CHAPTER 4-6

INVERTEBRATES: MOLLUSKS

Figure 1. Slug on a *Fissidens* species. Photo by Janice Glime.

Mollusca – Mollusks

Glistening trails of pearly mucous criss-cross mats and turfs of green, signalling the passing of snails and slugs on the low-growing bryophytes (Figure 1). In California, the white desert snail *Eremarionta immaculata* is more common on lichens and mosses than on other plant detritus and rocks (Wiesenborn 2003). Wiesenborn suggested that the snails might find more food and moisture there. Are these mollusks simply travelling from one place to another across the moist moss surface, or do they have a more dastardly purpose for traversing these miniature forests?

Quantitative information on snails and slugs among bryophytes is scarce, and often only mentions that bryophytes are abundant in the habitat (*e.g.* Nekola 2002), but we might be able to glean some information from a study by Grime and Blythe (1969). In collections totalling 82.4 g of moss, they examined snail populations in a 0.75 m^2 plot each morning on 7, 8, 9, & 12 September 1966. The copse snail, *Arianta arbustorum* (Figure 2), numbered 0, 7, 2, and 6 on those days, respectively, with weights of 0.0, 8.5, 2.4, & 7.3 per 100 g dry mass of moss. They were most abundant on the stinging nettle, *Urtica dioica*, which also seemed to be a preferred food. Perhaps we need to searach at night when the snails and slugs are more active.

Figure 2. The copse snail, *Arianta arbustorum*, in Stockholm, Sweden. Photo by Håkan Svensson through Wikimedia Commons.

In the Pacific Northwest, USA, unusual jumping slugs in the genus *Hemphillia* (Figure 3) prefer coarse woody debris or moss mats on decaying logs (Leonard & Ovaska 2003). Their ability to roll or flap violently may break their surface tension, permitting them to move quickly, and giving the appearance that they are jumping. Evidence also suggests that they smear their slime trail, confusing potential predators. In Canada, some of these species seem safe from extinction due to sufficient abundance, but others are endangered due to increasing patchiness of suitable habitats. The 1994 NW Forest Plan regulates ground disturbance activities on federal lands in northern California to Washington, protecting "survey and manage" species, including several species of jumping slugs. Hence, protection of these slugs can help in the protection of mosses in these areas. However, the Bush administration was not sympathetic to this protection and it could be lost at any time with a change in administrative philosophy.

Figure 3. *Hemphillia glandulosa*, the warty jumping slug, on moss. The two photos illustrate the variability in its coloration. Photos by Kristiina Ovaska.

Bryophytes as Home

Wiesenborn (2003) observed snails in the Riverside Mountains of California and found that the active snails preferred epiphytic mosses and lichens compared to plant detritus and four sizes of rocks. They suggested that the epiphytes could provide these snails with food or moisture.

In the sub-Antarctic Marion Island, the slug *Deroceros caruanae* lives in moist bryophyte communities as well as on decaying bryophytes (Smith 1992). In boggy habitats, gastropods have little choice but to travel across bryophytes (Stanisic 1996). In a study of bryophyte inhabitants in the Bükk Mountains of Hungary, Varga (2008) found the gastropods *Punctum pygmaeum* and *Pumilla muscorum* among the terrestrial mosses *Plagiobryum zieri*, *Hypnum cupressiforme* (Figure 4), and *Tortella tortuosa.* From my own observations, it appears that snails and slugs are common on moss clumps, but finding documentation on their use of moss evades even the aggressive Google search.

Snails can sometimes occur in significant numbers in moss habitats. Their need for a moist environment (Pratt 1935) would seemingly attract snails to the mosses as a moist substrate. Grime and Blythe (1969) found average morning populations of up to 8.5 *Arianta arbustorum* snails per 100 g dry weight of moss in early September at Winnats Pass in Derbyshire, England. This was surpassed only by those on *Urtica dioica* (stinging nettle) reaching 14.4 and *Mercurialis perennis* (dogs mercury) reaching 16.2. Nevertheless, it takes a lot of dry moss to make 100 g. However, nighttime activity by many snails is likely to be greater, although little snails may actually seek refuge in mosses during the day. Furthermore, snails like *Arianta arbustorum* typically climb, often to a considerable height, to obtain food. Bryophytes just don't fit into this behavior pattern, so the behavior of *Arianta arbustorum* may not reflect that of the small snails.

