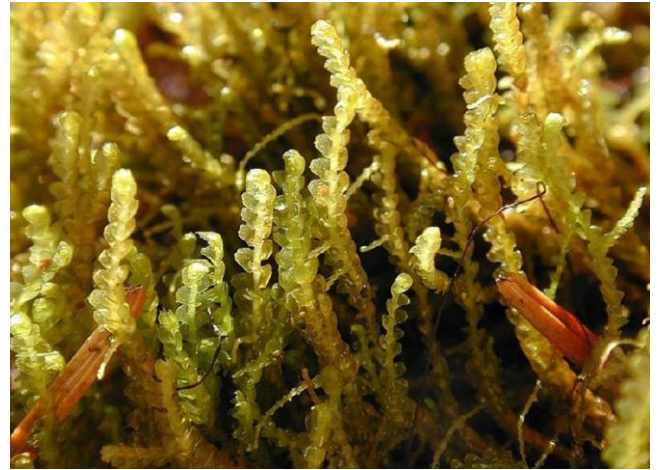


Figure 49. *Bazzania tricrenata*, food for *Caurinus deces* on logs. Photo by Michael Lüth, with permission.



Figure 47. *Radula bolanderi* growing epiphytically, a species that *Caurinus deces* would not eat. Photo by Ken-ichi Ueda, through Creative Commons.



Figure 50. *Ptilidium californicum*, a secondary choice for food by *Caurinus deces* on logs. Photo by Scot Loring, through Creative Commons.





Figure 51. *Lepidozia reptans*, a food choice refused by *Caurinus decetes* on logs, even when no other choice was available. Photo by David T. Holyoak, with permission.



Figure 54. *Scapania umbrosa* on an old log where it is an acceptable food for *Caurinus decetes*. Photo by Hermann Schachner, through Creative Commons.



Figure 52. *Calypogeia fissa*, an acceptable food for *Caurinus decetes* on older logs. Photo by Bernd Haynold, through Creative Commons.



Figure 55. *Scapania umbrosa*, an acceptable food for *Caurinus decetes* on older logs. Photo by Hermann Schachner, through Creative Commons.



Figure 53. *Calypogeia muelleriana*, an acceptable food for *Caurinus decetes* on older logs. Photo by Hermann Schachner, through Creative Commons.



Figure 56. *Lophocolea heterophylla* on a log that has lost its bark where it is an acceptable food for *Caurinus decetes*. Photo by Sture Hermansson, with online permission.





Figure 57. *Geocalyx graveolens*, a species on old logs that *Caurinus dectes* larvae eat when their primary host liverworts are not available. Photo by Michael Lüth, with permission.



Figure 58. *Lophozia incisa* with perianth, a species on older logs and that *Caurinus dectes* larvae eat when their primary host liverworts are not available. Photo by J. C. Schou, with permission.



Figure 59. *Cephalozia bicuspidata*, a species on older logs and that *Caurinus dectes* larvae (but not adults) eat when their primary host liverworts are not available. Photo by Christian Peters, with permission.



Figure 60. *Cephalozia lunulifolia*, a species on older logs and that *Caurinus dectes* adults (but not larvae) eat when their primary host liverworts are not available. Photo by Michael Lüth, with permission.



Figure 61. *Jamesoniella autumnalis*, a species on older logs and that *Caurinus dectes* eats when its primary host liverworts are not available. Photo by Michael Lüth, with permission.



Figure 62. *Jungermannia atrovirens*, a species on older logs and that *Caurinus dectes* eats when its primary host liverworts are not available. Photo by Hermann Schachner, through Creative Commons.





Figure 63. *Riccardia latifrons*, a species on older logs and that *Caurinus decetes* eats when its primary host liverworts are not available. Photo by Julita Klusa <daba.dziedava.lv>, with online permission.



Figure 64. *Blepharostoma trichophyllum*, although common on logs where *Caurinus decetes* lives, is an unacceptable food. Photo by Hermann Schachner, through public domain.



Figure 65. *Chiloscyphus pallescens*, although common on logs where *Caurinus decetes* lives, is an unacceptable food. Photo by Michael Lüth, with permission.