Figure 4. Slug on *Hypnum*. Photo by Janice Glime.

Szlavecz (1986) determined that snail size plays an important role in their behavior. Although one might think that larger animals need to eat more, it seems that larger *Monadenia hillebrandi mariposa* (see Figure 5) instead spends more time crawling and less time feeding, permitting it to travel farther. Although it prefers leaf litter, it consumes mosses as well (Figure 6). One would expect that size would also constrain movement among the bryophytes and restrict larger snails to the surface.

Because of their small movement space, bryophytes can serve as safe sites for smaller snails. Birds can be significant consumers of snails, particularly during migration (Shachak & Steinberger 1980), and bryophytes can make the snails less conspicuous, if not hiding them completely. In terrestrial habitats, arachnids such as spiders and daddy-long-legs (Opiliones) are also predators on snails (Nyffeler and Symondson 2001). While some spiders can probably navigate the spaces within the moss mat, it seems unlikely that mature daddy-long-legs could manage without getting caught. In addition to the arachnids, Carabid beetles prey on terrestrial gastropods

(Symondson 2004). Some of these beetles use a pump mechanism to extract the gastropod remains from its shell.

Figure 5. *Monadenia fidelis* on mosses. Photo by Walter Siegmund through Wikipedia.

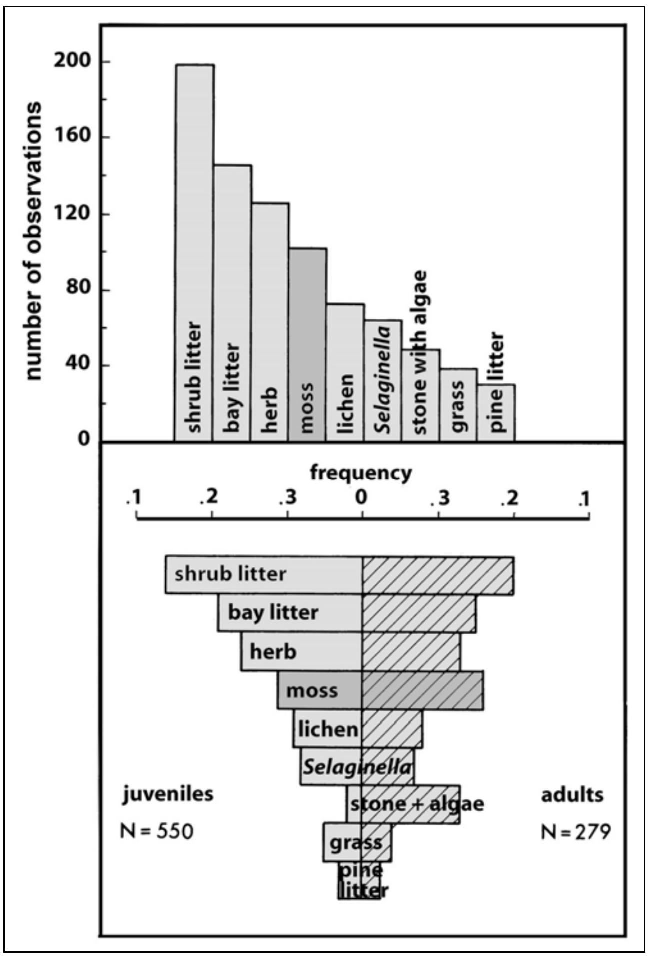

Figure 6. Laboratory selection of foods by the snail *Monadenia hillebrandi mariposa*. **Upper**: all data combined. **Lower:** juveniles vs adults. Redrawn from Szlavecz 1986.