On compacted soil, highly accepted food species for *Caurinus decetes* (Figure 28-Figure 30) included *Gyrothya underwoodiana* (Figure 66), *Nardia scalaris* (Figure 67),

*Diplophyllum albicans* (Figure 68), and *D. obtusifolium* (Figure 69), with secondary hosts of *Gyrothya underwoodiana* (adults only), *Jungermannia rubra* (Figure 70), and *Blasia pusilla* (Figure 71) (Russell 1979a). They did not accept *Pellia neesiana* (Figure 72), *Athalamia hyalina* (Figure 73), *Conocephalum conicum* (Figure 74), or *Anthoceros punctatus* (Figure 75), all thallose species. On boulders and outcrops they preferred *Plagiochila porelloides* (Figure 76), with *Porella cordaeana* (Figure 77) and *Scapania americana* (Figure 78) serving as alternatives when their preferred foods were unavailable. Even forest litter provided a suitable host in the form of *Plagiochila porelloides*.



Figure 66. *Gyrothya underwoodiana*, a highly accepted food for larvae and secondary food for adults of *Caurinus decetes* on compacted soil. Photo by Tab Tannery, through Creative Commons.



Figure 67. *Nardia scalaris*, a highly accepted food for *Caurinus decetes* on compacted soil. Photo by Hermann Schachner, through Creative Commons.





Figure 68. *Diplophyllum albicans*, a highly accepted food for *Caurinus dectes* on compacted soil. Photo by Hermann Schachner, through Creative Commons.



Figure 71. *Blasia pusilla*, a secondary food for *Caurinus dectes* on compacted soil. Photo by Tim Faasen, with permission.

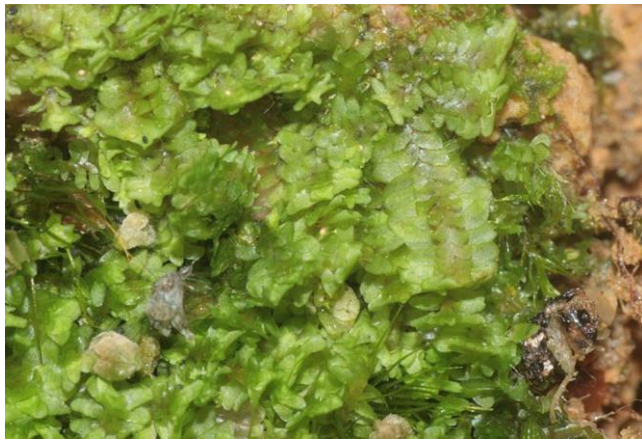


Figure 69. *Diplophyllum obtusifolium*, a highly accepted food for *Caurinus dectes* on compacted soil. Photo by Hermann Schachner, through Creative Commons.



Figure 72. *Pellia neesiana*, a potential food on highly compacted soil, but that is refused by *Caurinus dectes*. Photo by Bernd Haynold, through Creative Commons.



Figure 70. *Jungermannia rubra*, a secondary food for *Caurinus dectes* on compacted soil. Photo by Ken-Ichi Ueda, through Creative Commons.



Figure 73. *Athalamia hyalina*, a potential food on highly compacted soil, but that is refused by *Caurinus dectes*. Photo by Jason Hollinger, through Creative Commons.





Figure 74. *Conocephalum conicum*, a potential food on highly compacted soil, but that is refused by *Caurinus decetes*. Photo by Hermann Schachner, through Creative Commons.



Figure 77. *Porella cordaeana*, a secondary food for *Caurinus decetes* on rocks where the preferred foods are unavailable. Photo by Michael Lüth, with permission.



Figure 75. *Anthoceros punctatus*, a potential food on highly compacted soil and seepages, but that is refused by *Caurinus decetes*. Photo by Proyecto Musgo, through Creative Commons.



Figure 78. *Scapania americana*, a secondary food for *Caurinus decetes* on rocks where the preferred foods are unavailable. Photo by Chris Wagner, with permission.