The slug *Prophysaon vanattae* (scarletback taildropper; Figure 7) is one of those snails that seems to find a safe site under mosses on trees on Vancouver Island, Canada (Kristiina Ovaska, pers. comm. 30 June 2009). But it also hangs on epiphytic moss mats in the moist deciduous forest there and may even lay eggs there (Figure 8).

In streams, it is likely that snails find mosses as a safe site from the current. Habdija *et al.* (2004) rarely found any gastropods on bryophytes at velocities of greater than 70 cm s^{-1}, whereas oligochaetes became more abundant at higher velocities. Flow rates are much slower within the moss mats, thus providing a haven for feeding where the current is unlikely to dislodge the snails and slugs. This also provides them protection from predators such as fish (mostly), ducks, shore birds, and amphibians (Pennak 1953).

Figure 7. *Prophysaon vanattae*, the scarletback taildropper, can be found hiding under mosses. Photo by Kristiina Ovaska.

Figure 8. *Prophysaon vanattae* with eggs on a moss. Photo by Kristiina Ovaska.

Bryophytes as Food

Snails and slugs have a rasping tongue that destroys the epidermis of tracheophytes (Grime & Blythe 1969), but what does it do to moss leaves only one cell thick? Apparently it makes them potential food (Szlavecz 1986), enabling these mollusks to consume even the tough capsule (Davidson & Longton 1987, Davidson *et al.* 1990). Nevertheless, the palatability index for bryophytes is low (Jennings & Barkham 1975). And snails and slugs seem to be less interested in grazing things with awns than those without. Robin Stevenson (pers. comm. January 2008; Figure 9) has seen *Bryum argenteum* that is completely grazed over, but never observed such grazing on an awned *Grimmia* species. Could it just be that there is no nutrition in an awn, or do they have trouble gliding across the furry tips of leaves?

But awns may not deter all snails. Szlavecz (1986) was able to identify the awned *Grimmia trichophylla* in the feces of the California snail, *Monadenia hillebrandi mariposa* and also demonstrated that the spine tips of the tracheophyte *Selaginella hanseni* did not deter feeding or crawling. Michael Lüth has observed snails grazing on

Orthotrichum and Terry McIntosh has seen slugs grazing on other bryophytes, both indicating that the damage to the moss was similar to that shown in Figure 10 (Bryonet 12 January 2008). On the other hand, Frank Greven (Bryonet 13 January 2008) has seen this pattern as a result of grazing by isopods (wood lice). Robin Stevenson (pers. comm. 14 January 2008) agrees that isopods might be deterred by the awns, causing them to eat in such a pattern. But why would slugs or snails climb up the bridge coping to the moss for such a limited nutrient source?

Figure 9. *Bryum argenteum*, a moss with no awns and a food source for snails and slugs. Photo by Michael Lüth.

Figure 10. *Grimmia pulvinata* exhibiting grazing in a pattern typical of snail or slug grazing, but also known for isopods. Photo by Robin Stevenson.

That rasping tongue is not always enough to accomplish the task of obtaining nutrients from mosses. Oyesiku and Ogunkolade (2006) experimented with snails and the moss *Hyophila crenulata.* In their laboratory experiments, the snails (*Limicolaria aurora*; Figure 11) gained the most weight when fed with *H. crenulata* paste. The snails that had only unground moss actually lost weight. Those in the field experiment (restricted to *H. crenulata*) either lost weight or remained the same. Fecal matter of the field snails had fragments of moss that had lost the chlorophyll from their cells as well as that of abundant algae and Cyanobacteria. The presence of these snails on the moss was seasonal from April until October, when the moisture and lower temperature may have provided a favorable habitat. This experiment suggests that in this case the snail was unable to penetrate the cells of the moss, making it an unlikely food source in nature.

Figure 11. Shell of *Limicolaria aurora*. Photo by David G. Robinson, USDA APHIS PPQ at Bugwood.org.