Russell (1979a, b) was not able to locate any highly acceptable hosts for *Caurinus decetes* among liverworts from streams and seepages, but *Chiloscyphus polyanthos* (Figure 79), *Riccardia multifida* (Figure 80), and *Blasia pusilla* (Figure 71) served as "emergency" foods when others were not available. *Scapania undulata* (Figure 81) and *Anthoceros punctatus* (Figure 75) were rejected.



Figure 76. *Plagiochila porelloides*, a preferred food for *Caurinus decetes* on boulders. Photo by Bernd Haywold, through Creative Commons.



Figure 79. *Chiloscyphus polyanthos*, an emergency food for *Caurinus polyanthos* from streams and seepages. Photo by Kristian Peters, with permission.





Figure 80. *Riccardia multifida*, an emergency food for *Caurinus polyanthos* from streams and seepages. Photo by Hermann Schachner, through Creative Commons.



Figure 81. *Scapania undulata*, a rejected food for *Caurinus polyanthos* from streams and seepages. Note that some species of *Scapania* are eaten. Photo by Hermann Schachner, through Creative Commons.

One of the most interesting observations by Russell (1979a, b) was that although these boreids had accepted

*Porella navicularis* (Figure 32) as food, and readily tasted *Porella roellii* (Figure 82), they soon showed a distinct distaste for *P. roellii*. Evidence included regurgitation, signs of distress, and repeated grooming of their mouthparts. This behavior commenced within 30 seconds of tasting the *P. roellii*. Once eating this species, they subsequently would no longer eat *P. navicularis*, a previously staple food source for them in the lab. *Porella roellii* is known for its "violent, burning taste" which is evidenced after a few seconds of delay.

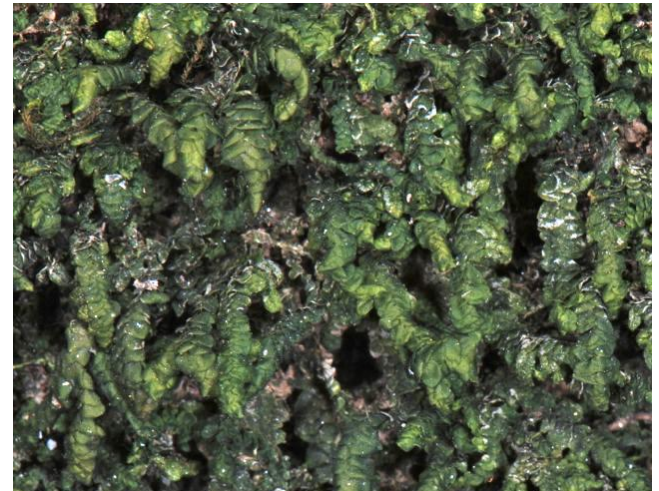


Figure 82. *Porella roellii*, a leafy liverwort that appears to be repugnant to *Caurinus dectes*. Photo by Paul Wilson, with permission.

Russell (1979a, b) rejected the hypothesis that liverworts provided better nutrient quality than the less preferred mosses. In fact, the liverworts seemed to have less nitrogen, an essential component of protein, and rarely exceeded the content of mosses for any of the nutrients tested (Table 1). The switch in some cases from larval to adult preferences is interesting. Also of interest is that this insect specializes on Jungermanniales, with 18 species accepted in laboratory tests.

Table 1. Macronutrient concentrations in the gametophytes of some bryophytes collected in *Caurinus dectes* habitat at Marys Peak, Oregon, USA. From Russell 1979a.