Algae growing on mosses, especially in the aquatic habitat, could be a prominent source of food. In the Negev Desert, adult desert snails (*Sphincterochila zonata*) fed exclusively on algae on the soil surface, creating an algal turnover of 142 kg hectare^{-1}, despite being active for only 8-27 days in winter during the rainy period (Shachak & Steinberger 1980). Other Negev Desert snails feed on the mosses themselves. *Trochoidea seetzeni* feeds on shrubs there, but its feces indicate that it also feeds on the moss *Desmatodon convolutus* (Yom-Tov & Galun 1971).

Clearly for some slugs and snails there are bryophytes that do indeed seem palatable. Ochi (1960) reported that *Conocephalum conicum* (Figure 12) served as food for a slug. Merrifield (2000) found evidence of heavy grazing on epiphytic bryophytes, particularly *Syntrichia laevipilus*, of Oregon white oaks (*Quercus garryana*) in the Willamette Valley, Oregon, USA, and considered that either springtails or slugs were likely responsible. She considered that the abundance of gemmae may be a response to this grazing.

Figure 12. *Conocephalum conicum*, a liverwort that can serve as slug food. Photo by Michael Lüth.

Szlavecz (1986) compared feeding preferences in 31 individuals of the snail *Monadenia hillebrandi mariposa.* Collections of field feces indicated that they consumed *Rhytidiadelphus* sp. (Figure 13) and *Grimmia trichophylla* (Figure 14) in nature, among other things. In the lab, they preferred shrub and bay litter over mosses, but preferred mosses and lichens over grasses and pine litter. Studies by Chatfield (1973), Williamson & Cameron (1976), and Richter (1976) indicate that at least juvenile snails might do best on a mixed diet.

Figure 13. *Rhytidiadelphus squarrosus*, a member of a genus that has been found in feces of the snail *Monadenia hillebrandi mariposa*. Photo by Michael Lüth.

Figure 14. *Grimmia trichophylla* showing awns. Photo by Michael Lüth.

Davidson and Longton (1985, 1988; Davidson 1988, 1989) reported that several species of generalist slugs consumed bryophytes. Protonemata were readily consumed (Grime 1979). In Great Britain, capsules and protonemata of several mosses (*Brachythecium rutabulum* (Figure 15), *Mnium hornum* (Figure 16), and *Funaria hygrometrica* (Figure 17) were eaten preferentially to leafy gametophores by slugs (*Arion* spp.; Figure 19) (Davidson & Longton 1987, Davidson *et al*. 1990).

Figure 15. Snail eating capsules of *Brachythecium*. Note the number of setae that are missing capsules. Photo by Janice Glime.

Figure 16. Capsules of *Mnium hornum*. **Upper:** Young, green capsules that are preferred by *Arion* slugs. Photo by Michael Lüth. **Lower:** Mature capsules. Photo by Janice Glime.

Figure 17. Capsules of *Funaria hygrometrica*. Photo by Michael Lüth.

Older capsules with spores were less preferred than the green ones (Figure 18; Davidson & Longton 1987; Davidson *et al*. 1990). Presence of moss cells of *Brachythecium rutabulum* and *Mnium hornum* in the feces of previously starved *Arion* suggest that the leafy mosses are not digested well (Davidson *et al*. 1990). Ferulic acid, present in shoots but absent in young capsules of *Mnium hornum*, is a phenolic compound that is only released after severe hydrolysis.