		P	N	Na	K	Ca	Mg
<b>Mosses</b>							
<i>Dicranum fuscescens</i>	Figure 83	.142	.932	.038	.546	.418	.145
<i>Rhizomnium glabrescens</i>	Figure 44	.251	2.083	.043	1.125	.972	.261
<i>Eurhynchium oreganum</i>	Figure 84-Figure 85	.146	.829	.056	.741	.518	.190
<i>Isoetecium spiculiferum</i>	Figure 43	.142	.949	.034	.512	.516	.177
<i>Antitrichia curtipendula</i>	Figure 40-Figure 41	.151	.686	.028	.631	.430	.170
<i>Rhytidiadelphus loreus</i>	Figure 33	.164	.727	.072	.770	.440	.171
<b>mean</b>		<b>.166</b>	<b>1.034</b>	<b>.045</b>	<b>.721</b>	<b>.551</b>	<b>.186</b>
<b>Liverworts</b>							
<i>Scapania bolanderi</i>	Figure 31	.072	.748	.035	.659	.275	.111
<i>Porella navicularis</i>	Figure 32	.155	.890	.026	1.040	.426	.156
<i>Frullania tamarisci</i>	Figure 46	.107	.874	.030	.904	.515	.134
ssp. <i>nisquallensis</i>							
<b>mean</b>		<b>.111</b>	<b>.834</b>	<b>.030</b>	<b>.868</b>	<b>.405</b>	<b>.134</b>





Figure 83. *Dicranum fuscescens*, a food species for adults of *Hesperoboreus brevicaudus*. Photo by Michael Lüth, with permission.



Figure 84. *Eurhynchium oregonum* habitat in area where *Caurinus dectes* lives. Photo by Matt Goff, with permission.



Figure 85. *Eurhynchium oregonum* in habitat where *Caurinus dectes* lives. Photo by Matt Goff, with permission.

### ***Hesperoboreus***

In Oregon, USA, *Hesperoboreus brevicaudus* (see Figure 89) larvae are inhabitants of epiphytic mosses, whereas adults may also occur among thick, matted mosses on rocks (Russell 1979a, b). Penny (2006) reported them from vertical moss banks and epiphytic mosses in

California, USA. In the lab, adults feed on *Polytrichum* (Figure 1, Figure 17) leaf lamellae (Figure 86), *Rhizomnium glabrescens* (Figure 44), and *Dicranum fuscescens* (Figure 83) (Russell 1979a). Larvae feed extensively on *Funaria hygrometrica* (Figure 87), *Rhytidiadelphus loreus* (Figure 33), *Antitrichia curtipendula* (Figure 40-Figure 41), and *Plagiothecium undulatum* (Figure 88) in the lab.

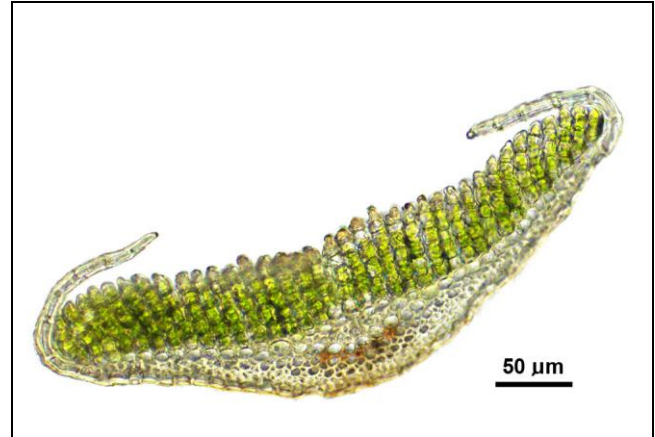


Figure 86. *Polytrichum juniperinum* leaf cs, showing lamellae that are eaten by adults of *Hesperoboreus brevicaudus*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 87. *Funaria hygrometrica*, food of *Hesperoboreus brevicaudus*. Photo by Malcolm Storey <[www.discoverlife.org](http://www.discoverlife.org)>, through Creative Commons.



Figure 88. *Plagiothecium undulatum*, food of *Hesperoboreus brevicaudus*. Photo by Walter Obermayer, with permission.



These mossy habitats, especially among epiphytic mosses, dry out in seasons with little rainfall (Gerson 1982). To accommodate for this unwelcome dryness, the larvae of *Hesperoboreus notoperates* (Figure 89) make hardened cells, using salivary secretions, among the moss rhizoids (Cooper 1974). These cells apparently conserve water until moisture returns. After sufficient rainfall, the larvae break out of the cells and begin feeding again.



Figure 89. *Hesperoboreus notoperates*, a species that prefers compact cushion mosses. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Cooper (1974) noted parasites, especially on *Hesperoboreus notoperates* (Figure 89) in Southern California. Living in such confined quarters may be dangerous for the young boreids because it most likely makes transfer of the parasites from one to another easy. Nevertheless, tight cushions of *Grimmiales* (Figure 23) and *Isobryales* (Figure 90) (Cooper 1974) seem preferable to open mats (Penny 1977), perhaps for greater conservation of moisture.



Figure 90. *Fontinalis antipyretica*, a member of *Isobryales*. Photo by Tab Tannery, through Creative Commons.

### Nannochoristidae

*Nannochorista* (Figure 91) has carnivorous aquatic larvae that feed on larvae of *Chironomidae* (midges) (Tillyard 1917; Byers & Thornhill 1983; Byers 1989; Palmer 2009). The adult diet is unknown. But during

pupation, *Nannochorista* sometimes uses damp mosses as a substrate, avoiding the need to make a special cell for that purpose (Pilgrim 1972; Byers & Thornhill 1983). Those larvae that migrate to soil or bark for pupation create a cell by excavating the soil or wet wood. They pupate above the water, but within 10-20 cm of it (Pilgrim 1972). *Nannochorista philpotti* (Figure 91) is a predatory species that sometimes spends part of its life among bryophytes.



Figure 91. *Nannochorista philpotti* adult, a predatory species that sometimes spends part of its life among bryophytes. Photo by Steve Kerr, with permission.

### Panorpidae

It is the **Panorpidae** that have earned the name of scorpionflies for the order **Mecoptera** (Wikipedia 2016). The genitalia of the males are enlarged and curved upward, arching over the back, much like the stinger of a scorpion (Figure 92).



Figure 92. *Panorpa nuptialis* male adult. Note the resemblance to a scorpion. Photo by Karen Perez, through Creative Commons.

The larvae of **Panorpidae** are unusual among holometabolous insects in having compound eyes with ommatidia, a trait shown by *Neopanorpa* (Figure 93) and *Panorpa* (Figure 94) (Ramel 2016). As Farkač *et al.* (2005) have reminded us, *Panorpa hybrida* (Figure 94) is an endangered species in the Czech Republic. And this species lives mostly among mosses.





Figure 93. *Neopanorpa* sp. adult, a species whose larval eyes are compound. Photo by E. S. Ross <www.discoverlife.com>, with online permission.

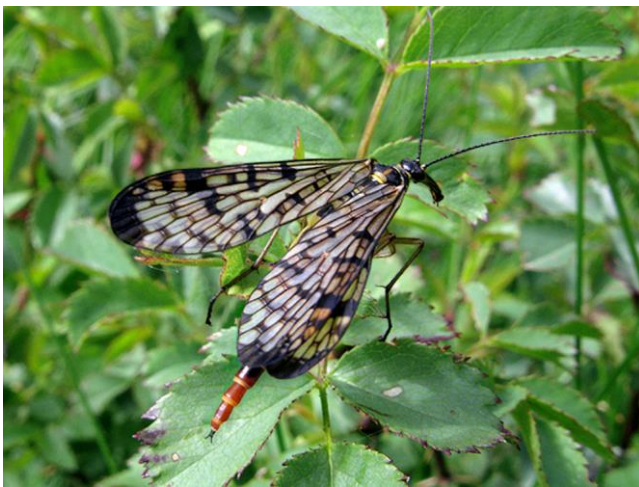


Figure 94. *Panorpa hybrida* adult, a moss dwelling species in Europe. Photo by Ivelina Assyova, with permission.

But the members of the genus *Panorpa* (Figure 94) are not all associated with bryophytes. Some are carnivores, eating freshly killed katydids, grasshoppers, and caterpillars in the lab (Cai & Hua 2009).