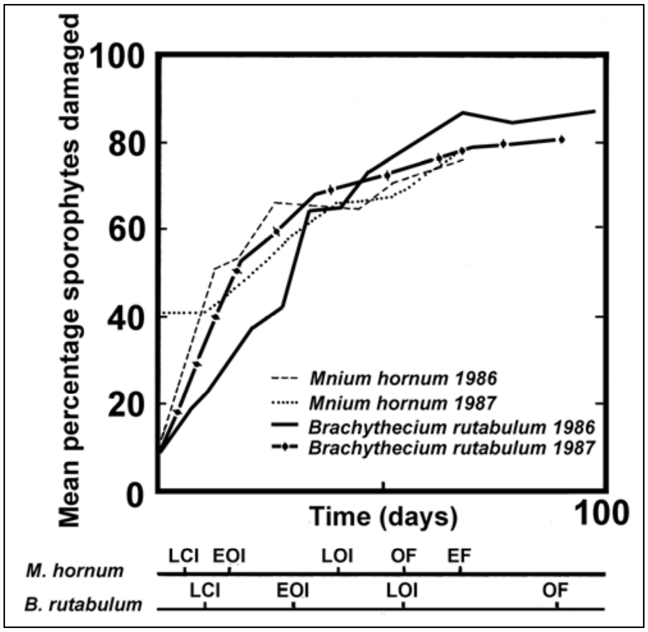

Figure 18. Relative damage by slugs of sporophyte stages of two species of bryophytes. n=300-500 at day 0. **LCI** = late calyptra stage; **EOI** = early operculum intact; **LOI** = late operculum intact; **OF =** operculum fallen; **EF** = empty and fresh. Redrawn from Davidson *et al*. 1990.

Only trivial amounts of *Brachythecium rutabulum* shoots were consumed (Davidson 1989; Figure 15). *Mnium hornum* (Figure 21) was also ignored, but after 5-7 days of starvation *Arion rufus* (10-15cm long; Figure 19) and *A. subfuscus* (5-7 cm long; Figure 20) ate significant quantities of shoots of this species. *Arion hortensis* still ignored the moss even after 7 days of starvation. On the other hand, all three species of slugs readily consumed *Funaria hygrometrica* (0.4-6.5 mg wet weight per slug) in overnight feeding trials.

Figure 19. *Arion rufus* amid protonemata and liverworts. Photo by Alekas through Wikipedia.

Longton (pers. comm. 1996) has speculated that phenolic compounds that protect the leafy gametophytes deter herbivory, especially on perennials. This could account for greater herbivory on the *Funaria hygrometrica* than on *Brachythecium rutabulum* or *Mnium hornum*. The phenolic compounds in the latter two species was released only after severe hydrolysis, leading Davidson *et al*. (1990) to suspect that the phenolic acids might be tightly bound to cellulose in the cell wall. The greater palatability of the *F. hygrometrica* (Figure 17, Figure 22) supports the general theory that perennials invest more resources in defense against herbivory than do annuals.

Figure 20. *Arion subfuscus*, a slug known to consume *Mnium hornum*. Photo by Gary Bernon, USDA APHIS at Bugwood.org.

Figure 21. *Mnium hornum* shoots – a species that was ignored in experiments until the slugs were starved. Photo by Janice Glime.

Figure 22. Young sporophytes of *Funaria hygrometrica* before spores form. Photo by Michael Lüth.

Given the choice of capsules or vegetative material, both *A. rufus* and *A. subfuscus* preferred immature capsules of all three mosses (see Figure 23), with *M. hornum* being top choice (Davidson 1989). Setae were generally ignored, but *A. subfuscus* did occasionally eat *M. hornum* and *B. rutabulum* setae. All three slugs also ate protonemata in the laboratory, and for *B. rutabulum* and *F. hygrometrica* the protonema was eaten just as much by *A. rufus* and *A. subfuscus* as were immature capsules. In fact, dry weight consumption exceeded that of immature capsules. Young shoots were also eaten, but less readily.

Figure 23. Slug browsing on *Leucolepis acanthoneuron*. Photo from UBC website, with permission.

Figure 24. Keeled slug, a common inhabitant of mosses in the Pacific Northwest, USA. Photo by Jeri Peck.