*Panorpa* (Figure 94) has three types of mating (Ramel 2016). In all cases, the male emits a **pheromone** that attracts females, and unfortunately, also other males. In one strategy, the male offers the female a gift, food of course (Figure 95), that she devours during copulation (perhaps helping to prevent her from eating her mate as is known in other carnivores such as the preying mantis). In fact, Cockle (1908) observed the female of *Boreus californicus* (Figure 19-Figure 20) drag the male around on his back until he died. The second strategy is similar – the male finds a dead arthropod, which he partially consumes (Ramel 2016). Then the male stands beside it and emits the pheromone attractant or secretes a salivary mass on a nearby leaf or other substrate, again resting beside it and secreting a pheromone. Copulation occurs while the female feeds, either on the arthropod or the salivary mass. In the third strategy, the male offers nothing – no food and no pheromones. Rather, he rushes at the female and attempts to mate with her, a strategy known as **forced copulation**, and often he succeeds. This latter strategy is most used by those males who lose to other males in their

attempt to gain food for a gift. Not surprisingly, females prefer the males with gifts, and those that do receive gifts lay more eggs than females that have had forced copulation.



Figure 95. Male *Panorpa communis* with prey item (*Diogma glabrata glabrata*) such as that offered to females before mating. Photo by Richard Bartz, through Creative Commons.

Kullmann and Sauer (2005) investigated other species of *Panorpa* and learned that other strategies are present as well. They found that the males of both *Panorpa similis* and *Panorpa connexa* carry out their copulations with one salivary mass as a nuptial gift or have copulations without any nuptial gift, but always without the use of force.

Earlier researchers reported that *Panorpa* oviposits loose clusters of eggs, using pre-existing cavities in moist soil (Miyake 1912; Tillyard 1926; Byers 1963; Riek 1970; Byers & Thornhill 1983). But *Panorpa communis* (Figure 95-Figure 96), the common scorpionfly that was named by Linnaeus, oviposits beneath mosses (Malyshev 1968). Byers (1963) found that in *P. nuptialis* (Figure 92, Figure 97) size increase is rapid in the young larvae, but the prepupal stage is prolonged. Adults emerge from pupae in about 20 days.



Figure 96. *Panorpa communis* male adult, a species that oviposits under mosses. Photo by Gail Hampshire, through Creative Commons.





Figure 97. *Panorpa nuptialis* adult. Photo by Robby Deans, through Creative Commons.

### Apteropanorpidae

This tiny family has only one genus (*Apteropanorpa*; Figure 99) with four species known as Tasmanian snow scorpionflies (Palmer *et al.* 2007; Wikipedia 2011). The larvae live among mosses in Tasmania and southern Australia (Byers & Yeates 1999; Wikipedia 2011). Adults are wingless predators, but likewise live among mosses (Kaltenbach 1978; Byers & Yeates 1999).

Like the **Boreidae**, the **Apteropanorpidae** are active in the cold of winter (Byers & Thornhill 1983). Both larvae and adults live among mosses (Kaltenbach 1978; Ferrington 2008) where conditions remain moist most of the time (Russell 1979a). Although Ferrington (2008) considered this family to be aquatic, Palmer (2009) argues that they are not, stating "There is no evidence suggesting that adults of any species of *Apteropanorpa* predictably occupy riparian or aquatic vegetation." Further, Evans (1942) collected two **Mecoptera** larvae from mosses at 600-900 m on Mt. Wellington and these have now been determined to be *Apteropanorpa* (Palmer 2009). Balian *et al.* (2008) noted the ability of mosses to retain a film of water that permits limnoterrestrial invertebrates to live there. But Palmer cautions that larval stages of this genus are poorly known and mosses may not be their only habitat.

But danger lurks among the bryophytes. Like several other mecopteran families, this one is plagued by parasitism. Adults of *Apteropanorpa tasmanica* (Figure 99-Figure 99) are parasitized by larvae of the mites *Leptus agrotis* and *Willungella rufusanus* (Seeman & Palmer 2011).



Figure 98. *Apteropanorpa tasmanica*, a species whose larvae live among mosses. Photo © Simon Grove, Tasmanian Museum and Art Gallery, with permission.



Figure 99. *Apteropanorpa tasmanica*, a species whose larvae live among mosses. Photo © Simon Grove, Tasmanian Museum and Art Gallery, with permission.

### Meropeidae

This tiny family has only two members, one in eastern USA – *Merope tuber* (Figure 100-Figure 101) and one in Australia – *Austromerope poultoni* (Byers 1973, 1988; Kaltenbach 1978). It appears to be an ancient family that was once more widespread.

*Merope tuber* (Figure 100-Figure 101) adults live among aquatic or riparian vegetation or bryophytes (Ferrington 2008). Presumably the bryophytes provide sufficient moisture for these terrestrial living sites.



Figure 100. *Merope tuber* adult, a species that includes bryophytes among its substrates. Photo by Tom Murray, through Creative Commons.





Figure 101. *Merope tuber* adult male showing claspers. Photo by R. Machado, R. Kawada, and J. Rafael, through Creative Commons.

*Merope tuber* is a poorly known species (Dunford *et al.* 2007). Its larvae have never been described and its habits are largely unknown. We do know that the adults are nocturnal, and flight traps have revealed that the species is more common than we had imagined (Byers 2005). Its range is from southeastern Canada to Florida and west to Kansas, Minnesota, and eastern Iowa Byers (1973, 1993; Dunford *et al.* 2007). The Appalachian Mountain range and eastern mesic forests provide it with suitable habitat (Dunford *et al.* 2007). Its presence in the more western and southern parts of its range suggest that these disjunct locations may be relict habitats where it found refuge during glacial advances (Byers 1969, 1993; Schiefer & Dunford 2005). The two species are able to survive in these two distant geographic locations on opposite sides of the Earth along streams in ravines (Killington 1933; Byers 1988) that provide temperatures that vary little from 20°C (Means 1985).

## Bittacidae

The **Bittacidae** are not true bryophyte associates, but they do occasionally feed on mosses (Setty 1931). More commonly they are **saprophagous** and feed on things like dead earthworms or dead insects (Setty 1931, 1940; Byers & Thornhill 1983). Like the **Nannochoristidae**, *Harpobittacus australis* (Figure 102) uses pheromones for attracting attraction (Crossley & Waterhouse 1969). Most of the bittacids hang on vegetation by their legs to drop their eggs to the ground (Ramel 2016). Hence, any association of eggs with bryophytes is probably coincidental.



Figure 102. *Harpobittacus australis* adult, a species that uses pheromones to attract his mate. Photo by John Tann, through Creative Commons.

Currie (1932) relates fascinating observations of the larval behavior of *Harpobittacus tillyardi* in the lab. In preparation for molting, the larvae move to a higher location on a soil mound or on a liverwort leaf. When the larvae molt, they move their body fluids forward, causing the anterior to swell. Eventually the head capsule splits and the larva crawls out, then eats its former skin. After a 10-minute rest, the larvae moved the posterior end up above the head capsule. They then proceeded to expell sand and soil from the anus and to cover the larval skin with it as they moved the anus backward. After about 20 minutes, this process was repeated. This covering rendered the larvae nearly invisible on its substrate. During feeding, which was almost entirely on dead matter, the larva occasionally took a bit of liverwort in the lab. Maintenance of moisture was important, and larvae would expel fluids from the mouth to spread over the body to keep it moist. If it ran out of this fluid, it would die in the dryness.

## Summary

The **Mecoptera** include the snow scorpionflies, and these typically feed on mosses or algae associated with them. **Chorista** (**Choristidae**) is among the bryophages. The **Boreidae** has three genera, all of which feed almost exclusively on bryophytes as both larvae and adults. In addition to food, the mosses may be important as a moist refuge. Many lay their eggs on mosses under the snow. For *Boreus*, mosses seem to be important, whereas for *Caurinus*, liverworts are important. *Hesperoboreus brevicaudus* species occur among epiphytic mosses as larvae but migrate to mosses on rocks as adults.

In the **Nannochoristidae**, has aquatic larvae that are carnivorous, but the larvae may move to damp mosses for pupation. The **Panorpidae** have compound eyes, unusual in this order, that may help them to detect motion in their dark bryophyte habitat. However, not all **Panorpidae** are bryophyte associates. Both larvae and adults of **Apteropanorpidae** live among mosses and are winter-active. *Merope* (**Meropeidae**) adults can live among aquatic vegetation or among bryophytes. The **Bittacidae** only occasionally associate with bryophytes and feed on them.

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