Davidson and Longton (1987) suggested that *Arion hortensis* was restricted by the physical structure of the capsule to consuming developing spores from broken capsules in *P. commune*; no spores were eaten from unbroken capsules. When approaching *Mnium hornum*, the slugs would withdraw their tentacles, then retreat, suggesting some sort of chemical deterrent; they behaved similarly in the presence of extracts from the capsule. It is likely that hydroxycinnamic and phenolic acids in this species and in *Brachythecium rutabulum* provided this chemical protection against herbivory (Davidson *et al*. 1989). Stems of both species were apparently protected by ferulic and possibly m- and p-coumaric acid bound in the cell walls of the shoots (Davidson *et al*. 1989), explaining the preference of the slugs for capsules. On the other hand, when moss extracts were placed on communion wafers, the slugs ate them more readily, suggesting that chemistry alone was not the likely deterrent (Anonymous 1987; Davidson *et al*. 1990). Rather, some physical feature of the mosses, perhaps the cell wall, deterred these slugs.

But what did the slugs derive from the consumed mosses? When they consume preferred foods such as lettuce leaf or carrot root, the resulting feces contain macerated, partially pigmented tissue (Davidson 1989). When they consumed bryophytes, on the other hand, large pieces of leaf, whole leaves, and even stem pieces remained. Most cells still contained green chloroplasts. Evidently the moss did little more than fill the gut. Even the preferred capsules were poorly digested, with capsule wall fragments, opercula, and peristome teeth remaining. Mature spores seemed unharmed, but immature spores seemed to have experienced some digestion, appearing broken, colorless, and shrivelled. Likewise, the protonema seemed to be digestible, resembling the lettuce and carrots in being macerated and colorless or brown.

Figure 25. Slug on moss. Photo by Janice Glime.

This raises the question of whether slugs and snails actually eat bryophytes in the field, or is this a laboratory phenomenon where they have no other choice. For example, Jennings and Barkham (1975) found that bryophytes all gave low palatability scores when six species of slugs, including the three in the Davidson (1989) study, had a choice of foods. For whatever reason, it appears that at least some snails do eat bryophytes in nature. Szlavecz (1986) found remnants of the mosses *Rhytidiadelphus* sp. and *Grimmia trichophylla* in feces from snails (*Monadenia hillebrandi mariposa*) that had been eating in the field. More green moss than brown occurred, whereas brown material was more common from consumed tracheophytes (Figure 26). Grime and Blythe (1969) found bryophytes in the feces of four species of snails out of the six examined from Winnats Pass, Derbyshire, England, on 13 October. But then, tracheophyte foods are often less nutritious as the plants prepare for winter.

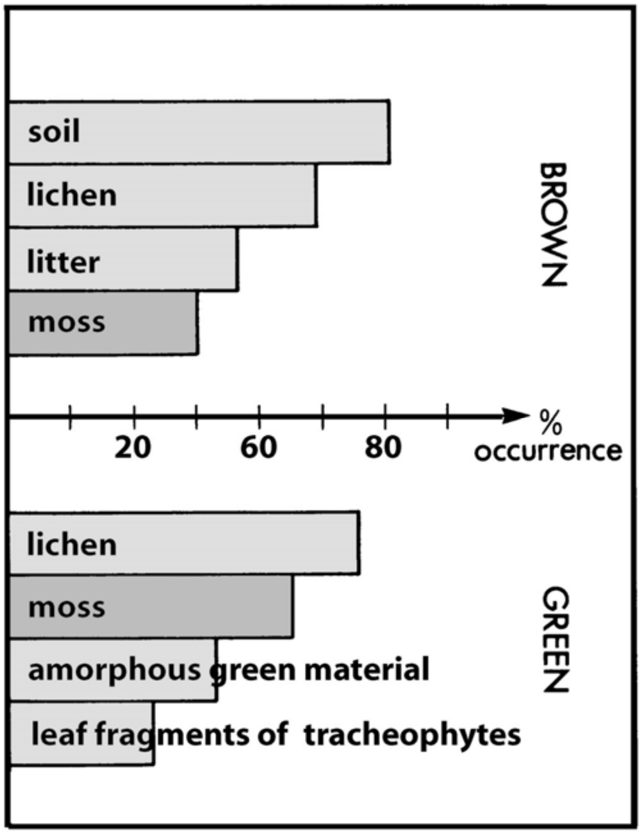

Figure 26. Comparison of green and brown portions of plant material eaten by the snail *Monadenia hillebrandi mariposa*. Modified from Szlavecz 1986.

Rosso and McCune (2003) found that mollusks on shrubs in the Pacific Northwest, USA, exhibited significant herbivore activity on the lichens. Bryophytes, on the other hand, had little change in cover between stems in exclusions and those available for herbivory. It appears that the mollusk herbivory on lichens may benefit the bryophytes by contributing to the successful competition of the bryophytes over the lichens in the understory of these forests.

Indirect evidence suggests that slugs and snails graze capsules of *Buxbaumia viridis* (Gordon Rothero, Birds feeding on moss capsules, Bryonet-l, 10 April 2003). Stark (1860) relayed a story of the ill fate of *Buxbaumia aphylla* specimens on their journey from Scotland to England. A slug had inadvertently been included in the package and it managed to destroy the specimens. However, I have discovered that what appeared to me to be grazing on capsules of *Buxbaumia aphylla* is really only the splitting of the capsule top as it dries, and that this occurs on nearly every capsule.

Grazing by slugs can be so severe as to define distribution of a species. Lohammar (1954) found that in northern Europe *Fissidens fontanus* (Figure 27) was absent in lakes where *Fontinalis antipyretica* was also absent. Others suggest that scarcity of *Fissidens* in some places is due to snail grazing (Gerson 1982). In the presence of *Fontinalis*, this smaller moss lives among the *Fontinalis* fronds where it is presumably protected from snail grazing by the inedible forest of *Fontinalis* surrounding it.

It may be that in the aquatic habitat the snail effect on some bryophytes is much greater than in the terrestrial habitat. But it is not necessarily all bad. Steinman (1994) opined that snail grazing could account for the apparent unresponsiveness of epiphytes following phosphorus enrichment in a woodland stream in Tennessee, USA, where bryophytes were prominent. And some bryophytes seem prepared to fight back. *Ricciocarpos natans* (Figure 28) exhibits molluscicidal properties that are active against the snail carrier of schistosomiasis (Wurzel *et al*. 1990).

Figure 27. *Fissidens* (*Octodiceras*) *fontanus*, a moss that seems to be vulnerable to snail grazing except it is protected by *Fontinalis*. Photo by Michael Lüth, modified by Janice Glime.

Figure 28. *Ricciocarpos natans* with holes where some invertebrate has been nibbling. Photo by Janice Glime.

Slugs also eat hornworts (Figure 29). Bisang (1996) reported that they especially eat the green sporophytes.

Figure 29. *Phaeoceros carolinianus* with mostly green sporophytes, a food source for slugs. Photo by Michael Lüth.

Mussels

Some mollusks and other organisms can actually turn the relationship around and provide a home for the bryophytes. Yes, some of these animals actually have mosses growing on them. Neumann and Vidrine (1978) found *Fissidens fontanus* (Figure 27) and *Amblystegium* (*Leptodictyum*) *riparium* (Figure 30) growing on freshwater mussel shells.

Figure 30. *Amblystegium* (*Leptodictyum*) *riparium*, a moss known to grow on freshwater mussel shells. Photo by Michael Lüth.

Antifeedants

Based on the fore-going discussion, it appears that at least some bryophytes are able to discourage browsing by slugs (Frahm & Kirchhoff 2002). Alcohol extracts of moss *Neckera crispa* (Figure 31) and liverwort *Porella obtusata* have antifeedant activity against *Arion lusitanicus* (Figure 33). Extracts of 0.5% dry weight of the moss had low activity, whereas those from the liverwort exhibited moderate activity at 0.05%. At 0.25% the antifeedant activity of *Porella obtusata* was complete. It is likely that this activity is not specific for slugs and may discourage insects, bacteria, and fungi as well.

Figure 31. *Neckera crispa*, a moss that has antifeedant activity against the slug *Arion lusitanicus*. Photo by Michael Lüth.

Dispersal Agents

It appears that slugs are not all bad in the bryophyte world and may instead be a necessary vector for some propaguliferous taxa (Stolzenburg 1995). Slugs and snails (Figure 32) leave a trail of mucous as they go, and as you well know if you have handled these mollusks, this secretion can be sticky. It is therefore no surprise that these animals have dispersal abilities.

Figure 32. Snails such as this one traversing epiphytic mosses in Japan may be effective dispersal agents. Photo by Janice Glime.

Slugs are able to disperse the brood branches of *Orthodicranum flagellare* (Kimmerer & Young 1995; Figure 34). These tiny branches become entrapped in the secretions and are deposited in the ensuing slime trail. Kimmerer and Young found that these can be transported at least 23 cm from the colony, although the mean distance in their study was only 3.7 cm.

And it appears that the secretion increases the ability of the propagule to adhere to its substrate without affecting the germination rate. In fact, experiments by Davidson (1989) suggest that passage through the slug may enhance germination success. All plates containing mature spores from slug (*Arion* spp.; Figure 33) fecal pellets produced shoots, whereas only 80% of the plates with uneaten mature *Mnium hornum* spores and 70% of those with uneaten *Brachythecium rutabulum* (Figure 35) spores produced shoots.

Figure 33. *Arion lusitanicus*, a slug that traverses mosses, but finds *Neckera crispa* and *Porella obtusata* unpalatable. Photo by Mogens Engelund, Wikipedia.

The ability of snails and slugs to glide across bryophytes and to climb setae to capsules suggests that these animals may be important dispersal agents. Although some experiments exist on ability of spores to survive the mollusk gut, more experiments are needed. How widespread are herbivory and dispersal among bryophytes that temporarily host these slow-moving animals?

Figure 34. *Orthodicranum flagellare* showing the tight flagellate branches that can be dispersed by slugs. Photo by Janice Glime.

Figure 35. *Brachythecium rutabulum*, for which the spores germinate better if they have passed through the gut of a slug (*Arion*). Photo by Michael Lüth.

Summary

Snails and slugs have often been observed on bryophytes. The white desert snail, *Eremarionta immaculata*, is common on bryophytes and seems to prefer them as a habitat. The copse snail, *Arianta arbustorum* is another known inhabitant. More quantitative studies have shown that some slugs and snails prefer bryophytes. More active snails might be found at night, whereas tiny snails might take refuge in the bryophytes during the day. Snails might use them as a safe site to escape spiders, daddy-long-legs, and beetles, whereas other predators may lurk among the bryophytes. In streams, bryophytes may protect them from fish, ducks, shore birds, and amphibians.

Bryophyte leafy plants and capsules can serve as food for snails and slugs, but some of these mollusks seem to avoid leaves with awns. In some cases the moss structure is such that the snails actually lose weight, whereas moss paste fosters a weight gain. But in many cases, the snails may gain their nutrition from adhering algae and Cyanobacteria. In some cases protonemata and green capsules are preferred to leafy plants. *Fissidens fontanus* can be virtually eliminated by snails in lakes where there is no *Fontinalis antipyretica* to protect it.

But some slugs won't eat the moss even when they have been starved for 7 days. They have even been observed retreating from a moss. Various phenolic compounds seem to be involved in their reluctance to eat some bryophyte species. *Ricciocarpos natans* has molluscicidal properties that are effective against snail vectors of schistosomiasis.

The moss may not offer any nutrition. Intact cells of leaves, capsules, and mature spores pass through the gut, and it seems that only young spores and protonemata become pale during their trip through the digestive system.

Because of their mucous trail, slugs and snails are able to disperse some bryophytes, including brood branches, spores, and leaf fragments. And it appears that the mucous helps the dispersed fragment to adhere to its new substrate. Spores can even pass through the digestive system and survive, thus adding another form of dispersal.

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